Evolution of Vertebrate Brains

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Introduction and Overview

The brains of living vertebrates are a reflection of the very diverse niches occupied by the different species that comprise each major taxon (Figure 1) – agnathans (jawless vertebrates) and three radiations of jawed vertebrates: (1) the cartilaginous fishes (chimaeras and sharks, skates, and rays), (2) the ray-finned fishes (bony fishes), and (3) the sarcopterygian (fleshy-finned fish) radiation, which includes tetrapods (amphibians, mammals, reptiles, and birds). Within each of these major taxa, brain structure varies substantially, with some brains smaller relative to body size and less elaborate in terms of cytoarchitecture and others larger and more elaborate. The former can be referred to as type I brains (Figure 2) and the latter as type II (Figure 3). This type I–type II distinction is a matter of degree, and where the line is drawn is necessarily somewhat arbitrary. However, within each radiation, there are clearly some species with highly complex and enlarged brains relative to other species. Thus, this distinction is of heuristic value in appreciating the range of variation of brain evolution that has occurred within each major radiation.

That brain enlargement and elaboration has occurred four times independently presents a very different reality of how brain evolution has operated than is perceived in the widely held folk-belief of a sort of scale of nature, or Scala Naturae, that ranks all vertebrates along a simplistic scale. Instead, the picture now appreciated is a much more sophisticated and fascinating one in terms of both evolutionary history and the mechanisms by which it has proceeded. It is also important to note that the strategy of retaining a relatively simple brain in terms of cytoarchitecture, and one that is of modest size in relation to the body, is a successful one for many species, just as brain enlargement and elaboration is for other species. The variation in complexity and relative brain size that exists across all living vertebrate groups and individual species is a direct function of the available niches and the adaptations of various species that successfully occupy them.

The three major radiations of jawed vertebrates, or gnathostomes, each comprise diverse species that occupy equally diverse niches. The jawless vertebrates number fewer species and less diversity of niche but nonetheless exhibit marked diversity of brain size and degree of elaboration. Of the jawless vertebrates, or agnathans, lampreys have a relatively simple, or type I, brain (Figure 2) in terms of its number of neurons and their degree of migration away from the ventricular surface where they are generated during embryological development. In contrast, hagfishes have an enlarged and elaborated type II brain (Figure 3), characterized by considerably more neurons that are produced in and also migrate away from the ventricular surface and that form large aggregations of nuclei and/or laminated structures. Within cartilaginous fishes, chimaeras (ratfishes), and squalomorph and squantinomorph sharks have type I brains (Figure 2), while galeomorph sharks and skates and rays have type II brains (Figure 3). Within ray-finned fishes, reedfishes (Cladistia), sturgeons and paddlefishes (Chondrostei), gars (Ginglimodi), and the bowfin (Halecomorphi) have type I brains (Figure 2), while teleosts (Teleostei) have type II brains (Figure 3). Among the latter, species that exhibit complex social and territorial behaviors, such as many of the reef fish, have exceptionally complex and enlarged brains relative to other species. Within the sarcopterygian radiation that gave rise to land vertebrates, lungfishes (Dipnoi), the crossopterygian fish *Latimeria* (Actinistia), and amphibians have type I brains (Figure 2), while reptiles, birds, and mammals have type II brains (Figure 3).

The ratio of brain size to body size also varies considerably across different vertebrate groups. As shown in Figure 4, thanks to the copious data collected and analyzed by Harry Jerison, agnathans – both lampreys and hagfishes – have relatively low brain: body ratios, as do amphibians. Ray-finned fishes exhibit a wide range, with a few species overlapping the lower range of mammals. Reptiles fall within a modest range, with both mammals and birds having the largest brain:body ratios, but a number of cartilaginous fishes overlap the bird–mammal range. These data also demonstrate the wide range of variation within multiple groups of vertebrates that is the result of independent evolutionary processes.

Most of the diversity in brain complexity occurs in the dorsal part of the brain, which is derived from the alar plate during embryological development, rather than in the derivatives of the more ventrally lying basal plate. The latter gives rise to the motor nuclei for cranial nerves and reticular formation components and, while some variation occurs among these structures, they are relatively conservative in their organization and degree of development across vertebrates. The alar plate gives rise to the dorsal part of the neural tube, including the sensory nuclei of
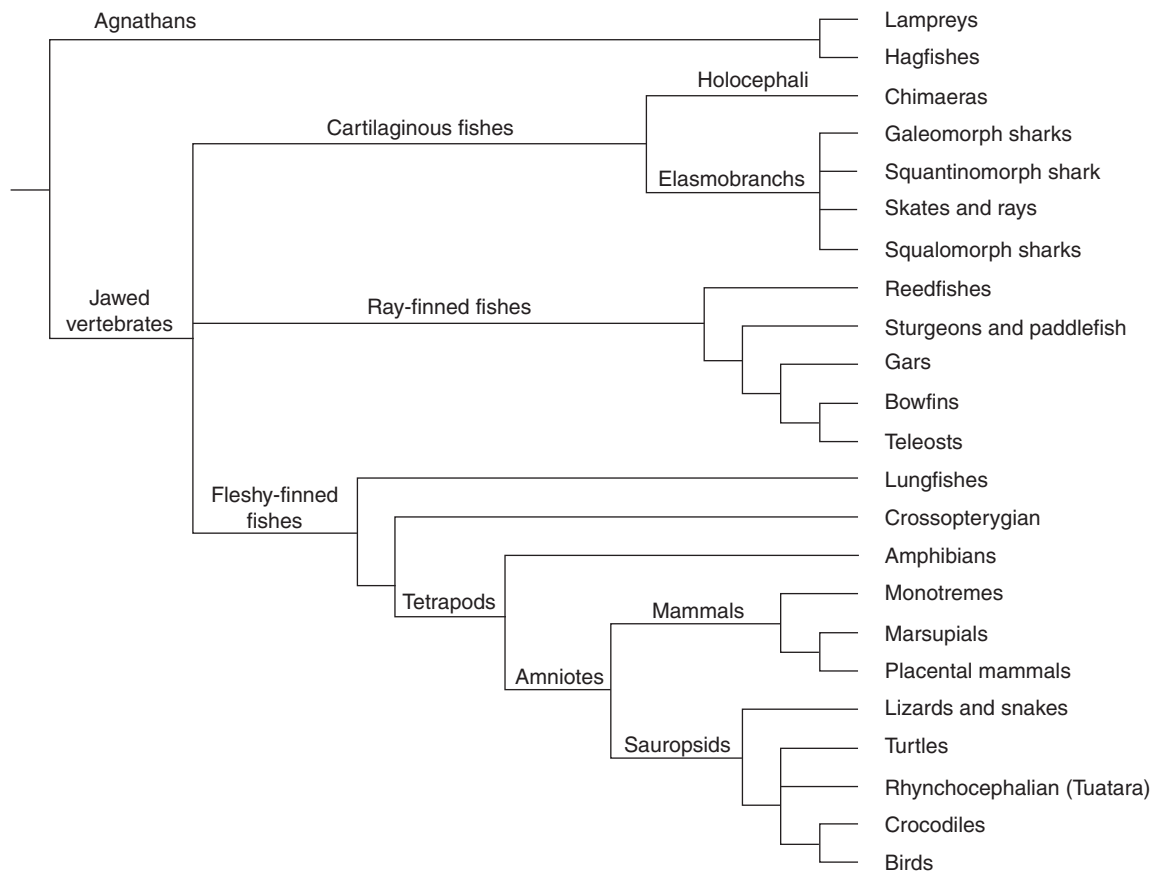
Figure 1 Cladogram showing the relationships of the four major groups of vertebrates – agnathans, cartilaginous fishes, ray-finned fishes, and the sarcopterygian radiation of fleshy-finned fishes.

cranial nerves, roof structures (cerebellum, midbrain tectum, much of the diencephalon, and all of the telencephalon), and cerebellar and basal-ganglia-related nuclei (inferior olivary nucleus, pontine nuclei, red nucleus, substantia nigra, etc.). Among the alar plate derivatives, the most variation occurs in the forebrain and particularly within the pallium, which is the dorsal part of the telencephalon. However, substantial variation also occurs in the roof of the midbrain, the tectum, and in the roof of the hindbrain, the cerebellum.

The simplistic Scala Naturae concept of evolution ranks organisms on an ascending scale that is presumed to reflect evolutionary history and that places humans in a position that is 'superior' to that of all other animals, as in fish-to-frog-to-rat-to-cat-to-monkey-to-human. While this concept is unfortunately widely and deeply embedded in the public consciousness, it is completely unsupported by the massive amount of data on evolution, not only for the brain but for all characters across the board. This concept not only errs in implying a direction to evolution, which it does not have except in terms of responses to externally driven selective pressures that vary over

space and time, but it incorrectly implies that some existing taxa are identical to shared ancestral taxa, such as extant ray-finned fishes being identical to the ancestors of both themselves and land vertebrates.

To the contrary, both evolution and embryological development proceed from the general to the specific. In regard to evolution, the common ancestor of all vertebrates, for example, gave rise to the radiation of jawless vertebrates on the one hand and to that of the jawed vertebrates on the other; lampreys did not give rise to hagfishes. The common ancestor of tetrapods gave rise to amphibians on the one hand and to amniotes (reptiles, birds, and mammals) on the other; neither frogs nor newts gave rise to reptiles, birds, or mammals. Among amniotes, mammals actually appear in the fossil record before reptiles; reptiles did not give rise to mammals any more than mammals gave rise to reptiles. In regard to embryological development, it likewise generally proceeds from the general (common ancestral features) to the specific (specializations of the taxon) – for example, for a cat: from features common to vertebrates to those common to jawed vertebrates to those common to sarcopterygians (the fleshy-finned radiation) to
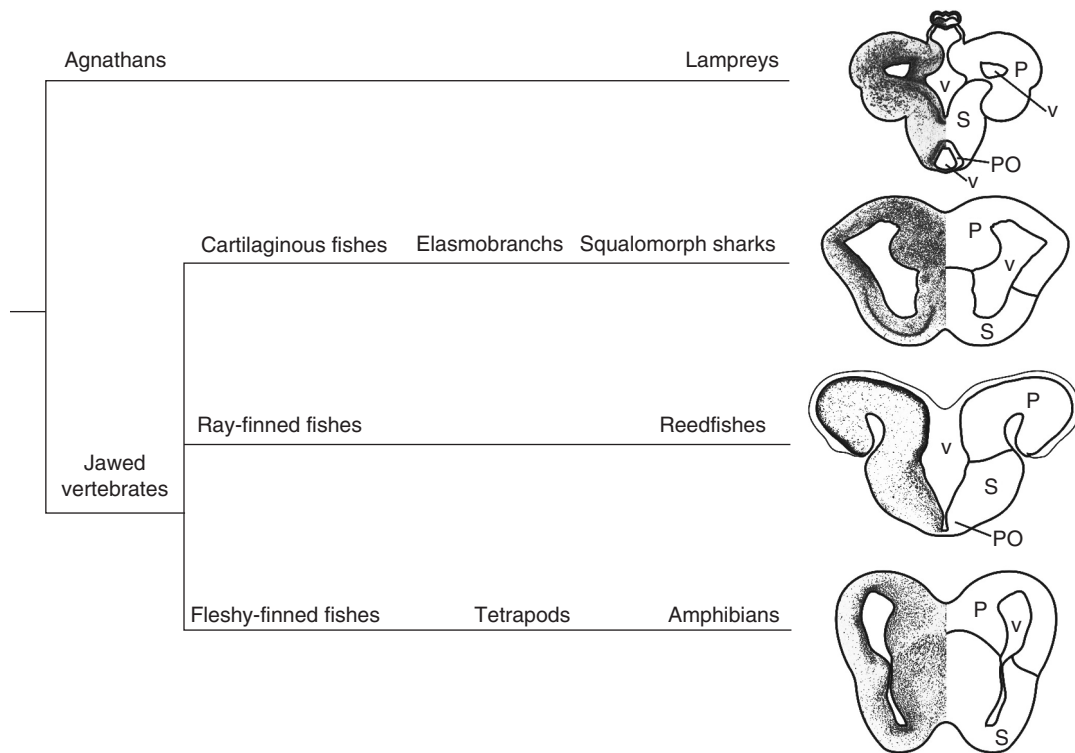
Figure 2 Simplified vertebrate cladogram showing examples of some of the taxa that have type I, cytoarchitectonically simple brains – lampreys (*Ichthyomyzon*), squalomorph sharks (the spiny dogfish shark *Squalus*), reedfishes (the bichir *Polypterus*), and amphibians (the bullfrog *Rana*). The photomicrographs of Nissl-stained hemisections with mirror-image line drawings shown at the right are through the telencephalon. D, diencephalon; H, habenula; P, pallium; Po, preoptic region; S, subpallium; v, ventricle. Most Nissl photomicrographs used in this figure were kindly provided by R Glenn Northcutt.

those common to tetrapods to those common to amniotes to those common to mammals to those specific to cats.

Understanding the basic process of evolution in these terms is essential to understanding brain evolution, since the structures present in the telencephalon of a modern reptile, for example, were not necessarily present in the common ancestor of mammals and reptiles. In order to reconstruct the evolution of a mammalian brain one must first deduce the condition of the ancestral brain, and only a comparative analysis of tetrapod brains can provide the clues necessary to do so. Features present in all tetrapod brains are those that can be hypothesized to have been present in the ancestral brain. Features present in only reptiles or only birds or only mammals are those features that can be hypothesized to be specializations of that particular taxon. Such hypotheses are not guaranteed to be correct, but they follow the principle of parsimony, which is accepted as the most conservative and probably most accurate method of dealing with the data. What is clearly established is that all taxa have their own specializations. Each taxon has a mix of primitive features – those that resemble what a distant ancestor had – and advanced features – those that

are unique specializations. The challenge is to determine which features are shared across several taxa and therefore probably primitive in order to reconstruct a model of the common ancestor, then identify the specializations in each taxon, and then investigate how such specializations might have arisen.

Evolution of the Brain in Ancestral Vertebrates

Lancelets, or amphioxus, are small invertebrate chordates that are the closest living relatives of vertebrates. They have a specialization at the rostral end of the neural tube, called the cerebral vesicle, that qualifies as a brain in terms of its position and several regional features that correspond to those of vertebrate brains. From reconstructions of thin sections analyzed at the electron microscope level by Thurston Lacalli and his colleagues, it is now known that these features include (1) a single, midline group of pigment cells and associated neuronlike cells called the frontal organ, which appears to be the homolog of the paired, retinal eyes of vertebrates; (2) a more caudally lying structure called the lamellar body, homologous to the vertebrate pineal organ; (3) a ventrally situated
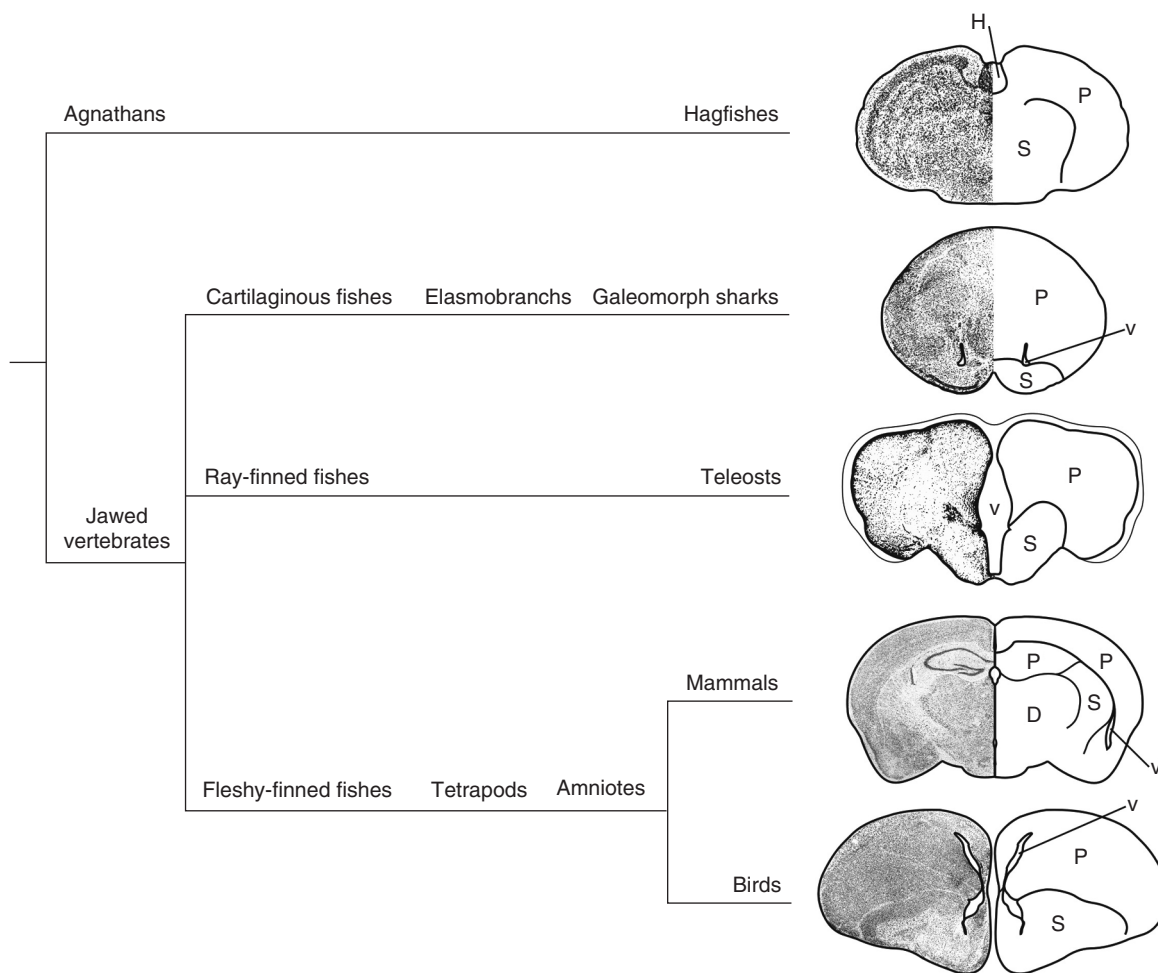
Figure 3 Simplified vertebrate cladogram showing examples of some of the taxa that have type II, cytoarchitectonically more complex and elaborated brains – hagfishes (*Eptatretus*), galeomorph sharks (the nurse shark *Ginglymostoma*), teleosts (the sunfish *Lepomis*), mammals (the mouse *Mus*), and birds (the pigeon *Columba*). The photomicrographs of Nissl-stained hemisections with mirror-image line drawings shown at the right are through the telencephalon. Most Nissl photomicrographs used in this figure were kindly provided by R Glenn Northcutt.

structure called the balance organ, homologous to at least part of the hypothalamus of mammals; and (4) associated infundibular cells, homologous to the vertebrate infundibulum (neurohypophysis). Recent findings from a cache of fossils of a small creature named *Haikouella lanceolatum*, discovered in Haikou, China and analyzed by Jon Mallatt and Jun-Yuan Chen, in addition to an array of other fossil evidence, have allowed several hypotheses on early brain evolution in the vertebrate line to be substantially clarified. *Haikouella* fossils exhibit a number of relevant features, including (1) an enlarged brain with a brain: body ratio comparable to that of lampreys, (2) brain components that consist mainly of a diencephalon and hindbrain, and (3) paired eyes. The scenario presented here may be modified in the future depending upon further fossil evidence but seems

the most likely one based on the multiple lines of evidence available to date.

At the origin of vertebrates, the nervous system would have had, like amphioxus, a rostral, forebrain region that contained at least the light-receptive and hypothalamic components of the diencephalon. It lacked a telencephalon and olfactory structures. The light-receptive components comprised paired eyes, like *Haikouella*, and also a pineal organ. While still small and relatively simple in construction, the paired eyes likely had a vertebrate retinal structure. The hypothalamic component included connections with an infundibulum. As evolution proceeded, subsequent gains included a host of features associated with the neurogenic placodal tissues of head and the neural crest tissue of the body and head. Together, these tissues generate the motor neurons of the autonomic
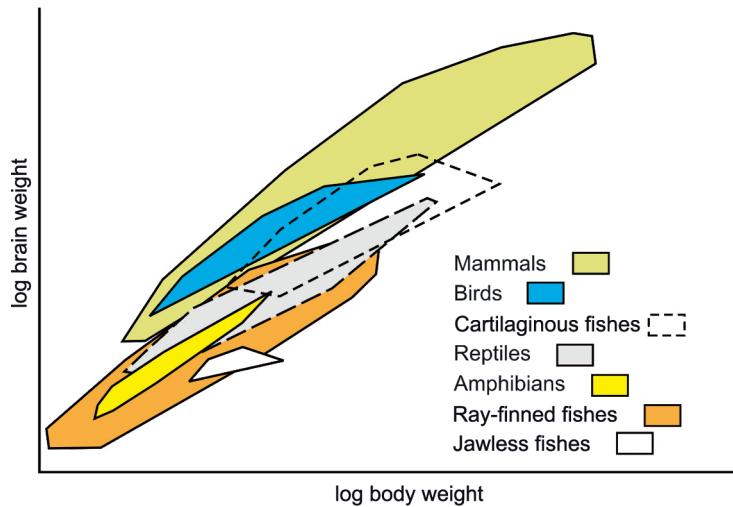
Figure 4 Convex polygons that enclose the log values for brain weight plotted against log values for body weight for a number of vertebrate taxa. Data kindly provided by Harry Jerison. Note that the polygon for birds almost completely overlaps that for mammals. The brain:body ratios for some groups of birds, including corvids (crows) and parrots, overlap the lower range of primates. Note also that the upper border of the polygon for ray-finned fishes also overlaps the lower border of the polygon for mammals and that the polygon for cartilaginous fishes substantially overlaps the polygons for both birds and mammals. These relationships demonstrate that brain elaboration and enlargement has occurred independently multiple times. Not all type II brains also show marked enlargement of brain:body ratio, however, since while hagfishes have type II brains, their brain:body ratio falls within the polygon for jawless fishes, which overlaps only the lower range for ray-finned fishes and is considerably below the polygons for cartilaginous fishes, birds, and mammals.

nervous system, the sensory neurons of cranial nerves I, V, VII, VIII, IX, and X, and the sensory neurons of the spinal nerves. Additionally, neural crest generates a host of other tissues, including the dermal bones and sensory capsules of the skull and the meninges that surround the central nervous system. Thus, with the bloom of these tissues at some point along the early vertebrate lineage, many of the structures that form the vertebrate head were gained, along with the peripheral nervous system of the head and body. Continued elaboration of the brain and spinal cord, in terms of sensory and motor nuclei and cell columns, the reticular formation, ascending and descending pathways, the telencephalon with olfactory bulbs, the dorsal and ventral thalamic components of the diencephalon, and a definitive midbrain region would likewise have been gained during this transition.

Type I Brains

As noted previously, brains that exhibit relatively little migration of neurons away from the ventricular surface and relatively simple cytoarchitecture, as compared to more complexly elaborated brains, can be classified as type I (Figure 2) for heuristic reasons. Taxa that have such brains include lampreys, some cartilaginous fishes (chimaeras, squantinomorph sharks, and squalomorph sharks), some ray-finned fishes (nonteleosts), and, among the sarcopterygian

radiation, lungfishes, the crossopterygian fish *Latimeria*, and amphibians. Only a brief overview of brain organization in these taxa with selected highlights can be presented here.

Lampreys

Lampreys have most of the cranial nerve and other central nervous system components that characterize vertebrate brains in general, although there are some minor differences in the innervation pattern of the extraocular muscles. Among alar plate derivatives, a cerebellum is present but of miniscule size, consisting only of a small region of gray matter in the dorsal part of the rostral medulla. The midbrain tectum is present, with both caudal, auditory and rostral, visual and somatosensory portions. The telencephalon is of very modest size, with cell bodies migrated away from the ventricular surface to only a limited extent (Figure 2). Pallial regions homologous to those of other vertebrates have not yet been identified with certainty. A striatopallidal complex is present in the subpallium (also an alar plate derivative).

Type I Cartilaginous Fishes

Type I cartilaginous fishes comprise chimaeras (ratfishes), squantinomorph sharks, and squalomorph sharks. The latter have been most studied, particularly the spiny dogfish shark *Squalus acanthias*. In general,

the brains of these taxa exhibit many of the cranial nerve and reticular formation components of other vertebrates, a well-developed cerebellum, a moderately developed midbrain roof, an unremarkable diencephalon, and a moderately developed telencephalon. The latter in particular is less extensively populated with neurons (**Figure 2**) than in type II cartilaginous fishes but contains all the basic pallial and subpallial components of other vertebrates.

Type I Ray-Finned Fishes

All ray-finned fishes, both type I and type II, undergo an almost unique process of telencephalic pallial development called eversion. The only other vertebrate that shares this developmental process, and that to a lesser extent, is the crossopterygian fish *Latimeria*. Rather than undergoing an outpouching process of hemispheric expansion during development, as occurs in other vertebrate groups, eversion causes the most medial part of the telencephalic pallium to lift upward and outward, eventually arching laterally. In evagination, the pallium enlarges like a balloon expanding, with its most medial part remaining in a medial position, the dorsal part arching dorsally, and the most lateral part remaining in its lateral position. In contrast, during eversion, the medial pallium comes to lie in the most lateral position, and the originally lateral pallium remains most medially and ventrally. The geometry of eversion is akin to that of a person doing a back bend, such that the head, arms, and upper torso curve upwards and then backwards. Thus, as shown for both the reedfish telencephalon shown in **Figure 2** and that of a teleost telencephalon shown in **Figure 3**, the ventricular surface lies dorsalmost over the dorsal aspect of the everted pallia, and the ventricular cavity extends laterally over each side to the point where the ependyma (shown as a thin line) attaches.

The brains of type I ray-finned fishes (reedfishes, sturgeons and paddlefishes, gars, and the bowfin *Amia*) are generally similar in plan and in their component parts to brains of other vertebrates, with similar cranial nerve and reticular formation components: cerebellum, midbrain roof, and forebrain components. As with other ray-finned fishes and, generally speaking cartilaginous fishes, the dorsal thalamus contains three nuclei, the more caudal two of which receive their predominant input from the midbrain roof, and the rostral one receives its predominant inputs directly from the retina, somatosensory system, and/or other sources, without relay first through the midbrain roof. The midbrain roof-recipient nuclei can be grouped as the collothalamus and the rostral dorsal thalamic component(s) can be grouped as the lemnothalamus – a basic feature of organization that applies at least to all jawed vertebrate brains.

Both ray-finned fishes and cartilaginous fishes have additional nuclei that are involved in the relay of ascending sensory information to the telencephalon, the preglomerular nuclear complex (or individual nuclei homologous to its various components), but these are better developed in type II brains than in type I brains. In reedfishes, a nucleus medianus is present that relays visual information to the pallium, and in gars and the bowfin *Amia*, a preglomerular nuclear complex is present. The latter generally relays lateral line and/or gustatory inputs to the telencephalon.

Lungfishes, Crossopterygian, and Amphibians

Less information is available for lungfish brains than for the brains of amphibians and most other major vertebrate groups, and very little information is available for the crossopterygian *Latimeria*, since this animal survives only at great ocean depths under conditions of high pressure. Nonetheless, the anatomical organization of lungfish and crossopterygian brains appears to be generally similar to that of amphibians. As already noted, the telencephalic pallium of *Latimeria* undergoes partial eversion during embryological development, whereas evagination occurs in lungfishes and amphibians.

Amphibian brains exhibit the basic structure and components of other vertebrate brains. Of note in terms of their type I development, more production and migration of neurons occurs in the medial (hippocampal) part of their pallium than in other pallial regions (**Figure 2**). The medial pallium is the major site to which the rostral part of their dorsal thalamus, nucleus anterior, projects. The latter nucleus constitutes the lemnothalamus, but, unlike the situation in amniotes, it does not receive direct input from either the retina or the somatosensory system (dorsal column nuclei), instead having these inputs relayed to it through the ventral thalamus. Also, the ventral thalamic projections to nucleus anterior are thought to be inhibitory, rather than excitatory as the direct inputs would be. Whether this condition represents the ancestral tetrapod condition or a secondary specialization within the amphibian lineage remains to be determined.

The collothalamus of amphibians is also different to a marked degree in its pattern of projections from the collothalamus of amniotes. These nuclei, which receive their predominant visual, somatosensory, and auditory inputs via relay through the midbrain roof, project almost exclusively to the striatum in the subpallium, with only a few fibers reaching the lateralmost aspect of the pallium. In contrast to the

medial pallium, the rest of the pallium in amphibians exhibits almost no migration of neurons away from the ventricular surface (Figure 2). Also in contrast to this pattern of projections, as will be noted subsequently, in amniotes, collothalamic projections give off collaterals to the striatum, but their heaviest targets are within the dorsolateral and lateral (lateral and ventral) portions of the pallium.

Type II Brains

As noted previously, brains that exhibit a relatively large production of neurons combined with substantial migration of most neurons away from the ventricular surface and relatively elaborate cytoarchitecture, as compared to the more simply constructed type I brains, can be classified as type II (Figure 3) for heuristic reasons. Taxa that have such brains include hagfishes, some cartilaginous fishes (galeomorph sharks, skates, and rays), many ray-finned fishes (telosts), and, among the sarcopterygian radiation, amniotes (mammals, reptiles, and birds). Only a brief overview of brain organization in these taxa, with selected highlights, can be presented here.

Hagfishes

The brain of hagfishes is largely terra incognita, due to the difficulty of obtaining and working with these animals (which are covered with a copious quantity of secreted mucus) in a laboratory setting. Also, the substantial amount of neuronal production and migration during development results in a highly complex brain in terms of its cytoarchitecture, and many features of the latter do not clearly correspond to those of other vertebrates. A telencephalon with a highly laminated pallium is present (Figure 3), and those pallial lamina are in receipt of olfactory information. A diencephalon is present with recognizable divisions of epithalamus (habenula), dorsal and (perhaps) ventral thalami, and hypothalamus. Eyes, however, are extremely reduced, and extraocular muscles are absent, with corresponding reduction of retinal projections and oculomotor nuclei. No cerebellar tissue has been identified. Instead of being similar to ancestral jawless vertebrates, a good case can be made for hagfish neural (and other) features being the consequence of evolutionary specializations.

Type II Cartilaginous Fishes

Galeomorph sharks, skates, and rays have exceptionally well-developed telencephalons, both in terms of size relative to their body size and in terms of complexity of cytoarchitecture (Figure 3). Less is known about their various neural systems and major

pathways than for some other vertebrate groups – particularly ray-finned fishes and tetrapods – due to the practical difficulties of working with many of these animals in a laboratory setting. One of the major breakthroughs in comparative studies of the past century was that achieved by Sven Ebbesson, Lennart Heimer, Dolores Schroeder, and their colleagues with their work on nurse shark (*Ginglymostoma cirratum*) behavior and sensory pathways, demonstrating that (1) olfactory projections are limited to a relatively small lateral pallial area (rather than being to most or all pallial areas as previously assumed), (2) two different visual pathways to the pallium are present, one lemnothalamic (via direct projections from the retinorecipient nucleus anterior) and one collothalamic via midbrain roof relay to the dorsal thalamus and thence to the pallium, and (3) visual form discrimination requires participation of these telencephalic visual areas rather than just that of the midbrain roof. These findings, along with those of Harvey Karten and his colleagues on bird sensory system pathways and telencephalic organization (see later, the section titled 'Forebrain evolution across amniotes'), precipitated a new era of comparative insights into the evolution of vertebrate brains.

Teleosts

The range of variation in brain structure across teleosts, an exceptionally large vertebrate taxon, is extremely broad. As with cartilaginous fishes and other ray-finned fishes, teleosts exhibit many of the basic cranial nerve, reticular formation, cerebellar, midbrain, and forebrain components of the brain typical of vertebrate brains in general. As in cartilaginous fishes, olfactory projections are restricted to a small part of the pallium, leaving large areas for other sensory system inputs. Various groups and species of teleosts also exhibit a large number of specializations, mostly of alar plate derivatives but some of the basal plate as well, a sampling of which can be presented here.

A derivative of the basal plate, the oculomotor nucleus, has a very specialized structure in the stargazer, one of a number of fishes that are capable of producing an electric discharge. Part of the oculomotor nuclear complex in this fish is called the electromotor division, and it innervates specialized electric organs that are developmentally derived from the extraocular muscle anlage. Both alar and basal plate derivatives are involved in the complex circuitry that supports the sonic motor systems of a number of fishes, such as the plainfin midshipman (*Porichthys notatus*). Other cranial nerve specializations include a massive expansion of the taste-receptive nuclei in

cyprinids (which include goldfishes) and silurids (cat-fishes). Rather than consisting of the relatively small gustatory nucleus as in mammals and most other vertebrates, the taste-receptive cell groups in these fishes are hypertrophied into large vagal, glossopharyngeal, and facial lobes, with over a dozen cellular layers and a highly complex pattern of connections. Likewise, the lateral line system is particularly elaborated in electroreceptive teleost fishes, with mormyrids being an extreme example. These fishes have an electroreceptive cerebellum that is massively expanded relative to all of the rest of the brain and also extreme in its degree of complexity of cytoarchitecture and connections. Mormyrids use their electrosensory communication system for individual identification to conspecifics and for highly complex behavioral feats, including group cooperation in the building of underwater nests.

In addition to these cranial nerve and hindbrain specializations, teleosts display a wide range of variation in the complexity and degree of elaboration of their telencephalons (**Figure 3**). As described above for type I ray-finned fishes, the telencephalon undergoes a process of eversion during embryological development, resulting in a reversal for the adult positions of the originally medial and lateral pallial regions. Recent studies by Cosme Salas and his colleagues have demonstrated that the originally medial (hippocampal) part of the pallium in goldfish is involved in the same types of functions as the amniote hippocampus, particularly spatial mapping. In contrast, the originally lateral (amygdalar) part of the pallium in goldfish is involved in emotional, associational learning, such as the pairing of a light stimulus with an aversive, moderate electric shock. Thus, despite the process of eversion and also despite markedly different cytoarchitecture, the basic functions of pallial regions in goldfish are remarkably similar to their homologs in land vertebrates.

Amniotes

Mammals The earliest mammals appear in the fossil record slightly before the earliest reptiles. Rather than thinking of the common ancestor of all amniotes as a stem reptile, which implies reptilian structures in the brain as well as elsewhere, it is correct to think of the common ancestor as a stem amniote. Some of the most salient features of the brains of sauropsids (reptiles and birds) and those of mammals represent divergences from the common ancestral condition rather than sequential evolution of either the extant mammalian or sauropsidian condition to the other.

Cranial nerve specializations do not only occur in fishes, such as those already noted. Among mammals, a remarkable adaptation of the trigeminal nerve also occurs in monotremes – platypus and echidna. Both, but better developed in the platypus, have electroreceptors – located on the snout of the echidna and the duckbill of the platypus. These are not innervated by the lateral line system, which is present only in anamniotes, but rather by the trigeminal nerve. The platypus in particular uses these electrosensory inputs to search for prey under debris in the muddy stream beds that it inhabits. Trigeminal-associated specializations also occur in mammals such as the star-nosed mole, innervating its highly specialized Eimer's organs that cover fleshy tentacles around the oral region, and such as the barreletts-barreloids-barrels cellular formations that are present within somatosensory nuclei and cortex of rodents and some marsupials with mustacial vibrissae.

In addition to a host of features similar to those of other vertebrates, the brains of mammals vary somewhat across their taxa (monotremes vs. marsupials vs. placental mammals) and also share several salient specializations, the most prominent of which is of course the six-layered and massively developed neocortex (**Figure 3**). Likewise, the mammalian dorsal thalamus is the most highly developed and elaborated of any major taxa, in placentals containing numerous sets of multiple nuclei each. It is likely that, as in extant monotremes and to a lesser degree in extant marsupials, the earliest mammals favored a substantial expansion of the lemnothalamus (anterior, medial, rostral intralaminar, and ventral nuclear groups and the dorsal lateral geniculate nucleus) and its pallial targets. This would be in accord with the importance for early, small-sized, crepuscular mammals of depending on limbic system functions such as spatial mapping and on their lemnothalamic visual pathway to striate cortex. Subsequently, within marsupials and to a greater degree in multiple orders of placental mammals, the collothalamic (medial geniculate body and the posterior intralaminar, posterior, and LP/pulvinar nuclear groups) pathways were markedly expanded, including the collothalamic-recipient extrastriate, auditory, and secondary, etc., somatosensory cortical areas as well as the higher order association cortical areas of the temporal and parietal lobes. Likewise, a pallial part of the amygdala in mammals, its basolateral component, is in receipt of ascending collothalamic projections.

Sauropsids Just as mammals diverged from the stem amniote stock, so did the sauropsid line that gave rise first to reptiles and, subsequently, birds, which actually are a specialized group of reptiles, just as are the other extant groups of this major taxon. In fact, recent genetic analyses have demonstrated that the thecodonts (crocodiles and birds), along with

turtles and the rhynchocephalian lizardlike animal *Sphenodon*, are clustered as a monophyletic group, while the squamates (lizards and snakes) constitute the outgroup to them (**Figure 1**).

Among sauropsids, as in mammals and other vertebrates, cranial nerve specializations occur. In two families of snakes, boids and crotalids, sensory pits are present on the head region that can detect infrared radiation. These pits are innervated by the trigeminal nerve, and, in crotalids, the trigeminal projections terminate within a brain stem nucleus (the lateral trigeminal nucleus) unique to them. The infrared sensory information is relayed to the optic tectum (directly in boids and via another unique nucleus, the nucleus reticularis caloris, in crotalids), where it is used in conjunction with visual input to locate and accurately strike prey. Yet another specialization of the trigeminal system – the ability of magnetodetection – occurs in birds and is shared with like specializations recently found in trout, salamanders, and loggerhead sea turtle hatchlings. Naturally available magnetic stimuli are used, often in conjunction with visual clues, for navigation and orientation to the earth's magnetic field.

The telencephalic pallium of both birds (**Figure 3**) and reptiles contains a dorsally lying region – the Wulst of birds and the general, or dorsal, cortex/pallial thickening of reptiles – that is well established as the homolog of at least some of the more medial, lemnothalamic-recipient regions of mammalian neocortex, that is, the primary somatosensory-motor and visual cortices. Likewise, the lemnothalamus of sauropsids contains a number of individual nuclei that are homologous as either a field or one-to-one basis with various lemnothalamic nuclei and/or nuclear groups of mammals. The pallium of sauropsids also contains a structure called the dorsal ventricular ridge (DVR, also called the nidopallium and mesopallium in birds) that receives several ascending collothalamic pathways – visual, auditory, and somatosensory – and, likewise, the sauropsid collothalamus contains nuclei that are homologous to the set of collothalamic nuclei of mammals.

Within the early sauropsid line, a sequence of dorsal thalamic and pallial elaboration occurred that was opposite to that in mammals. In early sauropsids, elaboration of the collothalamus and its pallial targets was favored over that of the lemnothalamus. In some extant reptiles, such as turtles, some lizards, snakes, and the rhynchocephalian *Sphenodon*, the DVR is structured as a corticoid (layered) border of cells that surrounds a central region that hasscattered neurons but is mostly neuropil. Ascending thalamic afferents terminate on the dendrites of neurons of the corticoid band that extend into the neuropil region. In other extant reptiles – particularly crocodiles and some lizards – and birds, the DVR is a greatly expanded structure, with much more extensive and migrated populations of neurons – an exaggeration of the type II brain category. In these taxa, the DVR is composed of a number of nuclear regions, some of which receive the various ascending collothalamic projections and others of which are expanded areas of association pallium. Within the sauropsid line, birds have secondarily expanded the lemnothalamus and its pallial target area, the Wulst, although still not to as great a degree as the collothalamic-DVR systems.

Forebrain evolution across amniotes   Controversy is ongoing as to the homology of the DVR with mammalian pallial components. The pioneering work of Harvey Karten and his colleagues that began in the 1960s established the pallial nature of this part of the telencephalon in birds and traced the ascending auditory and visual pathways to it, strongly indicating homology of these areas to the auditory and extrastriate visual cortices of mammals (specifically of the DVR thalamo-recipient cell populations and their efferent target cell groups to the cell populations within layer IV and the infragranular layers of neocortex, respectively). Similar pathways were then discovered in a number of reptilian taxa.

Recent embryological studies of gene expression patterns have yielded data that suggest a different correspondence – that of the sensory-recipient DVR to the basolateral amygdala of mammals. Neither of these one-to-one comparisons yet accounts for the evolution of the other structure, however; that is, the basolateral amygdala hypothesis does not yet satisfactorily explain the evolutionary derivation of the lateral neocortex, and vice versa. An alternative hypothesis that attempts to do so posits that the single DVR structure present in sauropsids is homologous, as the single derivative of a developmental field, to both of these structures in mammals. Still others argue that the pallial regions in sauropsids and mammals are so independently derived that sensible comparisons cannot be made at all. The argument also embraces the particular homologous relationships of the individual collothalamic nuclei between sauropsids and mammals and borders on becoming circular in that regard.

Whatever the outcome of the continuing research in this area in regard to phylogenetic homology of pallial areas and dorsal thalamic nuclei, it is now clearly established that the neocortex in mammals and the various pallial areas in birds, which exhibit dramatic differences in their cytoarchitecture

(Figure 3), both support highly complex cognitive abilities and may thus also both support high levels of consciousness, including working memory-related attributes such as anticipation of future events, sense of self, and theory of mind. A bounty of recent studies in birds, creatively designed to ask experimental questions of the birds in behavioral paradigms that are relevant to their response abilities, indicate extremely high levels of cognitive abilities in at least some taxa, particularly corvids (crows) and parrots. Since such abilities in humans are correlated with a high degree of consciousness, it is parsimonious to posit a similar correlation in birds. One important caveat is that high levels of consciousness also may be present but currently undetectable by us in other animal taxa, including reptiles, amphibians, and fishes, but, at least in birds, the high cognitive abilities that we can now appreciate indicate the capacity for high-level consciousness as well. A major question then becomes what role the cytoarchitecture of neocortex (six cell layers based on a pyramidal cell motif) plays in mammalian cognitive abilities and the generation of high-level consciousness and why and how a dramatically different cytoarchitecture of the DVR (nuclear) is able to support similarly high cognition and a possibly correlated high degree of consciousness as well.

See also: Brain Connectivity and Brain Size; Brain Development: The Generation of Large Brains; Brain Evolution: Developmental Constraints and Relative Developmental Growth; Brains of Primitive Chordates; Gene Expression in the Evolution of the Human Brain.

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