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Evolution of the Pallium in Birds and Reptiles

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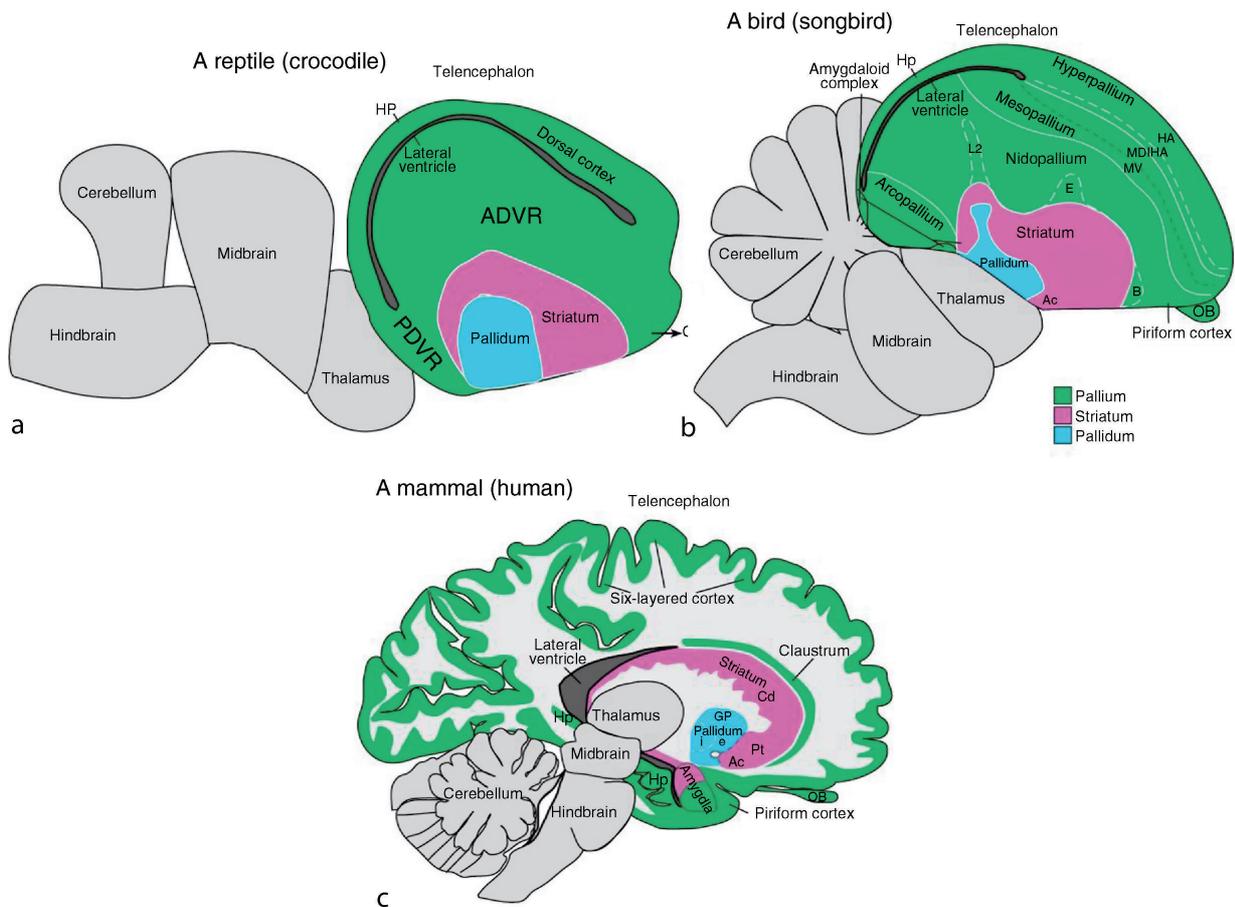
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Definition

The telencephalon of amniotes (reptiles, birds, and mammals) consists of two major subdivisions: the pallium and the subpallium. The subpallium, also called the basal ganglia, is further divided into two main subdivisions: the striatum and pallidum (Fig. 1). The striatum and pallidum are also thought to contribute to the septum and subpallial amygdala (central and medial nuclei). The subpallial components are relatively conserved in its organization among amniotes (Fig. 1). The pallium, however, which is the topic of this essay, is relatively diverse in its organization. The bird pallium consists of four major subdivisions – hyperpallium (hypertrophied pallium), mesopallium (middle pallium), nidopallium (nest pallium), and arcopallium (arched pallium)- as well as olfactory, hippocampal, and pallial amygdala regions (Fig. 1b) as defined in the new avian brain nomenclature [1,2]. The organization of the reptile pallium is not yet as well defined, but it consists of what has been called the dorsal cortex and the dorsal ventricular ridge (DVR), as well as olfactory, hippocampal, and pallial amygdala regions (Fig. 1a). Various hypotheses have been proposed for similarities and differences in the organization of the reptile, bird, and mammalian pallia, which contribute towards an understanding of the evolution of the pallium [1,2].

Characteristics

Reptiles and birds belong to the vertebrate class called sauropsids (Fig. 2). Although birds are now sometimes classified as reptiles, birds and reptiles are referred to here as separate groups belonging to sauropsids, one group with feathers and the other with scales, respectively. The sauropsids belong to the larger group



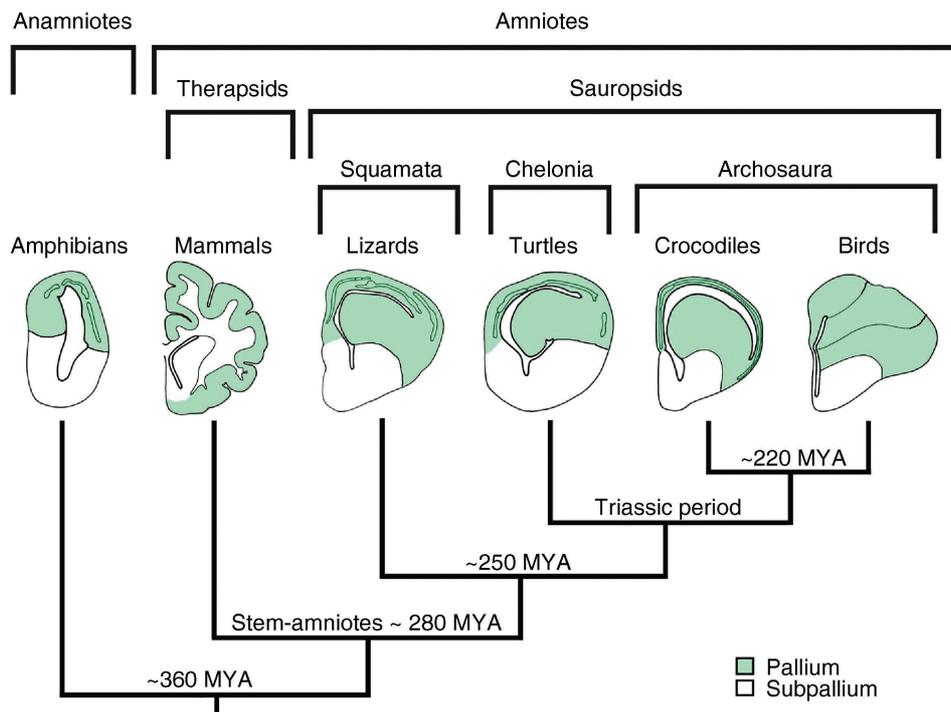
Evolution of the Pallium in Birds and Reptiles. Figure 1 Comparable organization of adult telencephalon of reptiles (a), birds (b), and mammals (c). Shown are sagittal views. Color-coding indicates pallial, striatal, and pallidal telencephalic domains. Pallial organization is well known for birds and mammals but not yet for most reptiles. The schematics represent the modern and recently revised view of vertebrate brain organization and evolution [1,2]. Abbreviations: *Ac* accumbens; *B* basorostralis; *Cd* caudate; *E* entopallium; *GP* globus pallidus, internal (i) and external (e) segments; *IHA* interstitial hyperpallium apicale; *HA* hyperpallium apicale; *Hp* hippocampus; *L2* field L2; *MD* dorsal mesopallium; *MV* ventral mesopallium; *OB* olfactory bulb; *Pt* putamen. For birds, some confusion exists in the literature as to whether the MD is hyperpallium densocellulare (HD) or is a separate structure.

called amniotes and share a stem amniote ancestor with mammals (Fig. 2). The pallia in developing embryos of reptiles, birds, and mammals are more similar than they are in their adult forms, consisting of a ventricular zone (VZ) and, in birds and mammals, a sub-ventricular zone (SVZ; Fig. 3), from which most pallial neurons emerge [3]. In the adult form, however, major differences are found in sauropsids relative to mammals. In sauropsids, the pallium is mostly nuclear in cellular organization, whereas in mammals it is mostly layered (Fig. 1) [1]. Among sauropsids, there are several types of nuclear organizations: type I found in turtles and some lizards, where neurons are relatively uniformly distributed within each brain subdivision, and type II found in other lizards, birds and crocodiles, where neurons are more concentrically organized relative to the lateral ventricle within brain subdivisions (Fig. 4) [4]. Despite these organizational differences,

neural connectivity and/or gene expression profiles indicate shared features in the type I and type II pallia of birds and reptiles and with the pallium of mammals. The shared features with mammals have led to investigators to propose differing hypotheses on the evolution of pallial subdivisions or neuron types from the stem amniote ancestor of birds and reptiles with mammals [1]. These features and hypotheses are discussed in this essay.

Development

The embryonic pallium of reptiles (studied mostly in turtles), birds, and mammals consists of a neurogenic zone near the lateral ventricle, the VZ (Fig. 3). Stem cells in the VZ divide to give rise to daughter stem cells, neurons, and glia. The neurons and glia migrate away from the VZ to make up the pallial parenchyma. In addition, mammals have a transient SVZ, and birds

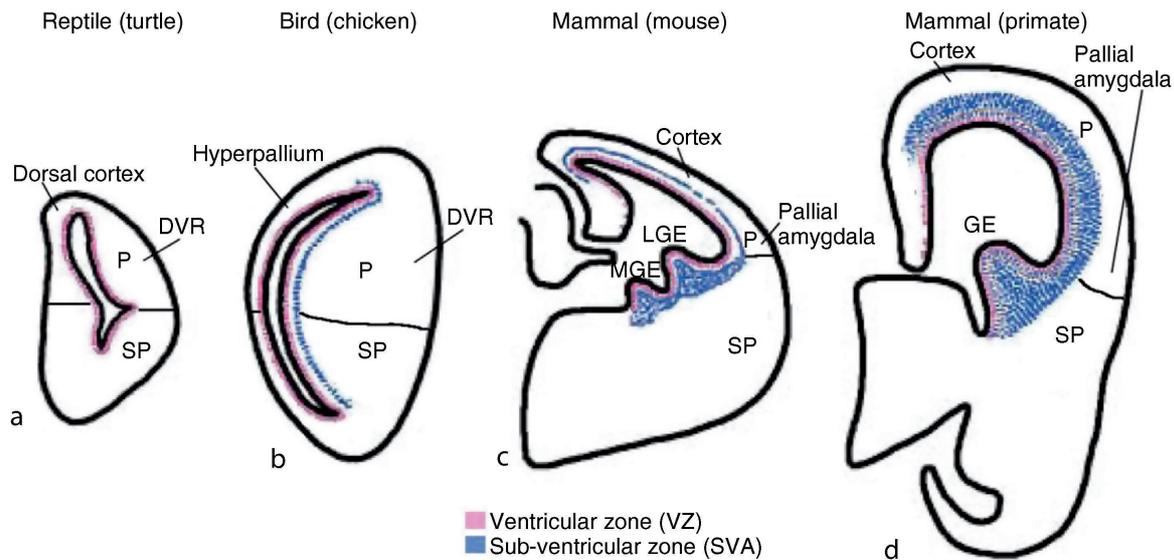


Evolution of the Pallium in Birds and Reptiles. Figure 2 Simplified modern view of tetrapod vertebrate evolution and general pallial shape in examples of living forms. As indicated by the phylogenetic trees, ancestral tetrapods are thought to have given rise to amphibians and to stem amniotes. Stem amniotes then split into at least two groups: the synapsid line leading to therapsids, which, through a series of now-extinct intermediate forms, evolved into mammals, and the diapsid line to sauropsids, which gave rise to all modern reptiles and birds. Among sauropsids, birds and crocodiles comprise the archosaurs and, along with the tuatara (not shown) and turtles, constitute one major clade, while the squamates, snakes (not shown) and lizards constitute the other major clade. This tree represents a recently revised view of reptilian phylogeny [8,9]. MYA, million years ago. For the brain examples, frontal views of anterior right hemispheres are shown; medial is left, dorsal is up. Note that the pallium (green) for large mammals (as shown here) is folded and thin; that of sauropsids below the lateral ventricle (open space) is nuclear and thick. For the sauropsids, only well-defined pallial subdivisions are known for birds. The subpallium in this plane of section includes the striatum (right of ventricle) and septum (left of ventricle, which is also thought to consist of striatal and pallidal parts). Figure modified from [10], with revisions based upon [1,2,8].

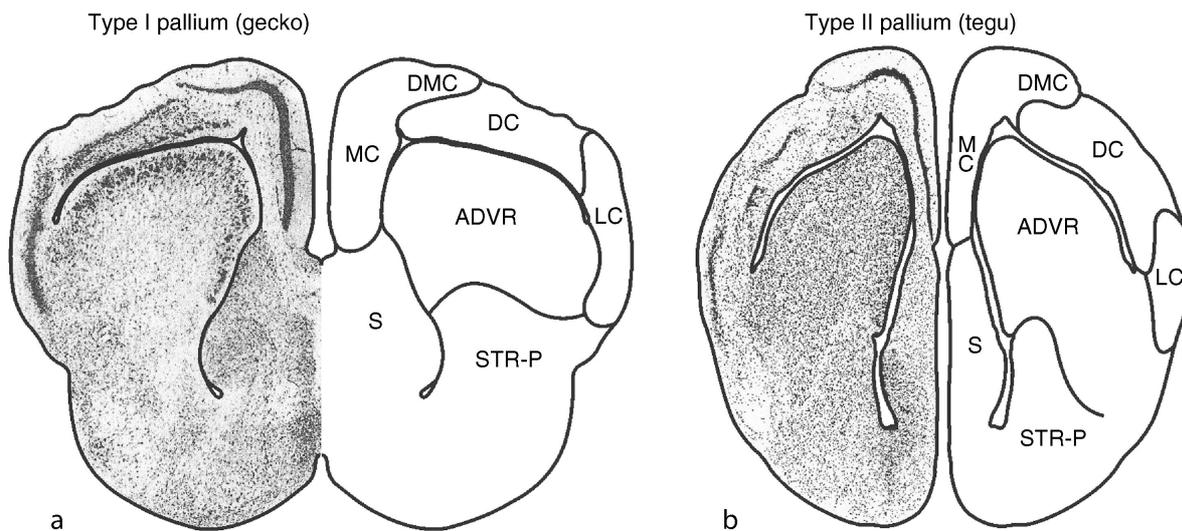
have a long-lasting SVZ located $\sim 100 \mu\text{m}$ away from the VZ that also gives rise to new neurons that contribute to the pallium. In mammals, the SVZ is present in pallial regions dorsal and ventral to the lateral ventricle and is transient, whereas in birds it is mainly ventral to the lateral ventricle and lasts throughout adulthood. In mammals, the thicker the SVZ, the larger the brain and cortical folding that develops, and this may also be the case for birds since their pallia tend to be relatively larger than many reptiles (Fig. 3) [3]. These findings suggest that either the SVZ evolved independently in birds and mammals or was lost in at least type I reptile (turtle) pallia. Neurons from the pallial VZ of developing birds and reptiles (and from the pallial SVZ of birds) are added to the pallium in an *outside-in* pattern as the pallium expands away from the lateral ventricle, with oldest neurons situated farthest away from the ventricle. In mammals, neurons are added instead in an *inside-out* pattern, with the oldest neurons

situated closest to the ventricle. These findings lead to the view that the similar connectivity and gene expression patterns found in adult avian and mammalian pallium may be the result of convergent evolution instead of features inherited from a common stem amniote ancestor [5].

Despite these differences in how the developing pallium is organized, developmentally regulated transcription factors have been used to demonstrate that the dorsal part of the telencephalon is homologous as pallium across vertebrates (Fig. 2). These transcription factors mostly have been studied in the brains of birds and mammals [6], but several also have been studied in reptiles [3,7]. The T-box transcription factor 2 (Tbr2) appears to be expressed in the pallial SVZ of both developing chicks and mice, whereas Tbr1 is expressed in more peripheral parts of the pallium lateral to the ventricle. In these peripheral parts, Tbr1 is lower in the later developing avian arcopallium and mammalian



Evolution of the Pallium in Birds and Reptiles. Figure 3 Comparable organization of embryonic telencephalon of reptiles (a), birds (b), and mammals (c and d) highlighting the ventricular zone (VZ) and the subventricular zone (SVZ). Shown are frontal views of the right hemisphere; medial is left, dorsal is up. A positive correlation exists between the presence and size of the SVZ and the size of the adjacent pallial regions. Labels outside of the telencephalons are the presumed adult regions to which these embryonic regions give rise. These and related findings were used to propose that the amygdala (and adjacent claustrum) of mammals is homologous to the DVR of reptiles and birds and that the six-layered cortex of mammals is homologous to the dorsal cortex of reptiles and hyperpallium of birds. The LGE and MGE in rodents give rise to the striatal and pallidal neuron types, respectively; in primates, the LGE and MGE are fused to form the GE. Abbreviations: DVR, dorsal ventricular ridge; GE, ganglionic eminence; LGE, lateral ganglionic eminence; MGE, medial ganglionic eminence; P, pallium; SP, subpallium. Figure modified from [3]; the medial part of the bird telencephalon is more vertically orientated than that shown, as in other species.



Evolution of the Pallium in Birds and Reptiles. Figure 4 Examples of type I and type II reptile pallia. Shown are frontal sections with mirror-image drawings through the telencephalon of a type I lizard (a, the gecko) and a type II lizard (b, the black tegu). Note the differences in the pallium, the ADVR, of each. Type I species have a high density of cells clustered near the ventricle surface. Abbreviations: ADVR, anterior dorsal ventricular ridge; DC, dorsal cortex; DMC, dorsal medial cortex; LC, lateral cortex; MC, medial cortex; S, septum; STR-P, Striatal-pallidal region. Figure from [9, figs.19–21] and used with permission.

pallial amygdala. The empty spiracles 1 (Emx1) homeobox transcription factor is expressed in dorsal pallial regions during development in chick, turtles, and mice, but appears to be absent in the later stages of embryonic avian nidopallium, mammalian claustrum, and parts of reptile pallium. The paired box 6 (Pax6) transcription factor is expressed along the entire developing pallial VZ in birds, reptiles, and mammals, but it is also differentially expressed in other forebrain areas among these groups. These findings have led some investigators to conclude that the avian arcopallium or parts of the avian arcopallium and a similar posterior pallial region in reptiles is homologous to the mammalian pallial amygdala, and that the avian nidopallium and parts of the mesopallium are homologous to mammalian claustrum, if not to other parts of the pallial amygdala [6,7]. I call this the nuclear-to-claustrum/amygdala hypothesis [1], which is described in further detail at the end of this essay.

Adult Organization

The organization of the adult avian pallium has been well studied and that of reptiles somewhat studied. Based upon Nissl staining patterns of embryonic and adult brains, Ulinksi and others defined a general organization of the bird and reptile pallia [4]. This includes a dorsal part, called the dorsal cortex in reptiles and the Wulst or hyperpallium in birds, and a lateroventral part called the dorsal ventricular ridge (DVR) that grows into the lateral ventricle (Fig. 1a and 1b). In birds the ventricular space between the DVR and hyperpallium is fused during development; in reptiles, the DVR and dorsal cortex remain separate into adulthood (Fig. 1a and b). Ulinksi further subdivided the DVR into anterior (ADVR) and posterior (PDVR) parts (Fig. 1a). He then defined two types of ADVR: type I, which consists of concentrically organized neurons with a higher density nearer the lateral ventricle, as found in turtles, the tuatara (the rhynchocephalian *Sphenodon*), and some lizards (such as the gecko; Fig. 4a); and type II, which consists of more uniformly distributed neurons, as found in birds, crocodiles, snakes, and other lizards (such as black tegu; Fig. 4b). As a result, the type II pallium is thought to have been derived multiple times independently (see ►[Evolution, of the Brain: in Reptiles](#)).

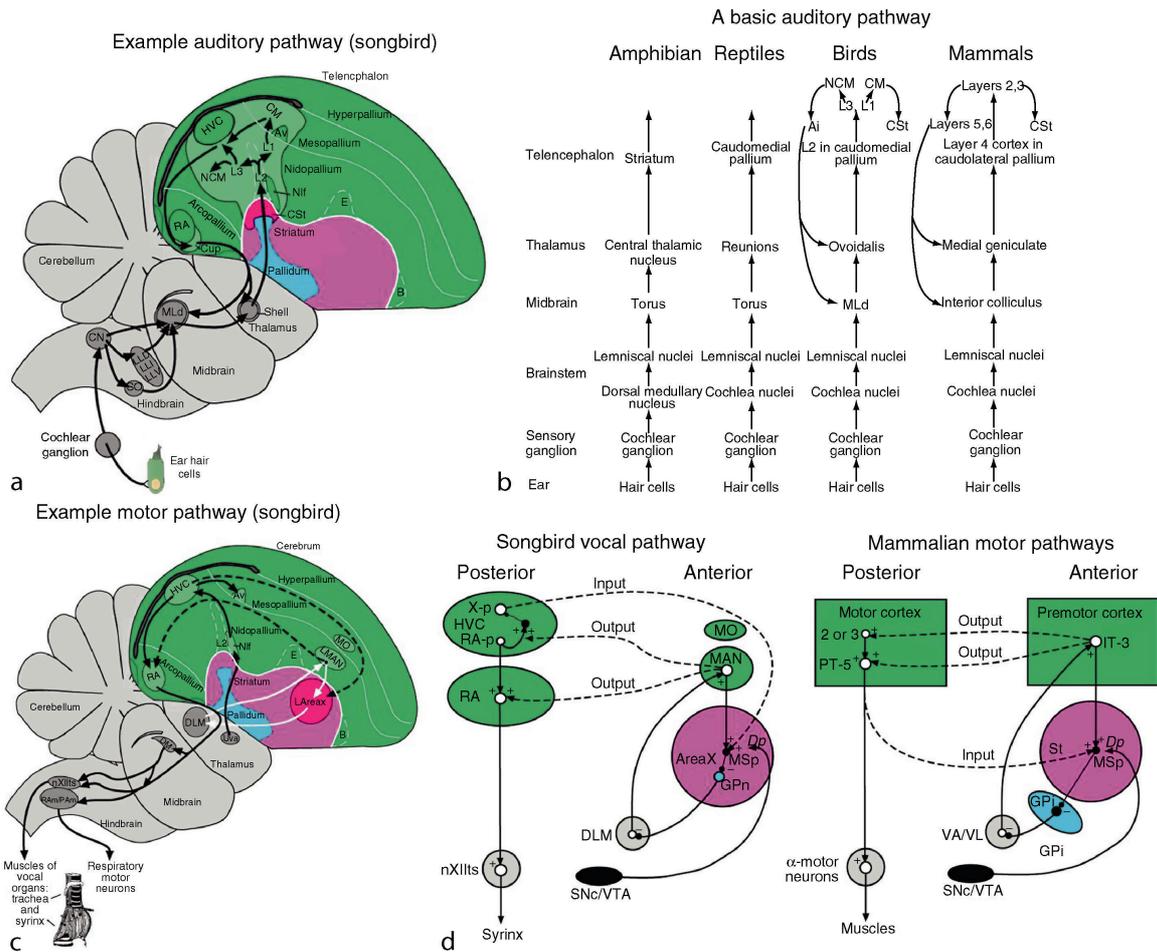
Which pallial subdivisions constitute the ADVR, PDVR, and dorsal cortex in birds is not clear, although it is often reported as clearly defined. For reptiles, detailed subdivision definitions have not yet been clearly delineated for any species, due in part to more diffuse Nissl staining of boundaries relative to birds [6]. Thus we do not yet know which pallial subdivisions in birds truly constitute presumably homologous subdivisions in reptiles. Approximate comparisons, however, have been given. One view holds that the homologue of the reptilian dorsal cortex is the highly differentiated

avian hyperpallium (including the hyperpallium apicale [HA], intercalated hyperpallium apicale [IHA], and hyperpallium densocellulare [HD]), that the homologue of the reptilian ADVR is the avian mesopallium and nidopallium, and that the homologue of the reptilian PDVR is the avian arcopallium [1,4]. However, this view may be too simplistic [4]. Comparative gene expression studies indicate that crocodiles like birds have a mesopallium [11], but that in both the mesopallium may consist of dorsal and ventral parts above and below the ventricle, as described further below. Differences certainly exist between birds and some reptiles. For example, snakes and lizards have a relatively unique feature in the medial part of their PDVR called the nucleus sphericus, which is involved in accessory olfactory bulb function and is not found in avians, crocodilians, or turtles [4,9]; nucleus sphericus is thought to be the homologue of portions of mammalian pallial amygdala nuclei (basal lateral amygdala and lateral amygdala) that receives input from the accessory olfactory bulb. Additional studies are needed to determine further similarities and differences in pallial organization between birds and reptiles, especially with the advent of the new avian brain nomenclature [1,2].

Connectivity: Sensory and Motor Pathways

Comparative analyses of sensory pathways in birds and various reptile species indicate that all have sensory pathways that reach the pallium [4,9]. These consist of at least two visual pathways, two somatosensory pathways, and one or possibly two auditory pathways. Two different types of sensory pathways have been defined as either collothamalic (sensory input serially connecting to midbrain to thalamus to pallium) or lemnothamalic (sensory input skipping midbrain serially connecting thalamus to pallium).

The auditory pathway is collothamalic, where in birds, crocodiles, turtles, and lizards, a midbrain auditory nucleus projects to the thalamic auditory nucleus, which in turn projects to a defined cell population in the caudomedial pallium (Fig. 5a and b). The exact location of this cell population differs across species of mammals, but it also differs across species of birds [12], where the subsequent connectivity has been well studied [13]. This pallial, thalamo-recipient cell population in birds is called field L2, which then projects to surrounding caudomedial nidopallium (NCM), which in turn projects to the caudomedial mesopallium (CM, in the ventral mesopallium). The surrounding nidopallium also has a descending auditory pathway to the arcopallium and thence to the surrounding shell regions of the thalamic and midbrain auditory nuclei. This descending auditory system is similar in connectivity to a descending auditory pathway found in mammals. The collothamalic visual pathway has a similar organization as the auditory pathway, as found in birds, crocodiles, turtles, and lizard,

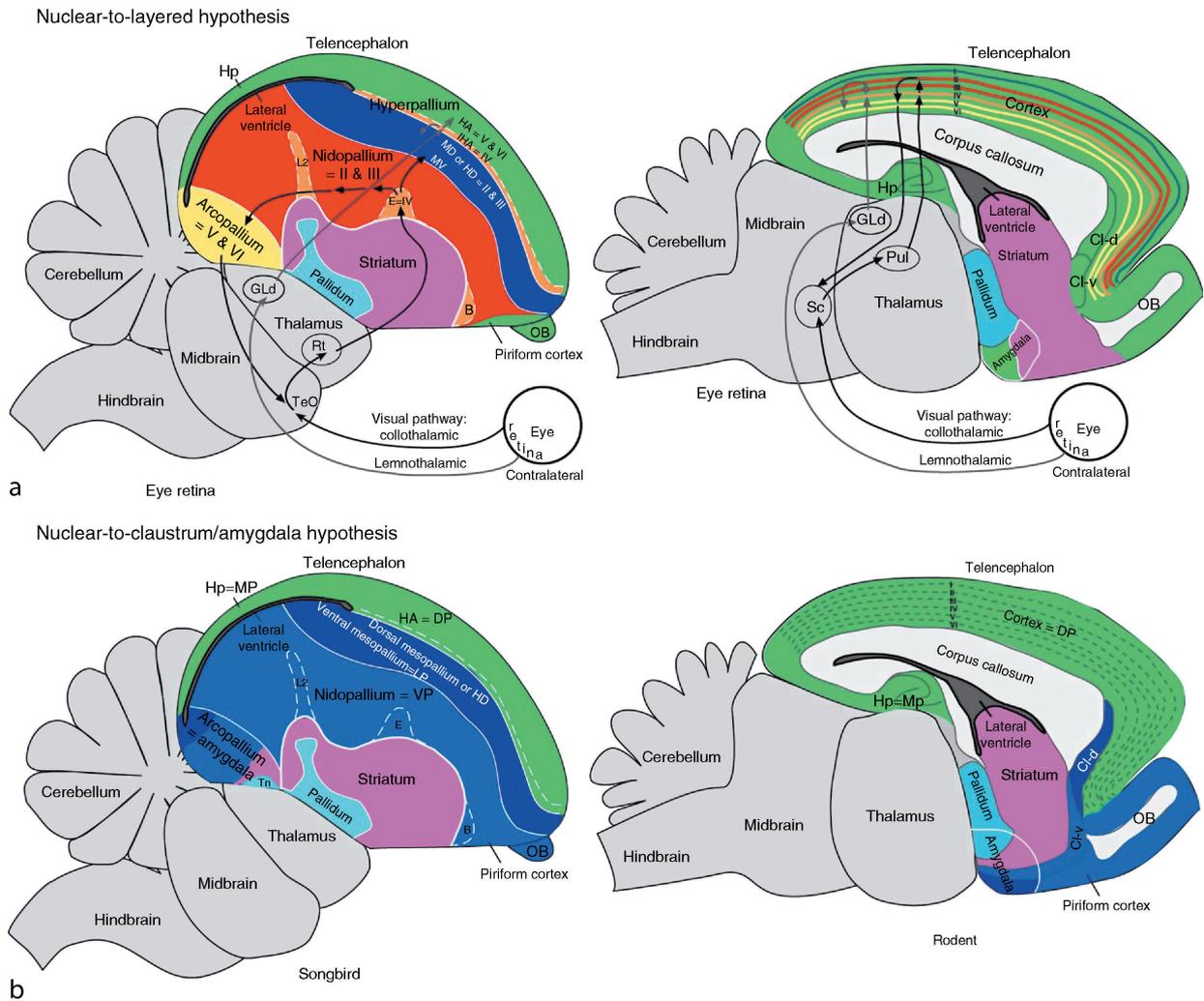


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Evolution of the Pallium in Birds and Reptiles. Figure 5 Example sensory (auditory) and motor (vocal) pathways in songbirds, in comparison with other vertebrates. (a) Auditory pathway in the songbird showing ascending and descending input. (b) Similar auditory pathways, but sometimes with different nomenclature used for individual nuclei, can be found for all amniotes examined. Only a sub-pathway through the cochlea and lateral lemniscal nuclei are shown. Once in the telencephalon, parallels can be found in cell type connectivity, although the pallial organizations are different and projections in amphibians are mostly to the striatum. (c) Vocal pathway of songbirds consisting of the vocal motor pathway (*black arrows*), the vocal pallial-basal-ganglia-thalamic loop (*white arrows*), and the connections between the two (*dashed arrows*). (d and e) Comparisons of cell types and connectivity of the vocal pathway in songbirds and forebrain motor pathways in mammals. Also shown is dopaminergic input from the SNc/VTA. Abbreviations: *Av* avalanche; *B* basorostralis; *CM* caudal mesopallium; *CN* cochlear nucleus; *CSt* caudal striatum; *DLM* dorsal lateral nucleus of the medial thalamus; *DM* dorsal medial nucleus; *E* entopallium; *GPI* globus pallidus, internal segment; *HVC* (a letter-based name); *L1*, *L2*, *L3* fields L1, L2 and L3; *LAreaX* lateral AreaX of the striatum; *LLD* lateral lemniscus, dorsal nucleus; *LLI* lateral lemniscus, intermediate nucleus; *LLV* lateral lemniscus, ventral nucleus; *LMAN* lateral magnocellular nucleus of the anterior nidopallium; *MO* oval nucleus of the mesopallium; *MLd* dorsal lateral nucleus of the mesencephalon; *NCM* caudal medial nidopallium; *Nif* interfacial nucleus of the nidopallium; *nXIIts* nucleus XII, tracheosyringal part; *Ov* ovoidalis; *PAm* para-ambiguous; *RA* robust nucleus of the arcopallium; *RAM* retroambiguous; *SO* superior olive; *Uva* nucleus uvaeformis. For panels (d) and (e) – + excitatory neurons; – inhibitory neurons; *MSP* medium spiny neuron; *GPn* globus pallidus-like neuron in songbird AreaX; *X-p* X-projecting neuron of HVC; *RA-p* RA-projecting neuron of HVC; *PT-5* pyramidal tract neuron of motor cortex layer 5; *IT-3* intratelencephalic projecting neuron of layer 3. (a) and (c) modified from [1]; (b) and (d) modified from [12].

with the projection field of all suaropsids tested located more anteriorly within the nidopallium adjacent or near to the striatum; the specific pallial, thalamo-recipient target is called the entopallium in birds (Fig. 6a). A

pseudo-collothalamic somatosensory pathway exists in birds, from the trigeminal sensory nucleus, innervated by the upper neck and face. The ascending trigeminal somatosensory pathway in birds does not involve a



Evolution of the Pallium in Birds and Reptiles. Figure 6 One-to-one homology hypotheses between avian and mammalian brains in the context of the new avian brain nomenclature. (a) An example of a nuclear-to-layered hypothesis. Connectivity of collothalamic and lemnothalamic visual pathways in avian (*left*) and mammalian (*right*) brains are shown. The hypothesis illustrated is a combination of Karten [18] and Medina and Reiner [5]. (b) An example of a nuclear-to-claustrum/amygdala nuclei hypothesis. The hypothesis illustrated is that of Puelles et al. [6]. In both hypotheses, color-coding indicates proposed homologies between birds and mammals, but the relationship of the newly named mesopallium needs further study and clarification. Abbreviations: I–VI cortical layers I–VI; B basorostralis; Cl-d claustrum, dorsal part; Cl-v claustrum, ventral part; DP dorsal pallium; E entopallium; GLd dorsal lateral geniculate nucleus; HA hyperpallium apicale; HD hyperpallium densocellulare; Hp hippocampus; IHA interstitial hyperpallium apicale; L2 field L2; LP lateral pallium; MD dorsal mesopallium; MP medial pallium; MV ventral mesopallium; OB olfactory bulb; Pul pulvinal nucleus; Rt nucleus rotundus; Sc superior colliculus; TeO optic tectum; Tn nucleus taenia; VP ventral pallium. Figure updated from Jarvis et al. [1].

connection through the midbrain or dorsal thalamus. But like collothalamic pathways, its pallial target, basorostralis, is within the nidopallium (Fig. 5a). The connectivity from basorostralis is similar thereafter to the collothalamic auditory and visual pathways. In contrast, in mammals, the trigeminal somatosensory pathway for the face and neck regions is clearly lemnothalamic; its connections in reptiles are unknown.

The lemnothalamic visual pathway projects directly from a thalamic nucleus to the posterior part of the

IHA lamina within the Wulst in birds (Fig. 6a) and to the outer layer of the dorsal cortex as well to an adjacent lateral region called the pallial thickening in turtles. After reaching the dorsal telencephalon, there are significant differences in intra-pallial connectivity between birds and turtles, suggesting that they evolved divergent pallial connectivity for the lemnothalamic visual pathway [5]. A lemnothalamic somatosensory pathway projects from the body receptors to the dorsal column nuclei to the somatosensory thalamus to the anterior IHA within

the Wulst in birds, and to part of the dorsal cortex in turtles and lizards. Very little is known for intra-pallial sensory pathway connectivity in reptiles, and thus further comparisons with birds will have to await further studies. Ulinski [4] proposed, however, that type II ADVRs in reptiles (like in birds) have more discrete sensory projections into the pallium than type I ADVRs, which have more diffuse projections that radiate out from a central recipient zone. Thus, there could be several types of sensory pathway organization in the reptile pallium.

As for the motor pathways of the pallium, very little is known for birds and reptiles. A pyramidal tract-like pathway from the anterior HA has been identified in birds, but it is suggested to possibly be a modulatory feedback projection to somatosensory nuclei of the spinal cord [14]. The best known sauropsid motor pathway is the songbird vocal pathway. This pathway consists of two sub-pathways: (i) a posterior vocal motor pathway that connects a series of nuclei in the ventral mesopallium, nidopallium, and arcopallium, which then projects to the vocal motor neurons of the medulla that control the syrinx; and (ii) an anterior vocal pathway that forms a pallial-basal-ganglia thalamic loop through the anterior nidopallium (and possibly ventral mesopallium) to the anterior striatum to anterior dorsal thalamus and back to the anterior nidopallium (Fig. 6c) [1]. This pathway is used for vocal learning of songs. A similar vocal pathway is found in the forebrain of parrots, and similar connectivity is found adjacent to the vocal nuclei in songbirds [15]. These and many other findings have led to the theory that the vocal learning systems may be motor pathways that evolved out of pre-existing non-vocal motor pathway in birds [12,16] (Feenders et al. unpublished observations). The songbird arcopallium adjacent to the arcopallial vocal nucleus projects to medullary reticular premotor neurons that in other avian orders have been shown to control wing and leg movements [17].

The above findings suggest that birds inherited their existing auditory, visual, and somatosensory pathways from their reptilian ancestor. A similar, but not identical auditory pathway exist in amphibians (Fig. 6b) [9]; a major difference is that the thalamic nuclei project heavily to the striatum, and only weakly to the medial pallium. This medial pallium region is thought to be the homologue of the mammalian hippocampus, but it could also include homologues of sensory areas (►[Evolution of the Auditory System in Anamniotes](#)). This suggests that sauropsids may have inherited a rudimentary form of their forebrain auditory pathway from their common stem amniote ancestor. As for the visual pathways, differences between birds and reptiles in the pallial connectivity of the lemnothalamic visual pathway suggest that they diverged after the split of birds from their common reptilian ancestor. As for the motor pathways, the posterior vocal pathways of

avian vocal learners have been noted to be similar to descending motor pathways of mammals, and the anterior vocal pathway is similar to motor cortico-basal-ganglia-thalamic loops of mammals (Fig. 6d) [12], indicating possible inheritance from the stem amniote ancestor. It has been recently said that reptiles lack such loops (►[Evolution, of the Brain: At the Reptile-Bird Transition](#)), but Ulinski discovered their existence in turtles and lizards [4] before they were popularly studied in mammals. Therefore, if Ulinski is correct, the presence of such forebrain loops in reptiles, birds, and mammals indicate that they may have been inherited from their common stem amniote ancestor.

Harvey Karten noted that the sensory pathways to the pallium in birds share similarities with sensory pathways in mammals, and based upon these findings he and others proposed a hypothesis on the cellular homologies in pallial neuron types of birds with mammals (Fig. 5a) [5,18]. This hypothesis states that the primary thalamic recipient zones in bird pallium is homologous to layer IV neurons of primary auditory, visual, and somatosensory cortices; the second order neurons in the surrounding nidopallium are homologous to layers II and III; the third order neurons of the arcopallium that also send descending projections out of the telencephalon is homologous to layer V. I call this the nuclear-to-layered hypothesis [1], which is described in further detail at the end of this essay.

Molecular Profiles

Not many studies have compared molecular gene expression profiles of adult pallia in their fully differentiated forms between birds and reptiles. We compared the expression of the fork-head transcription factors FoxP1 and FoxP2 in adult birds and crocodiles [11]. FoxP2 is implicated in spoken language function in humans and in vocal learning in birds, and it is highly expressed in the striatum of both birds and mammals. We found similarly enriched FoxP2 expression in the striatum of crocodiles. FoxP1 is also expressed in the striatum in birds and mammals, but is further enriched in the avian mesopallium and mammalian cortical layer VI neurons. In crocodiles, FoxP1 expression shows very similar profiles, including enrichment in a pallial region similar to the avian ventral and dorsal mesopallium, with the ventral part below the lateral ventricle and the dorsal part above it. These findings suggest that mesopallium was inherited in birds from a common reptilian archosaur ancestor with at least crocodiles and that pallial organization of archosaurs may be very similar, although difficult to detect in the crocodile brain with Nissl staining. They also support an idea that the dorsal cortex and the ADVR may be continuous structures 6, where the lateral ventricle is not a functional boundary between brain subdivisions. Further gene expression studies are necessary to test these ideas and to determine the

similarities and differences in the organization of avian, crocodylian, and other reptilian pallia.

Function

The connectivity findings are supported by electrophysiology and lesion studies in birds and reptiles, and activity-dependent gene expression studies in birds. They show that there are auditory processing neurons in the caudal pallium, visual processing neurons in anterior and dorsal pallium regions of the two visual pathways, and somatosensory processing neurons in anterior and dorsal pallium regions of the two somatosensory pathways [4,9,12] (Feenders et al. unpublished observations). It is not yet clear whether these pathways in birds and reptiles process their sensory modality-specific information in the same manner. As for possible motor pathways, stimulation of the arcopallium in birds can induce crouching or running movements [4]. Stimulation of ADVR regions in reptiles leads to modulation of movements. However, lesions of ADVR in reptiles and anterior nidopallium in birds indicate that these regions are not essential for the generation of movement. These types of studies parallel the more detailed findings on the songbird vocal pathway, where lesions of the posterior vocal pathway nuclei show that they are necessary for the production of learned song, whereas the lesions of the anterior vocal pathway nuclei show that they are not necessary for song production but are necessary for song learning and the generation of variability in song production [12]. Further experiments are necessary to define non-vocal motor pathways of the pallium in birds and reptiles.

Evolution Hypotheses on Homologies with Mammals

Based upon comparative neurobiology studies, modern hypotheses on avian (as well as reptilian) brain homologies with mammals fall into two categories that I named nuclear-to-layered and nuclear-to-claustrum/amygdala hypotheses (Fig. 5) [1]. These hypotheses are sometimes presented as final in the literature, but each has its strengths and weaknesses, and thus each needs further testing. Both hypotheses agree on pallial regions that are widely recognized to be homologous among birds, reptiles, mammals and other vertebrates: the hippocampus, olfactory cortex, and olfactory bulb – brain regions covered in other essays (see ► [Evolution, of the Hippocampus](#); ► [Martínez-Marcos and Halpern, Evolution, of Olfactory and Vomeronasal Systems](#)). They disagree, however, on homologies of other pallial regions. To appreciate these disagreements, it is useful to consider general organization principles that appear to be unique to each vertebrate group. The avian hyperpallium possesses a more semi-layered organization not found in reptile dorsal cortex to date and thus might have evolved complexity more recently than the mammalian six-layered cortex, since birds evolved well

after mammals [by ~50–100 million years (Fig. 2)]. The DVR, with its nuclear organization, is found only in birds and reptiles and thus may have evolved after sauropsids split from stem amniotes. The six-layered cortex is a pallial organization found only in mammals (monotremes, marsupials, and placentals), and thus it was presumably inherited from their common therapsid ancestor over 200 million years ago (Fig. 2). As all non-mammalian therapsids are now extinct, it is difficult to trace from stem amniotes to mammals the evolutionary history of mammalian pallial organization – layered, nuclear, or otherwise. Thus, the reptilian nuclear pallial organization cannot be assumed to represent the ancestral condition for mammals, as it is for birds. The evidence suggests that in contrast to conserved striatal and pallidal domains, there are fewer constraints on how the pallium can be organized [1].

Nuclear-to-Layered Hypotheses

First proposed by Karten [18], this hypothesis states that the common ancestor of birds, reptiles, and mammals possessed a nuclear pallium that was transformed into a layered pallium early in the mammalian lineage, maintaining connectivity of the ancestral nuclear network. In this regard, he argued that the avian pallium is divided into three sets of serially connected types of neurons – thalamo-recipient neurons (Field L2, entopallium, and basorostralis), pallio-pallial neurons (other parts of nidopallium) and extra-telencephalic projection neurons (arcopallium), with cell types and interconnectivity similar to those of mammalian cortical layers IV, II-III, and V-VI, respectively. Similar arguments were made by others for the avian hyperpallium divisions (Fig. 6a) [5]. Supporting this hypothesis, gene expression studies on adult brains have shown that avian thalamo-recipient nuclear fields (L2, entopallium, basorostralis, and IHA) and the mammalian thalamo-recipient layer IV of cortex selectively express some of the same genes. Avian extra-telencephalic projection neurons (in the arcopallium, but not in the hyperpallium) and mammalian extra-telencephalic projection neurons (layer V neurons of cortex) both selectively express some of the same genes [1]. Thus, although the avian pallium is not organized cytoarchitectonically into layers, its nuclear subdivisions bear marked similarities in connectivity and some molecular profiles to different layers of the mammalian cortex. A weakness of this hypothesis is that developmental neural fate mapping studies have not revealed that the specific neurons precursors that give rise to the different layers of the mammalian six-layered cortex also give rise to the different pallial subdivisions of the avian telencephalon [6]; such studies have also not been able to falsify the hypothesis. Another weakness is that since the avian hyperpallium organization appears to be different than the turtle, it is possible that the hyperpallium

organization is novel instead of inherited from a common ancestor with mammals. Falsifying the nuclear-to-layered hypothesis may require the use of novel gene manipulation and fate mapping tools to determine if precursor nuclear-specific neurons or genes of sauropsids and layer-specific neurons or genes of mammals will be incorporated into each other's palliums in the expected manner according to the hypothesis.

Nuclear-to-Clastrum/Amygdala Hypotheses

First proposed by Bruce and Neary [19], these hypotheses propose that the DVR represents an elaboration of parts of the mammalian pallial amygdala and claustrum, and that the connectivity that the avian DVR shares with the six-layered cortex evolved independently. This view is based on findings that both the avian DVR and mammalian claustrum-amygdala are nuclear in organization, that both the avian DVR and part of the mammalian pallial amygdala have similar connections, and that both have conserved developmental expression patterns of regulatory genes that play key roles in brain regionalization and morphogenesis. Based on these gene expression patterns, Puelles et al. [6] and Smith-Fernandez et al. [7] proposed that the avian mesopallium and the mammalian dorsal claustrum and basolateral amygdala develop from the lateral pallium and are homologous structures, that the avian nidopallium and the mammalian ventral claustrum and lateral anterior amygdala arose from the ventral pallium and are homologous structures, and that the avian arcopallium and mammalian amygdala consists of pallial and subpallial parts derived from striatal and pallidal cell groups and are homologous to the mammalian amygdala (Fig. 6b). Weaknesses of these hypotheses are that the details vary greatly from author to author, from including only a part of the arcopallium to the entire DVR as the homologue of the mammalian amygdala/claustrum, that there is as yet no clear definition of the amygdala in birds or reptiles, that definitions of the amygdala in mammals varies (e.g. Fig. 6a vs. Fig. 6b.), and that some developmental fate mapping studies have been ambiguous in the context of the new avian brain nomenclature. For example, the expression of *Emx1* gene (*I note here*) is restricted to the newly defined embryonic mesopallium and arcopallium, but not hyperpallium and nidopallium, which would then lead to revisions of the proposed homologies between birds and mammals. Falsifying the nuclear-to-claustrum/amygdala hypothesis may also require the same novel tools and experiments as mentioned above for falsifying the nuclear-to-layered hypothesis.

It is possible that both hypotheses are partially correct. The mammalian amygdala and claustrum share many similarities with the six-layered cortex and as such has been proposed to be extensions of the

six-layered cortex [20]. If true, then the similarities of pallial regions shared with birds and possibly with reptiles would indicate that either the sauropsid pallium has both six-layered and amygdala/claustrum mammalian homologues that are extensions of each other within each brain subdivision or that the sauropsid and mammalian palliums use a pre-existing neural substrate present in their embryonic forms that then diverged into different pallial organizations in their adult forms but maintain basic principles. These hypotheses are testable.

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Evolution of the Pallium in Fishes

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Synonyms

Dorsal telencephalic area; Dorsal telencephalon

Definition

The pallium is the dorsal part of the telencephalic lobes. In the telencephalon of vertebrates two main regions have been distinguished, the olfactory bulbs and the telencephalic lobes. The telencephalic lobes consist of a dorsal region or pallium and a ventral region or subpallium. Cytoarchitecture, histochemistry, hodology (connections) and/or gene expression are currently

used for setting the boundaries with the ventral part of the telencephalic lobe (subpallium) and between the various pallial regions.

The term “fishes” applies to living representatives of jawless vertebrates, the Agnathans (Petromyzontids or lampreys and Myxinooids or hagfish) and to various groups of jawed fishes (Gnathostomata) included in the large radiations of Chondrichthyes (cartilaginous fishes) and of Osteichthyes (bony fishes). Cartilaginous fishes include the ratfish (holocephali), and sharks, skates and rays (elasmobranchs). Bony fishes include the Actinopterygians, or ►ray-finned fishes (Cladistia or bichirs, sturgeons, garfish and a large number of modern species, the teleosts) and the Sarcopterygians, which include the ►lobe-finned fishes (the coelacanth *Latimeria* and the lungfishes), living fossils thought to be closely related to primitive land vertebrates, as well as the land vertebrates, amphibians and amniotes. Fig. 1 depicts a simplified schema of phylogeny of fishes and the morphology of their telencephalic lobes.

Characteristics The Pallium in Fishes

The long evolutionary history of fishes has resulted in the pallium being very heterogeneous in appearance in the different lines (Fig. 1). For most groups, relevant information on its development, neurochemistry and connections is scant and knowledge on evolution of the pallium is quite incomplete. Modern studies of the telencephalon are centered on a few species of fishes, mainly teleosts, cartilaginous fishes, lampreys and lungs. Neurogenetic studies support the distinction between pallium and subpallium in fishes based on a gene expression program similar to the one observed in other vertebrates. Thus, in early embryo stages of species as different as lampreys, dogfish, zebrafish, frog, chick and mouse, the pallium and subpallium express similar transcription factors. The *Emx1/3* genes are expressed in the primordium of the pallium, whereas *Dlx-1/2* genes characterize the primordium of the subpallium [1,2]. Further distinction of pallium regions by genetic markers in developing fishes is lacking. In the Future paragraphs will describe some of the characteristics of the pallium of fishes using the phylogenetic schema presented above.

Agnathans

Hagfish The forebrain of adult hagfish is well-differentiated cytoarchitecturally but lacks a well-developed ventricular system, which obscures the location of the pallial–subpallial boundary. The pallium lies over a massive “central prosencephalic complex,” a structure unique to hagfishes that some authors have interpreted as medial pallium, striatum or even as thalamus. The pallium consists of a superficial “cortical” mantle of gray matter that is subdivided into