

Review

Forebrain evolution in bony fishes

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Abstract

The bony fishes consist of ray-finned fishes and lobe-finned fishes. In ray-finned fishes, the forebrain forms a morphocline from the cladistian bichirs through teleosts regarding the number and increasing complexity of pallial connections. The nuclei of the posterior tubercle parallel this increase in complexity, but the dorsal thalamic nuclei do not. The primary targets of the dorsal thalamic nuclei are the subpallial nuclei, whereas the primary targets of the posterior tubercle are various pallial divisions. Primitively, nucleus medianus is the primary projection nucleus of the posterior tubercle. It is either reduced or lost in teleosts, and its role is taken over by the preglomerular complex, which appears to develop from proliferative zones in both the thalamic alar plate and the posterior tubercle. Although there are numerous hodological data for the pallium in ray-finned fishes, there is no consensus regarding its homologies with other vertebrates. In contrast to ray-finned fishes, very few experimental data exist for lobe-finned fishes. The coelacanth, *Latimeria*, is extremely rare, and lungfishes are the best source for new experimental data. At this point, there are sufficient data to suggest that lungfishes are characterized by a pallium that is divided into four components, separate dorsal and ventral striatopallidal systems, and an amygdala that consists of anterior, central, lateral, and medial nuclei. The data suggest that telencephalic organization in lungfishes is far more similar to that in amphibians than was previously suspected.

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1. Introduction

The bony fishes represent approximately half of all living vertebrates and constitute more than 30,000 living species. These fishes form two great clades: the actinopterygians or ray-finned fishes, which include most bony fishes, and the sarcopterygians or lobe-finned fishes, which are restricted to only seven or eight living species (Fig. 1). Given the large number of species and their long phylogenetic history, it is not surprising that the brains of bony fishes exhibit a remarkable range of variation [57,58,64,106,112]. Much of that variation occurs in the forebrain. In this review, evolutionary trends in forebrain variation will be summarized first for the ray-finned fishes and subsequently for the lobe-finned fishes.

2. Ray-finned fishes

The forebrains of ray-finned fishes form a morphocline of increasing complexity [71,72] from bichirs (cladistians), through sturgeons and paddlefishes (chondrosteans), to the neopterygians, which comprise the gars (ginglymodes), bowfins (halecomorphs), and the teleosts, which represent the largest group of living vertebrates. Due to extensive research in several laboratories, there is considerable experimental data on forebrain organization in one cladistian (*Polypterus*), two chondrosteans (*Acipenser*, *Scaphirhynchus*), and several teleosts (*Carassius*, *Cyprinus*, *Danio*, *Oncorhynchus*, *Oreochromis*, *Sebastiscus*). Unfortunately, almost nothing is known about the histochemistry and connections of the forebrain in gars (ginglymodes) and bowfins (halecomorphs). Forebrain organization in ray-finned fishes will therefore be summarized in three genera (Fig. 2) for which substantial experimental data exist: *Polypterus* (a cladistian), *Acipenser* (a chondrostean), and *Carassius* (a teleost).

2.1. *Polypterus*, a cladistian ray-finned fish

The telencephalon of *Polypterus*, like that of other ray-finned fishes, does not evaginate, but undergoes pallial eversion [63], so that the most morphologically dorsal pallial division comes to lie far laterally (Fig. 2A). The pallium (area dorsalis) is relatively simple; most of its neuronal cell bodies are located in a periventricular layer and send apical dendrites into a more superficial neuropil. The pallium can be divided into dorsolateral and dorsomedial divisions (lateral and medial positions are reversed due to pallial eversion), based on histochemistry [9,82] and connectional data [9,34,75,102]. The dorsolateral pallium is the primary target of the secondary olfactory projections, although the dorsomedial pallium also receives sparse olfactory input [8,34,102]. The main input to the dorsomedial pallium, however, arises from nucleus medianus, a diencephalic nucleus (Fig. 2B).

The diencephalon of *Polypterus*, like that of other vertebrates develops from two segmental neuromeres, the anterior and posterior parencephalic neuromeres [79,108,109]. The anterior parencephalon primarily forms the ventral thalamus, whereas the posterior parencephalon forms the epithalamus (haben-

lar nuclei), the dorsal thalamus, and the posterior tubercle. In *Polypterus*, the retina projects to the rostral dorsal thalamus (anterior thalamic nucleus) and the optic tectum (Fig. 2B) as well as several other diencephalic targets [10,83]. The optic tectum also projects to the dorsal thalamus [75], primarily to the more caudally located posterior dorsal and posterior central thalamic nuclei, and to nucleus medianus within the posterior tubercle, and to a number of other diencephalic and medullar targets. Surprisingly, none of the dorsal thalamic nuclei appear to project to the pallium, as in many vertebrates, but only terminate in the nuclei of area ventralis or the subpallium [33,34]. Thus, nucleus medianus, not the dorsal thalamic nuclei, represents the primary, if not sole, source of ascending sensory information to the pallium.

2.2. *Acipenser*, a chondrostean ray-finned fish

In sturgeons, the pallium or area dorsalis (D) can be divided into at least three, if not four divisions [1,2,3,36,37,71,77]. The pallium of sturgeons is far thicker than that of *Polypterus* and is characterized by large numbers of neurons that have migrated from the ependymal layer (Fig. 2C). Rostrally, the pallium can be divided into lateral (Dl) and medial (Dm) divisions; caudally, Dm is replaced by a posterior (Dp) pallial division which is the primary pallial target of the secondary olfactory projections [37,71]. A fourth pallial division, a central (Dc) division, has been recognized in sturgeons, but further study may indicate that the large neurons that constitute Dc are only the deeper, larger cells of the other three pallial divisions, as appears to be the case in teleosts [7,70].

As in *Polypterus*, the retina in sturgeons projects to the anterior thalamic nucleus and the optic tectum (Fig. 2D) as well as to a number of other diencephalic targets [84]. Again as in *Polypterus*, the optic tectum in sturgeons projects to the more caudal nuclei of the dorsal thalamus and, probably, to two posterior tubercular nuclei as well as additional diencephalic and medullar targets [116]. Rupp and Northcutt [91] recognized an extensive nucleus medianus in *Acipenser*, as well as a more rostrally migrated but poorly defined nucleus within the posterior tubercle which they homologized to the preglomerular complex of teleosts (Fig. 2D). Although Yamamoto et al. [116] did not delineate these nuclei within the posterior tubercle of *Acipenser*, their chartings indicate that these nuclei do receive tectal input.

The primary projection target of the nuclei of the dorsal thalamus appears to be the nuclei of area ventralis (Fig. 2D), with the exception of a sparse projection from the posterior central thalamic nucleus to the pallium [37; unpublished observations]. On the other hand, the cells of nucleus medianus and the preglomerular nucleus in *Acipenser* form a substantial projection to the pallium [37]. In contrast to these results, Albert et al. [5] failed to find projections from these nuclei in *Acipenser* but claimed that cells located just beneath the pial surface of the dorsal thalamus are the only cells that project to the pallium. Given the general pattern of diencephalic pallial projections emerging from a number of laboratories, Albert et al.'s results [5] appear highly suspect.

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