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Sensory Biology of Aquatic Animals

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This volume is dedicated to

Sven Dijkgraaf
Karl von Frisch
C. Judson Herrick
Erich von Holst
George H. Parker
Jacob von Uexkull
J. Z. Young

Each of these investigators delved deeply and broadly into the sensory biology of aquatic animals. Their contributions to the study of sensory systems of aquatic animals have directly and indirectly influenced all of the work reported in this volume.

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Chapter 21

The Visual System in Teleost Fishes: Morphological Patterns and Trends

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Information on the organization of the nervous system in vertebrates has increased tremendously during the past twenty years, primarily spurred by new experimental techniques for tracing pathways (Nauta and Ebbesson 1970; Cowan and Cuenod 1975; Heimer and RoBards 1981). One focus of this experimental flurry has been the visual system of teleost fishes (Table 21.1). However, most of these studies have focused on cypriniform teleosts, specifically the common goldfish, *Carassius auratus,* whose visual system has been adopted as a model in the analysis of general problems of development and plasticity. Alternatively, one or another species has been the focus of an opportunistic analysis, in which some particularly well-developed visual character facilitates recognition of its biological role. Phyletic analyses, representing a third approach, have been infrequent and usually lack rigor. Such analyses should include the following steps: (1) an examination of the characters in a number of taxa; (2) recognition of the patterns of character distribution; (3) determination of the polarity of character transformations (i.e., recognizing homologous characters and determining which are primitive—plesiomorphic—and which are derived—apomorphic); (4) formulation and testing of hypotheses regarding these transformations and their underlying mechanisms. The theory and practice of phylogenetic systematics (Hennig 1966; Eldredge and Cracraft 1980; Wiley 1981; Northcutt 1984a, 1985) appear to provide the most rigorous criteria for such analyses.

A phyletic analysis not only allows one to recognize character patterns and trends, but by posing hypotheses regarding their history, one can frequently reveal structural and functional relationships not otherwise apparent and reveal gaps in our knowledge of the characters being examined, as well as related characters, that alter the course of our research (Northcutt 1986). For these reasons, we attempt to review the extensive literature on the primary visual projections in teleost fishes within the framework of a phyletic analysis and emphasize what additional studies are needed. This review considers aspects of the optic nerve and retinofugal and retinopetal projections of the retina, as well as higher-order visually related centers and pathways, to the extent that such centers and pathways

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Table 21.1. Experimental Retinofugal Studies of Actinopterygian Fishes

Reference	Method[a]	Species Described[b]
Cladistia		
Repérant, Rio, and Amouzou 1979	A	*Polypterus senegalus*
Repérant et al. 1981	A,D	*Polypterus senegalus*
Braford and Northcutt 1983	A	*Polypterus palmas*
Chondrostei		
Repérant et al. 1982	A,D,H	*Acipenser guldenstadti*
Ginglymodi		
Northcutt and Butler 1976	A,D	*Lepisosteus osseus*
Braford and Northcutt 1983	A	*Lepisosteus osseus*
Teleostei		
Osteoglossomorpha		
Lázár, Libouban, and Szabo 1984	A,D,Cl,H	*Gnathonemus petersii*
Elopomorpha		
Ebbesson 1968	D	*Gymnothorax funebris*[*]
Ekström 1982	C	*Anguilla anguilla*
Euteleostei		
Esocae		
Repérant et al. 1976	A	*Esox lucius*[*]
Ostariophysi		
Characiformes		
Voneida and Sligar 1976	A,D	*Astyanax hubbsi* *Astyanax mexicanus*
Ebbesson and Ito 1980	A,D	*Serrasalmus niger*
Cypriniformes		
Roth 1969	D	*Carassius auratus*[*] *Idus melanotus*[*]
Sharma 1972	D	*Carassius auratus*
Repérant and Lemire 1976	A,D,	*Rutilus rutilus* *Cyprinus macrolepidotus*[*] *Cyprinus carpio*[*]
Repérant et al. 1976	A	*Scardinius erythrophthalmus* *Alburnus alburnus*[*] *Cyprinus carpio*[*] *Phoxinus phoxinus*[*] *Rutilus rutilus*[*] *Tinca tinca*[*]
Peyrichoux et al 1977	H	*Scardinius erythrophthalmus* *Alburnus alburnus*[*] *Leuciscus rutilus*[*] *Rutilus rutilus*[*] *Tinca tinca*[*]
Springer and Gaffney 1981	Cl	*Carassius auratus*
Braford and Northcutt 1983	A	*Carassius auratus*
Fraley and Sharma 1984	H	*Carassius auratus*
Siluriformes		
Ebbesson and O'Donnel 1980	D	*Malapterurus electricus*
Meyer and Ebbesson 1981	A,D,H	*Synodontis nigriventris*
Prasada Rao and Sharma 1982	A,H	*Ictalurus punctatus*

Table 21.1. (*Continued*)

Reference	Method[a]	Species Described[b]
Salmonidae		
Pinganaud and Clairambault 1975	D	*Salmo irideus*
Lemire and Repérant 1976	A	*Salmo irideus*
Repérant et al. 1976	A	*Salmo irideus**
Pinganaud and Clairambault 1979	A,D	*Salmo irideus*
Paracanthopterygii		
Ebbesson 1968	D	*Opsanus tau*
Percomorpha		
Gasterosteiformes		
Ekström 1984	H	*Gasterosteus aculeatus*
Scorpaeniformes		
Ito et al. 1984	H	*Sebastiscus marmoratus*
Perciformes		
Roth 1969	D	*Aequadens portalogensis** *Astronotus ocellatus** *Cichlasoma meeki**
Vanegas and Ebbesson 1973	D	*Eugerres plumieri*
Anders and Hibbard 1974	D	*Cichlasoma biocellatum*
Repérant et al. 1976	A	*Perca fluviatilis**
Butler and Northcutt 1981	A	*Lepomis cyanellus**
Fernald 1982	D,H	*Haplochromis burtoni*
Finck 1984	H	*Coris julis*
Presson, Fernald, and Max 1985	Cl,H	*Haplochromis burtoni*
Springer and Mednick 1985d	A,Cl	*Astronotus ocellatus*
Tetraodontiformes		
Ito et al. 1984	H	*Navodon modestus*
Pleuronectiformes		
Gulley, Cochran, and Ebbesson 1975	D	*Achirus lineatus*
Beryciformes		
Campbell and Ebbesson 1969	D	*Holocentrus sp.*

[a] A = autoradiography; D = degeneration; H = horseradish peroxidase; C = cobalt; Cl = cobaltous lysine.

[b] * = described but not illustrated.

resolve discrepancies, but not details of the retina nor the development and plasticity of these visual centers.

While an accepted, uniform nomenclature does not exist for the nervous system in ray-finned fishes, we shall use the nomenclature developed by Northcutt (1983) for the optic tectum; Braford and Northcutt (1983) for the diencephalon; and Northcutt and Davis (1983) (modified from Nieuwenhuys 1963) and Northcutt and Braford (1980) for the telencephalon, with modifications as necessitated by new observations.

A phyletic analysis is strongly affected by the genealogical relationships of the taxa involved and thus frequently entails distinguishing among hypotheses of such relationships. The present analysis assumes that the hypotheses regarding

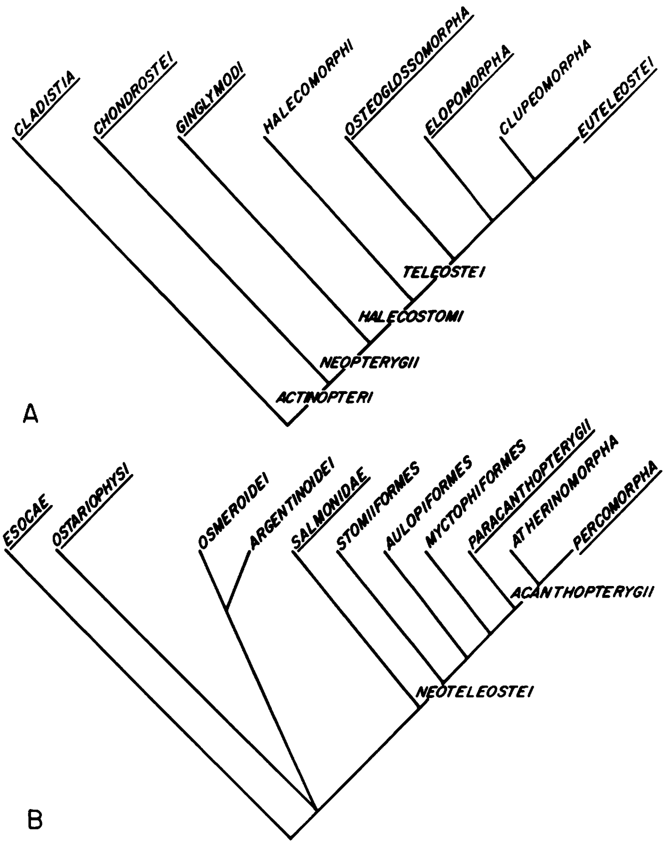


Figure 21.1. The actinopterygian (A) and euteleost (B) fishes. Experimental retinofugal studies exist only for members of underlined taxa.

the genealogy of ray-finned fishes proposed by Lauder and Liem (1983a, 1983b) and illustrated in Figure 21.1 are the most corroborated. Visually related characters that are possible synapomorphies (shared derived characters) that would support or invalidate these hypotheses are noted.

Optic Nerve

The detailed structure of the optic nerve in teleosts has been examined in an ostariophysan, *Carassius* (Rusoff and Easter 1980; Bunt 1982; Easter, Rusoff, and Kish 1981) and the percomorphs *Aequidens*, *Astronotus*, and *Tilapia* (Scholes 1979), *Eugerres* (Tapp 1973, 1974), *Haplochromis* (Presson, Fernald, and Max 1985), *Helostoma*, and *Lepomis* (Rusoff 1984). In *Carassius* and *Eugerres* the optic nerve consists of approximately 200,000 axons, one-fourth of which are unmyelinated. The optic nerve in many teleosts appears to add axons throughout life by the addition of new ganglion cells in the retina, and the unmyelinated fibers appear to be the axons of the youngest retinal ganglion cells. In *Carassius* the youngest optic axons, arising from the periphery of the retina, occupy the center of the head of the optic nerve, whereas the oldest axons occupy the periphery. As the optic nerve is traced centrally, the fibers are rearranged so that the axons of the central and peripheral parts of the optic head form distinct ventral and dorsal groups, respectively, within the optic nerve. As the optic nerve is traced toward the optic chiasm, the compact optic nerve of *Carassius* divides into a series of loosely connected fascicules, forming an indistinct, transversely folded, band, with the younger fibers growing over the surface of the older so that the older fibers are ventromedial within each nerve. In many percomorph teleosts, ganglion cells are added to the peripheral retina, but—unlike in *Carassius*—the younger axons immediately occupy a ventral position in the optic head. Furthermore, the optic nerve in many percomorph teleosts is not subdivided into separate fascicules, as in *Carassius,* but forms a distinctly pleated ribbon beginning immediately beyond the head of the optic nerve.

Examination of the optic nerve in a number of ray-finned fishes (Table 21.2) reveals that both fasciculated and complexly pleated optic nerves occur in all radiations except ginglymodes, halecomorphs, and clupeomorphs, where the optic nerve appears to be always pleated. A cladistic analysis of these characters suggests one of two scenarios: (1) if a fasciculated optic nerve was the plesiomorphic condition for ray-finned fishes, pleated nerves must have arisen at least twice, and reversals must have occurred four times independently; (2) if a pleated optic nerve was the plesiomorphic condition for ray-finned fishes, then a fasciculated nerve must have arisen five times independently. Assuming that gains and losses are equally probable and that the lowest number of character transformations is most parsimonious, a pleated nerve would be assumed to be the plesiomorphic condition for ray-finned fishes. An out-group analysis of other vertebrates, including lampreys and cartilaginous fishes, suggests that a fasciculated nerve is the plesiomorphic condition for all vertebrates and that a pleated optic nerve is a synapomorphy for ray-finned fishes. Given the large number of teleost groups whose optic nerves have not been examined and the presence of a pleated nerve in ginglymodes and halecomorphs, it is probable that a pleated nerve was present in ancestral teleosts and became fasciculated independently in each teleost radiation. It should be possible to determine the polarity of this transformation by a more detailed examination of the distribution of these characters in each teleost radiation and by comparing the development of the optic nerve in several teleost species.

It is claimed that a pleated optic nerve is an adaptation for maintaining constant electrical properties in the nerve in spite of extensive movements of the eye (Fernald 1980). Loose folds in the optic nerve would allow the nerve to lengthen during extensive rotation of the eye, without stretching individual optic axons, thus avoiding transient distortions in the electrical properties of the fibers. Although a pleated optic nerve may be so adapted, other possibilities should be considered. A pleated optic nerve may be exaptive (Gould and Vrba 1982; Northcutt, Chapter 34), and its effect may be due to other historical reasons. For example, fasciculated

Table 21.2. Variation in Visually Related Characters

Species Examined	Fasciculated (f) vs. Pleated (p) Optic Nerve	PSp	PSm	PSi	PSp/p	Nucleus Corticalis	Nucleus Glomerulosus
Cladistia							
Polypterus palmas	p	+	–	–	–	–	–
Erpetoichthys calabaricus	f	+	–	–	–	–	–
Chondrostei							
Polyodon spathula	p	+	–	–	–	–	–
Scaphirhynchus platyrynchus	f	+	–	–	–	–	–
Ginglymodi							
Lepisosteus osseus	p	+	+	–	–	–	–
Halecomorpha							
Amia calva	p	+	+	–	–	–	–
Teleostei							
Osteoglossomorpha							
Osteoglossum bicirrhosum	p	+	+	+?	+	?	–
Pantodon buchholzi	f	+	+	–	–	–	–
Elopomorpha							
Elops saurus	p	+	+	+?	+	–	–
Gymnothorax moringa	p	–	+	–	–	–	–
Anguilla rostrata	f	+	+	?	–	–	–
Clupeomorpha							
Clupea harengus	p	+	+	+	+	–	–
Brevoortia tyrranus	p	+	+	+	–	–	–
Engraulis mordax	p	+	+	+	+	–	–
Chirocentrus dorab	p	+	+	+	+	–	–
Euteleostei							
Esocidae							
Umbra limi	f	+	+	–	+	–	
Esox lucius	f	+	+	–	+	–	–
Ostariophysi							
Cypriniformes							

Carassius auratus	f	+	+	−	−	−	−
Characiformes							
Crenuchus spilurus	p	+	+	+?	+	+?	+?
Serrasalmus nattereri	p	+	+	+?	−	+?	+?
Gymnotoidei							
Eigenmannia virescens	f	−?	+	−	−	−	−
Siluriformes							
Ictalurus melas	f	−	+	−	−	+?	−
Sorubim lima	f	−	+	−	−	−	−
Salmonidae							
Salmo gairdneri	p	+	+	+	+	−	−
Paracanthopterygii							
Opsanus tau	f	+	+	?	−	+	+
Atherinomorpha							
Leuresthes tenuis	p	+	+	+	+	+	+
Strongylura notata	p	+	+	+	+	+	+
Percomorpha							
Lepomis cyanellus	p	+	+	+	+	+	+
Toxotes jaculatrix	p	+	+	+	+	+	+
Trachinotus falcatus	p	+	+	+	+	+	+
Astronotus ocellatus	p	+	+	+	+	+	+
Oreochromis mossambica	?	+	+	+	+	+	+
Hemichromis bimaculatus	p	+	+	+	+	+	+
Cichlasoma erythraeum	?	+	+	+	+	+	+
Coris julis	p	+	+	+	+	+	+
Embiotoca jacksoni	p	+	+	+	+	+	+
Cymatogaster aggregata	p	+	+	+	+	+	+
Astroscopus y-graeceum	f	+	+	+	−	+	+
Sphyraena baraccuda	p	+	+	+	+	+	+
Anabas testudineus	p	+	+	+	+	+	+
Ophicephalus africanus	p	+	+	+	+	+	+
Rhinecanthus aculeatus	p	+	+	+	+	+	+

NOTE: +, character present; −, character absent; ±?, probable condition; ?, condition unknown; PSp, PSm, PSi, pars parvocellularis, pars magnocellularis and pars intermedius, respectively, of the superficial pretectal nucleus; Psp/p, pleated pars parvocellularis.

lated and pleated nerves appear to be correlated, respectively, with punctate and elliptical optic nerve heads (S. S. Easter pers. com.). An elliptical optic head may be an efficient configuration for packing a large number of retinal axons, while minimizing reduction of the visual field. Thus, pleating of the optic nerve may be a mechanical consequence of an elliptical optic head, which, in turn, may be an adaptation to minimize reduction of the visual field in species under strong selection to increase the number of retinal receptors. In this case, a pleated nerve may effect electrical constancy in retinal axons, but could not be said to be adaptive. These hypotheses, as well as others, can be tested by examining the distribution and correlations of the relevant anatomical and functional characters among various fishes (see Northcutt, Chapter 34).

Connections of the Retina

Anatomical (Ito and Murakami 1984; Ito et al. 1984) and physiological (Vanegas, Essayag-Millán, and Laufer 1971; Vanegas, Amat, and Essayag-Millán 1973; Sandemann and Rosenthal 1974; Schmidt 1979; Vanegas 1983) studies indicate that the optic nerve in teleosts comprises both retinofugal and retinopetal fibers. Six classes of different-sized retinal ganglion cells have been identified in the percomorphs *Navodon* and *Sebastiscus,* and the diameter of an optic nerve axon appears to be closely linked to its cell class: type I cells, with small round or oval somata and small dendritic fields in the inner plexiform layer, give off thin axons (mean diameter 0.8 μm), as do type II cells, with small somata and dendrites that arborize in the innermost region of the inner plexiform layer; type III cells, with medium-sized round somata and extensively branching dendrites, give off medium-sized axons (mean diameter 1.3 μm), as do type IV cells, with large somata and dendrites in the innermost part of the inner plexiform layer; type V cells, with large, variously shaped, somata, usually dislocated in the inner plexiform or granular layer, give off thick axons (mean diameter 2.5 μm), as do type VI cells, which have the largest somata, also dislocated.

Anatomical studies of *Navodon* and *Sebastiscus* (Ito et al. 1984) demonstrate that axons of all three size groups include retinofugal fibers that terminate in various diencephalic and mesencephalic visual centers. However, electrophysiological evidence suggests that the largest axons include retinopetal fibers that arise from the optic tectum and, possibly, other neural centers (Vanegas, Amat, and Essayag-Millán 1973; Schmidt 1979).

The occurrence of three classes of retinofugal fibers and at least one class of retinopetal fibers is probably widespread among euteleosts, given the occurrence of these classes in cyprinids and percomorphs. However, it is presently impossible to determine if this is a plesiomorphic or apomorphic condition for teleosts or ray-finned fishes, as other groups have not been examined. Given considerable variation in the retinorecipient laminae of the optic tectum (Northcutt 1983) and pretectum (Braford and Northcutt 1983) in ray-finned fishes, it is particularly important to determine the physiological properties of the different classes of optic nerve fibers and their phylogeny.

Retinofugal Projections

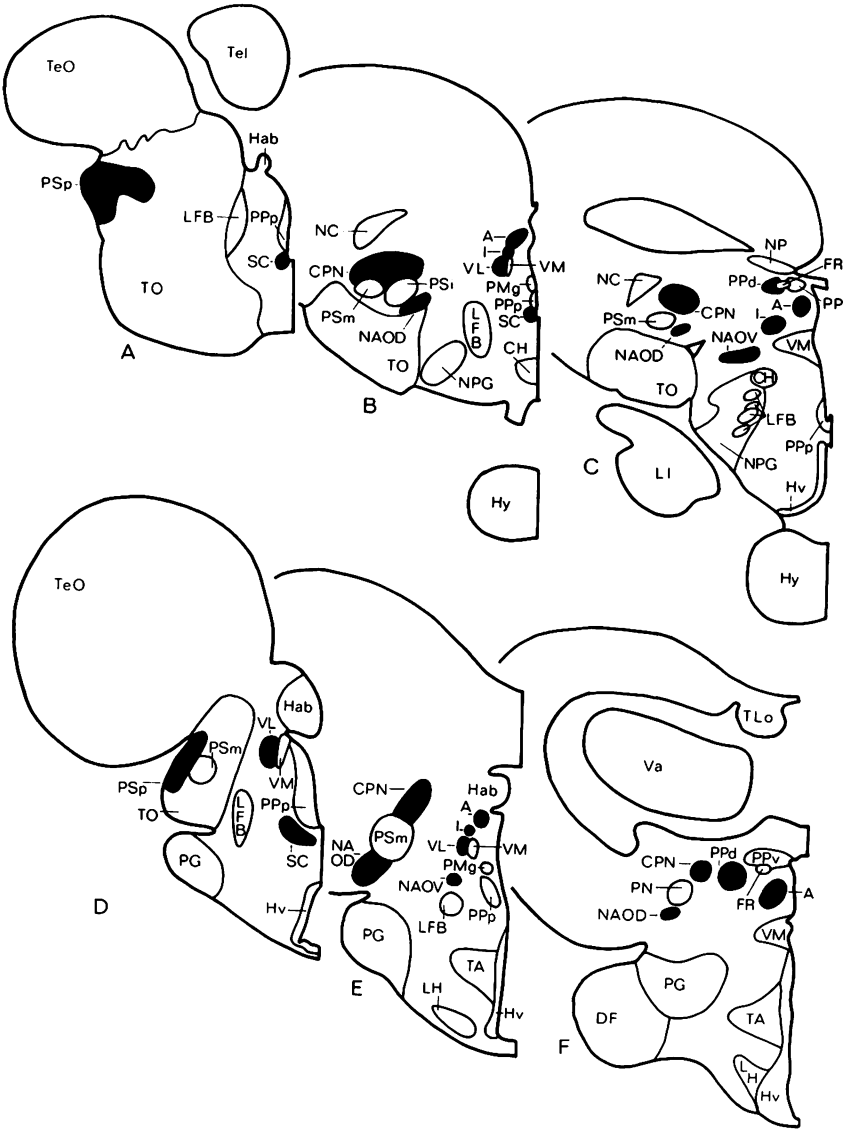
The extensive literature covering experimental studies of retinofugal projections in ray-finned fishes (Table 21.1) and reviews of same (Braford and Northcutt 1983; Northcutt 1983; Vanegas 1983; Vanegas and Ito 1983) report from seven (Vanegas and Ito 1983) to fourteen (Springer and Gaffney 1981) distinct centers, including the optic tectum, that receive contralateral retinofugal projections. Reports vary because of several factors: different experimental methods, different interpretations of the number and boundaries of various cell groups, and differences between species. A consensus does exist, however, regarding retinofugal terminal fields, and most of the differences in interpretation appear to relate to the number of cell groups, particularly in the thalamic and pretectal regions, and their homologues among various species of teleosts. Figure 21.2 summarizes the primary targets of the contralateral retinofugal projections in a cyprinid, *Carassius* (Sharma 1972; Springer and Gaffney 1981; Braford and Northcutt 1983; Fraley and Sharma 1984) and a centrarchid, *Lepomis* (Butler and Northcutt 1981), whose retinofugal projections are comparable to other percomorphs such as *Astronotus* (Springer and Mednick 1985a), *Haplochromis* (Fernald 1982; Presson, Fernald, and Max 1985), *Gasterosteus* (Ekström 1984), *Navodon* (Ito et al. 1984) and *Sebastiscus* (Ito et al. 1984). The nomenclature used is modified from Braford and Northcutt (1983). Differing anatomical names used for several of these retinofugal targets in other studies are noted, and some higher-order visual pathways that bear on these nomenclatural differences and their phylogenetic implications are discussed.

Preoptic Centers

The fibers of the optic nerve in teleosts, as in other anamniotes, form a lateral marginal and a medial axial optic tract caudal to the optic chiasm. As the optic fibers decussate in the chiasm, some of them turn dorsally to terminate in the suprachiasmatic nucleus (Fig. 21.2A, B, and D; *hypothalamic optic nucleus* of Meyer and Ebbesson 1981). Similarly, dorsomedially directed optic fibers also arise from the axial optic tract and innervate the caudal portion of the suprachiasmatic nucleus. Presson, Fernald, and Max (1985) claim that the suprachiasmatic nucleus of *Haplochromis* receives retinal projections only from the axial optic tract, which they believe consists solely of axons of ganglion cells located in the central portion of the retina, dorsal to the optic papilla. Fraley and Sharma (1984) similarly report that the axial optic tract, which they term the *medial fascicle of the optic tract,* innervates the suprachiasmatic nucleus in *Carassius,* but they claim that the axial tract consists of ganglion axons from all retinal quadrants that terminate in the suprachiasmatic nucleus, with the ventral retinal projections, not the central ones, as in *Haplochromis,* being the most extensive. Furthermore, Springer and Gaffney (1981) noted, in the preoptic region in *Carassius,* additional optic fascicles that innervate not only the suprachiasmatic nucleus, but also more dorsally located cellular fields that Braford and Northcutt (1983) termed the *nucleus preopticus parvocellularis posterioris* (Fig. 21.2A, B, D, and E) and a rostral tuberal region (Fig. 21.2E) of the hypothalamus. After contributing fibers to the suprachiasmatic nucleus, the axial optic tract continues dorsally to contribute fibers to the medial optic tract (Fig. 21.3B) and then joins the marginal optic tract.

Thalamic and Periventricular Pretectal Centers

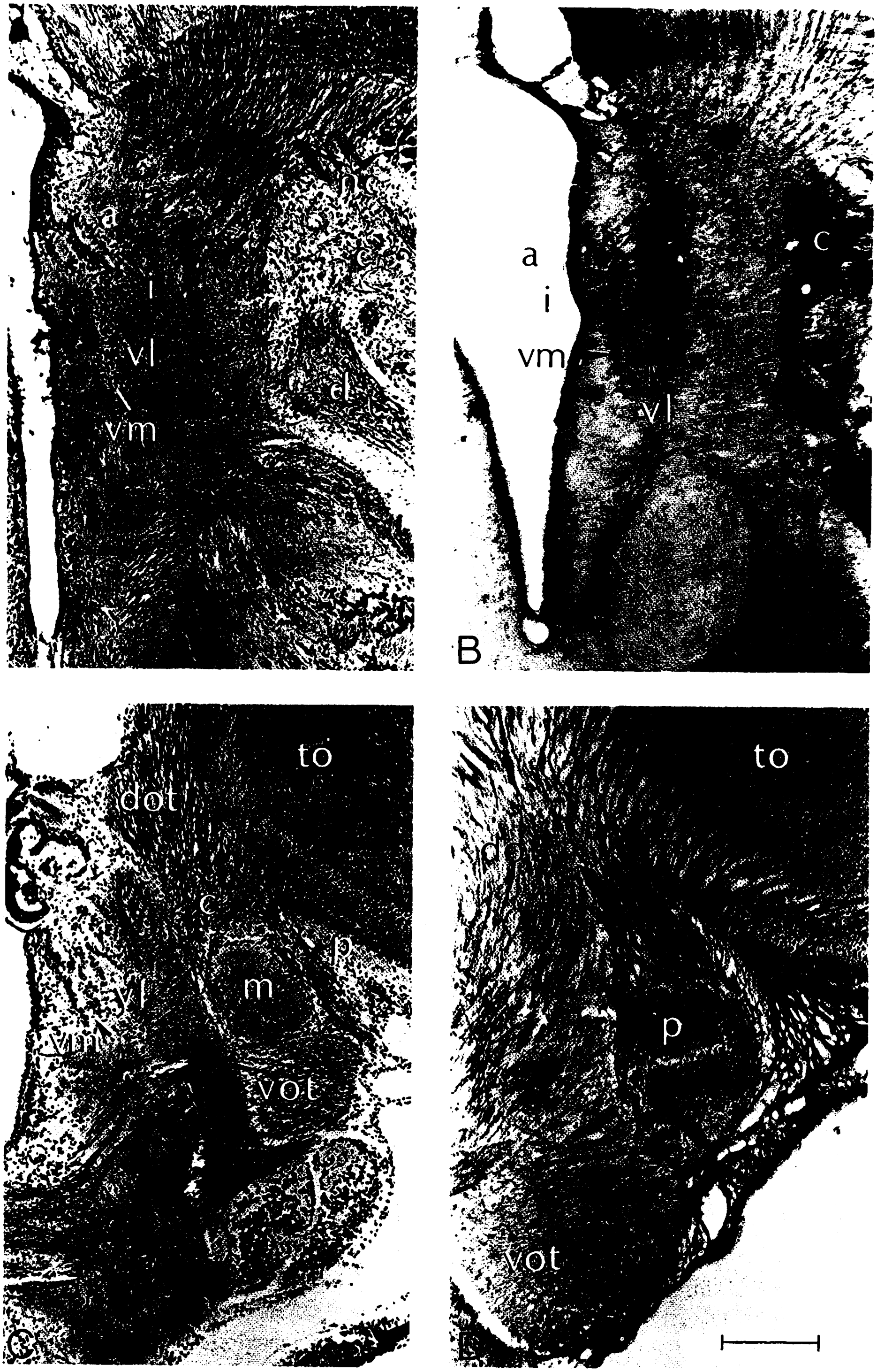
As fibers of the marginal optic tract are traced dorsally at a level comparableto that of Figure 21.2D, fibers turn medially to form a medial optic tract (*fasciculus dorsalis tractus opticus* of Springer and Gaffney 1981), which turns caudallyto



innervate the anterior, intermediate, and ventrolateral thalamic nuclei (Figs. 21.2B–F, 21.3A –C, 21.5, and 21.6; collectively termed the *dorsomedial optic nucleus* by Meyer and Ebbesson 1981, the *dorsolateral and ventrolateral optic nucleus* by Springer and Gaffney 1981, and the *dorsolateral thalamic nucleus* by Ito et al. 1984), the pars dorsalis of the periventricular pretectal nucleus (Fig. 21.2C and F; termed the *caudal part of the dorsomedial optic nucleus* by Meyer and Ebbesson 1981, the *caudal part of area pretectalis* Ekström 1984, and the *nucleus of the posterior commissure* by most other authors) before terminating in the optic tectum. In *Haplochromis* the medial optic tract is composed of axons arising from ganglion cells of all retinal quadrants, but no retinotopic termination is apparent in any of the terminal fields of this tract (Presson, Fernald, and Max 1985). However, Fraley and Sharma (1984) report that retinotopic terminations of axons of the medial optic tract, which they term the *dorsomedial optic tract,* exist in *Carassius.* Rostal (*nucleus opticus dorsolateralis*) and caudal (*nucleus of the posterior commissure*) terminal fields were recognized with axons of the dorsal and ventral retinal quadrants projecting onto the dorsorostral and ventrocaudal portions, respectively, and the axons of the nasal and temporal retinal quadrants projecting onto the dorsocaudal and ventrorostral portions, respectively, of the *dorsolateral optic nucleus.* Retinotopic projections to the *nucleus of the posterior commissure* were not so clear. Axons of the temporal and ventral retinal quadrants appear to innervate the caudal and rostral portions of the nucleus, respectively, but there is no clear topography for the termination of axons of the dorsal and nasal retinal quadrants.

Braford and Northcutt (1983) recognized the periventricular zone adjacent to the posterior commissure as a periventricular pretectal nucleus (*caudal dorsolateral optic nucleus* or *nucleus of the posterior commissure* of most studies) and subdivided this region into a pars dorsalis and a pars ventralis (Fig. 21.2C, and F). The pars dorsalis is the main site of the termination of the caudally coursing

Figure 21.2. Schematic drawings of transverse sections through one-half of the diencephalon and mesencephalon of a percomorph, *Lepomis* (A–C), and a cyprinid, *Carassius* (D–F), illustrating the position and relative development of primary retinofugal terminal fields (nuclei in black); *A*, nucleus anterioris thalami; *CH*, commissura horizontalis; *CPN*, nucleus pretectalis centralis; *DF*, nucleus diffusus lobi inferiores; *FR*, fasciculus retroflexus; *Hab*, habenula; *Hy*, hypophysis; *Hv*, ventral zone of periventricular hypothalamus; *I*, nucleus intermedius thalami; *LFB*, lateral forebrain bundle; *LH*, nucleus lateralis hypothalami; *LI*, lobus inferior; *NAOD*, nucleus accessorius opticus dorsalis; *NAOV*, nucleus accessorius opticus ventralis; *NC*, nucleus corticalis; *NPG*, nucleus preglomerulosus; *PG*, preglomerular nuclear complex; *PMg*, nucleus preopticus magnocellularis pars gigantocellularis; *PN*, nucleus pretectalis posterioris; *PPd*, nucleus pretectalis periventricularis pars dorsalis; *PPp*, nucleus preopticus parvocellularis posterioris; *PPv*, nucleus pretectalis periventricularis pars ventralis; *PSi*, nucleus pretectalis superficialis pars intermedius; *PSm*, nucleus pretectalis superficialis pars magnocellularis; *PSp*, nucleus pretectalis superficialis pars parvocellularis; *SC*, nucleus suprachiasmaticus; *TA*, nucleus tuberis anterior; *Tel*, telencephalon; *TLo*, torus longitudinalis; *TO*, tractus opticus; *TeO*, tectum opticum; *Va*, valvula cerebelli; *VL*, nucleus ventrolateralis thalami; *Vm*, nucleus medialis thalami.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medial optic tract; however, cells of pars ventralis may also receive a retinal input if their dendrites extend laterally. Pars ventralis is a major target of ascending cerebellar efferents in *Carassius* (Braford 1971) and in *Lepisosteus* (Braford and Northcutt 1983), and the cells of the periventricular pretectal nucleus (Fig. 21.7B and 21.8B) appear to project to the optic tectum (Luiten 1981; Northcutt 1982a, 1982b; Fiebig, Ebbesson, and Meyer 1983) and cerebellum (Finger 1978a; Luiten 1981; Northcutt 1982c; Wullimann and Northcutt 1985).

There is substantial evidence that the thalamic region generally identified as the *dorsolateral optic* or *thalamic nucleus* consists of at least four nuclei rostrally (the anterior, intermediate, ventrolateral, and ventromedial thalamic nuclei of Braford and Northcutt 1983). The thalamic wall immediately beneath the rostral habenular nuclei consists of obliquely oriented cellular laminae that Braford and Northcutt (1983) termed the *ventrolateral and ventromedial nuclei of the ventral thalamus* (Fig. 21.3C). The ventrolateral nucleus is distinguished from the ventromedial nucleus by its more loosely organized cellular laminae and by a dense neuropil composed of retinofugal and tectal terminals. The ventromedial thalamic nucleus may also receive retinofugal terminals, as the dendrites of its cells extend laterally into the neuropil of the ventrolateral thalamic nucleus. It is these rostral portions of the ventrolateral and ventromedial thalamic nuclei that many studies describe as the rostral pole of the *dorsolateral thalamic nucleus*. However, the cells of this rostral thalamic region (Fig. 21.6), like the more caudally and ventrally located cells described as the *ventrolateral optic nucleus* by Springer and Gaffney (1981), the *nucleus preopticus* by Luiten (1981), and the *dorsomedial optic nucleus* by Fiebig, Ebbesson, and Meyer (1983), receive a dense cerebellar input throughout their rostrocaudal extent (Braford 1971; Braford and Northcutt 1983), whereas the anterior and intermediate thalamic nuclei do not. Although the ventrolateral and ventromedial thalamic nuclei project to the optic tectum (Grover and Sharma 1981; Luiten 1981; Fiebig, Ebbesson, and Meyer 1983), as does the anterior thalamic nucleus (Figs. 21.5 and 21.6), the last-named also projects to the telencephalon (Echteler and Saidel 1981; Northcutt 1981a). Projections to the telencephalon from a cell group identified as a *ventromedial thalamic nucleus* have been reported in *Sebastiscus* (Murakami, Fukuoka, and Ito 1986), but other studies (Braford and Northcutt 1983; Echteler 1984, 1985) have identified these cells as

Figure 21.3. Photomicrographs of transverse sections through the diencephalon and optic tectum of *Lepomis* (A, B, and D) and *Carassius* (C) illustrating relative development of retinofugal recipient nuclei of the rostral thalamus and pretectum. A, C, and D are Bodian-stained preparations; B illustrates the course and termination of retinofugal fibers labeled with horseradish peroxidase. Dorsal and lateral surfaces in A–D are to the *top* and *right*, respectively. Bar scale equals 200 um; *a*, nucleus anterioris thalami; *ax*, axial optic tract; *c*, nucleus pretectalis centralis; *d;* nucleus accessorius opticus dorsalis; *dot*, dorsal optic tract; *i*, nucleus intermedius thalami; *m*, nucleus pretectalis superficialis pars magnocellularis; *nc*, nucleus corticalis; *p*, nucleus pretectalis superficialis pars parvocellularis; *to*, tectum opticum; *vl*, nucleus ventrolateralis thalami; *vm*, nucleus ventromedialis thalami; *vot*, ventral optic tract.

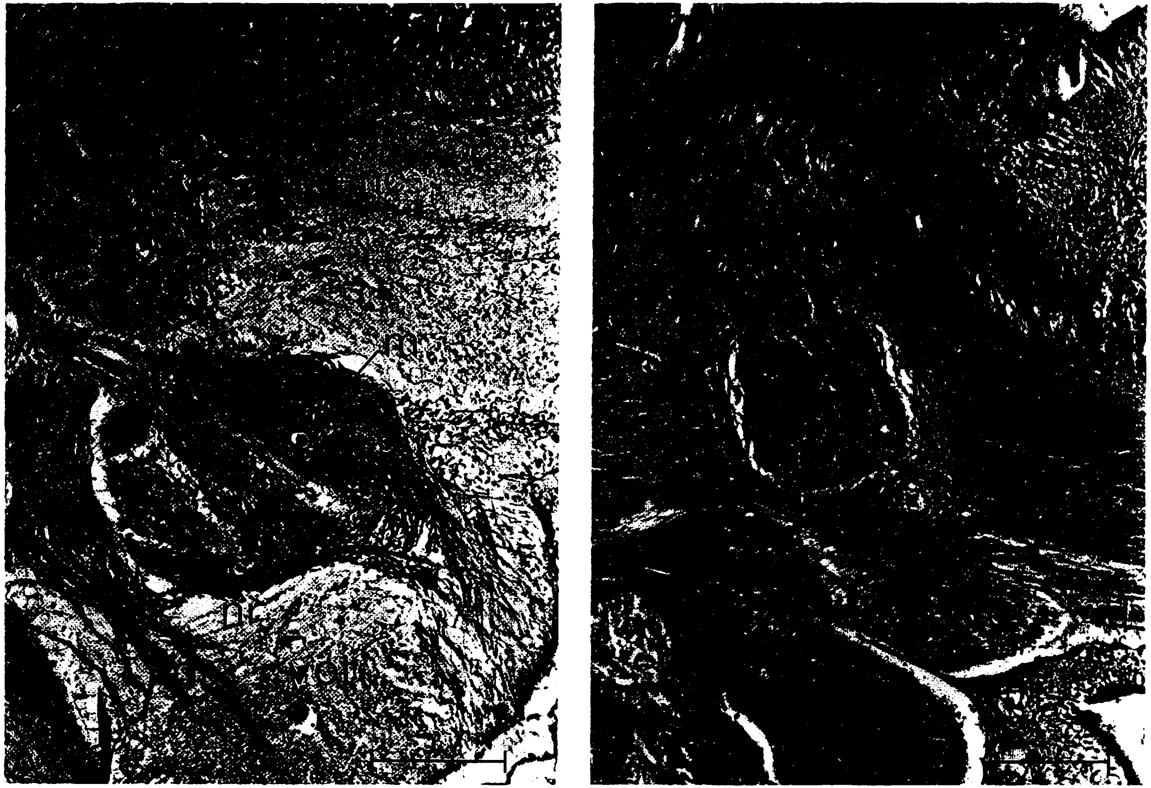

Figure 21.4. Photomicrographs of transverse Bodian-stained section through the pretectum of *Lepomis* (A) and a Nissl-stained section through the pretectum of *Carassius* (B). Dorsal and lateral brain surfaces are to the *top* and *right*, respectively. Bar scales equal 200 um; *c*, nucleus pretectalis centralis; *d*, nucleus accessorius opticus dorsalis; *m*, nucleus pretectalis superficialis pars magnocellularis; *ni*, nucleus pretectalis superficialis pars intermedius; *nc*, nucleus corticalis; *vot*, ventral optic tract.

part of the posterior central nucleus, a more caudal and dorsal division of the dorsal thalamus.

Pretectal Centers

At approximately the same level that the medial optic tract arises from the medial edge of the marginal optic tract, the main portion of the marginal optic tract divides into dorsal and ventral optic tracts (Fig. 21.3C and D) that continue caudally to innervate the rostromedial and caudolateral portions of the optic tectum. Bifurcation of the marginal optic tract is approximately coincident with the rostral border of the pretectum, and a number of pretectal nuclei also receive retinofugal input. The most superficial of these pretectal centers is the pars parvocellularis (*nucleus geniculatus lateralis* of most studies) of the superficial pretectal nucleus, which, in *Carassius* (Figs. 21.2D and 21.3C) and many other cyprinids, consists of a sphere folded dorsoventrally with the lips of the folds directed rostrally. In cichlids and many other teleosts (Table 21.2), the pars parvocellularis (Figs. 21.2A and 21.3D) is located more rostrally in the marginal optic tract and consists of multiple folds similar to a pleated optic nerve. A cladistic analysis of the occurrence and degree of folding of the pars parvocellularis (Table 21.2) suggests that the superficial pretectal nucleus of cladistians and chondrosteans is homologous to the pars parvocellularis of neopterygians, and that an nonfolded or simply folded pars parvocellularis is the plesiomorphic condition in neopterygians. Furthermore, a complexly folded pars parvocellularis appears to be plesiomorphic for teleosts, and the reduction or loss of the nucleus in several groups of teleosts (Table 21.2) is an independently occurring apomorphy.

Retinofugal projections to the pars parvocellularis of the superficial pretectal nucleus are known to be retinotopically organized in *Carassius* (Fraley and Sharma 1984; Springer and Mednick 1985b) and *Haplochromis* (Presson, Fernald, and Max 1985), with the dorsal and ventral retinal quadrants terminating laterally and medially, respectively; the nasal and temporal quadrants, caudally and rostrally, respectively. There is a slight discrepancy in the sites of termination of the projections of the nasal and temporal quadrants in *Carassius* and *Haplochromis*, but these are likely due to differences in the degree of folding of this nucleus in these two genera. The pars parvocellularis also receives input from the optic tectum (Sligar and Voneida 1976; Grover and Sharma 1979a; Northcutt and Butler 1980; Luiten 1981; Striedter and Northcutt 1986) and from the ipsilateral nucleus isthmi (Striedter and Northcutt 1986). Although the pars parvocellularis has frequently been termed the *lateral geniculate nucleus*, it does not project to the telencephalon (Ito and Kishida 1978; Grover and Sharma 1979b; Northcutt and Braford 1984), as would be expected if it were homologous to the lateral geniculate nucleus in amniotes. Instead, pars parvocellularis in *Lepomis* (Fig. 21.7) projects bilaterally to another pretectal center, nucleus intermedius of Brickner (1929), and to the inferior raphe nucleus (Striedter and Northcutt 1986). A projection to the retina has been reported in *Tetraodon* and *Julidochromis* (Ebbesson and Meyer 1981), but has not been observed in other teleosts (Münz and

Claas 1981; Springer and Gaffney 1981; Uchiyama, Sakamoto, and Ito 1981; Ekström 1984; Springer and Mednick 1985a).

In cyprinids, such as *Carassius*, an additional large spherical nucleus, termed *nucleus rotundus* by Schnitzlein (1962), is closely associated with pars parvocellularis and is easily recognized by its extensive central neuropil ringed by medium-sized cells (Figs. 21.2D, and 21.3C). Schnitzlein (1962) assumed that this nucleus occupied a central position within the dorsal thalamus and homologized it to the same-named nucleus in birds and reptiles, in which it receives bilateral input from the optic tectum and projects to a subdivision (dorsal ventricular ridge) of the telencephalic pallium. Although Sharma (1972) reported that this cell group receives primary retinal input in *Carassius*, subsequent studies (Springer and Gaffney 1981; Braford and Northcutt 1983) have failed to confirm this observation. Braford and Northcutt (1983) argued that, although the *nucleus rotundus* of Schnitzlein does receive a bilateral tectal input (Grover and Sharma 1979a; Northcutt and Butler 1980; Luiten 1981), its topographical position is incompatible with that of the nucleus rotundus in amniotes and it should be considered a pretectal nucleus, which they termed *pars magnocellularis* of the superficial pretectal nucleus because of its close association with the smaller-celled pars parvocellularis in ginglymodes and halecomorphs, as well as in cyprinids. Subsequently, the pars magnocellularis in cyprinids has been demonstrated (Northcutt and Braford 1984) to project ipsilaterally to a caudal hypothalamic nucleus (the so-called mammillary body) and to the nucleus lateralis valvulae (Fig. 21.8B). Thus both its topography and its efferent projections are incompatible with its' being the homologue of nucleus rotundus in amniotes.

Although a *nucleus rotundus*, or pars magnocellularis, has been recognized in percomorphs (Fernald 1982; Springer and Mednick 1985a), the comparable pretectal region of these fishes is more complex (Fig. 21.4A). In many percomorphs, such as *Lepomis*, there are two distinct neuropils, one of which contains medium-sized cells and the other large cells, rather than a single neuropil ringed by cells, as in *Carassius*. The dorsolateral neuropil contains cells as large as those of nucleus corticalis (Fig. 21.4A) and is easily distinguished from those of the finer-fibered ventromedial neuropil, which contains smaller neurons. We term these two neuronal populations the pars magnocellularis and pars intermedius, respectively, of the superficial pretectal nucleus (Fig. 21.7). The pars magnocellularis (*nucleus geniculatus posterior pars ventralis* of Ebbesson and Vanegas 1976 and *nucleus pretectalis* of Ito et al. 1981; Ito, Sakamoto, and Takatsuji 1982) receives ipsilateral input from the optic tectum (Ebbesson and Vanegas 1976) and projects bilaterally to nucleus isthmi (Ito et al. 1981; Ito, Sakamoto, and Takatsuji 1982; Striedter and Northcutt 1986), whereas pars intermedius (*nucleus intermedius* of Brickner 1929 and Sakamoto and Ito 1982) receives a bilateral input from pars parvocellularis (Striedter and Northcutt 1986) and projects ipsilaterally to nucleus glomerulosus (Sakamoto and Ito 1982). We believe that the pars magnocellularis is homologous in cyprinids and percomorphs, because in each case the nucleus occupies a comparable topographical position, consists of similar neurons, and receives tectal input (Figs. 21.7 and 21.8). However, there is no evidence that the pars magnocellularis of cyprinids projects to nucleus isthmi (Northcutt and Braford 1984) nor that the pars magnocellularis of percomorphs projects to the mammillary body and nucleus lateralis valvulae (Ito, Sakamoto, and Takatsuji 1982; Sakamoto and Ito 1982). The known efferents of the pars magnocellularis in the percomorph *Navodon* were determined by injecting horseradish peroxidase (HRP) into nucleus isthmi and not into pars magnocellularis. It is thus possible that there are other efferents from pars magnocellularis in percomorphs and that projections exist to the mammillary body and nucleus lateralis valvulae. Nucleus intermedius may not exist in cyprinids because these teleosts do not possess a nucleus glomerulosus (Sakamoto and Ito 1982; Braford and Northcutt 1983) and yet they may still exhibit a pars parvocellularis owing to its projections to conserved targets. Similarly, a projection to nucleus isthmi from pars magnocellularis may not exist in *Carassius,* as nucleus isthmi in that genus is poorly differentiated relative to that in most percomorphs. Because of these differences in efferent projections of the proposed homologues, pars magnocellularis in cyprinids and in percomorphs, it is necessary to consider several alternative hypotheses: (1) pars magnocellularis in cyprinids is a field homologue of pars intermedius and pars magnocellularis of percomorphs; (2) pars intermedius or pars magnocellularis in percomorphs is a de novo nucleus; and (3) both nuclei in percomorphs possess separate homologues, not yet identified, in cyprinids. Although additional experimental studies are needed to evaluate these hypotheses, a cladistic analysis of the distribution of a recognizable pars intermedius and pars magnocellularis among ray-finned fishes (Table 21.2) suggests that a pars magnocellularis arose with the origin of neopterygians and that a pars intermedius is a plesiomorphic character of teleosts or possibly only of clupeomorphs and euteleosts. If this hypothesis is correct, the absence of a pars intermedius in cypriniform, gymnotoid, and siluriform teleosts is an apomorphic condition rather than a plesiomorphic one.

At least three additional nuclei (the central pretectal nucleus and dorsal and ventral accessory optic nuclei) occur within the pretectal region in teleosts (Fig. 21.2) but have been differently named in various studies. A distinct population of medium-sized neurons occurs within the marginal optic tract or begins caudally in the dorsal optic tract immediately after bifurcation of the marginal optic tract; this cell population has been termed the central pretectal nucleus (Northcutt and Butler 1976; Braford and Northcutt 1983; Presson, Fernald, and Max 1985). The central pretectal nucleus (Figs. 21.3C, 21.4, 21.7B, and 21.8B) receives bilateral tectal input (Ebbesson and Vanegas 1976; Grover and Sharma 1979a; Northcutt and Butler 1980) and projects to the optic tectum (Luiten 1981; Northcutt 1982b; Fiebig, Ebbesson, and Meyer 1983) and the corpus of the cerebellum (Finger 1978a; Finger and Karten 1978; Luiten 1981; Northcutt 1982c; Wullimann and Northcutt 1985). This nucleus has been identified as a pretectal (P1) nucleus in *Carassius* and *Ictalurus* (Finger and Karten 1978), as the *pretectal nucleus* in *Serrasalmus* (Fiebig, Ebbesson, and Meyer 1983), as the *pars dorsalis of nucleus* and *area opticus pretectalis dorsalis* in *Carassius* (Springer and Gaffney 1981), as the *dorsal pretectal area and nucleus* in *Carassius* (Fraley and Sharma 1984), as *nucleus pretectalis medialis* in *Astronotus* (Springer and Mednick 1985a), and as *pars dorsalis of area pretectalis* in various teleosts (Vanegas and Ito

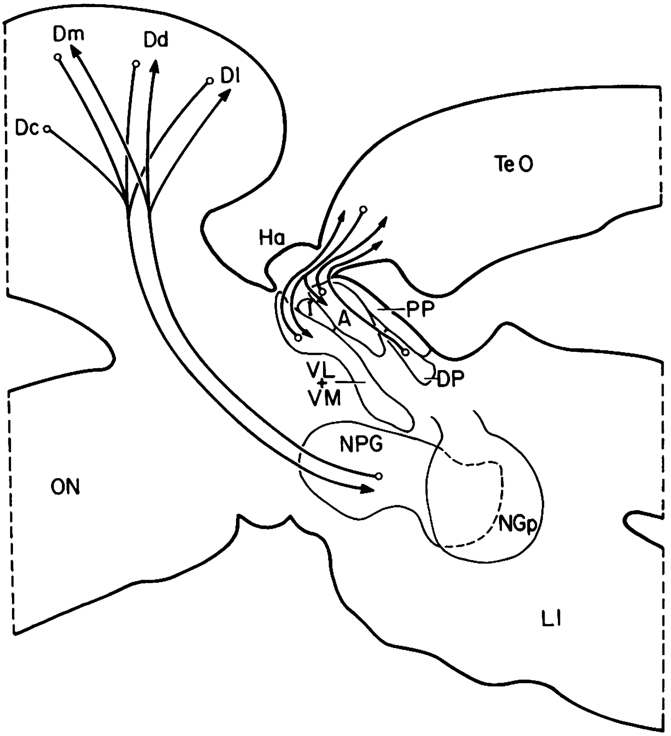

Figure 21.5. Diagram of some of the afferent and efferent projections of thalamic and preglomerular nuclei of *Lepomis* viewed in sagittal plane; *A*, nucleus anterioris thalami; *Dc*, central zone of area dorsalis telencephali; *Dd*, dorsal zone of area dorsalis telencephali; *Dl*, lateral zone of area dorsalis telencephali; *Dm*, medial zone of area dorsalis telencephali; *DP*, nucleus dorsalis posterioris thalami; *Ha*, habenula; *I*, nucleus intermedius thalami; *LI*, lobus inferior; *NGp*, nucleus glomerulosus pars posterior; *NPG*, nucleus preglomerulosus; *ON*, optic nerve; *PP*, nucleus pretectalis periventricularis; *Te O*, tectum opticum; *VL*, nucleus ventrolateralis thalami; *VM*, nucleus ventromedialis thalami.

1983). Presson, Fernald, and Max (1985) report that the central pretectal nucleus in *Haplochromis* receives retinofugal projections solely from the ventral hemiretina; while Fraley and Sharma (1984) report that the comparable retinofugal terminal field in *Carassius* is richly innervated by the ventral hemiretina, they also claim that this area receives projections from the dorsal hemiretina. A central pretectal nucleus apparently occurs in all radiations of ray-finned fishes, and no striking apomorphy has been noted among the species examined (Table 21.2).

A dorsal accessory optic nucleus occurs in *Carassius* (Figs. 21.2E and F and 21.4B) and *Lepomis* (Figs. 21.2B and C and 21.3A), adjacent to the dorsomedial border of the ventral optic tract, and a ventral accessory optic nucleus (Fig. 21.2C, E) occurs in both genera slightly more caudally and receives retinofugal fibers that diverge medially from the ventral optic tract as a distinct bundle termed the *accessory optic tract* by Springer and Gaffney (1981). The dorsal accessory

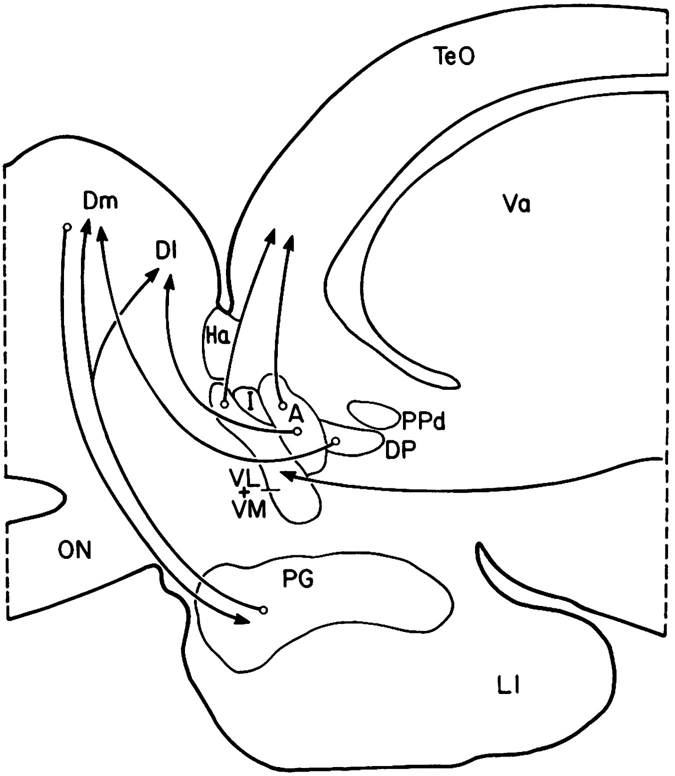

Figure 21.6. Diagram of some of the afferent and efferent connections of the thalamus and preglomerular complex of *Carassius* viewed in sagittal plane. Ascending brain stem tract to *VL* + *VM* is the so-called mesencephalocerebellar tract, which carries efferents to the thalamus; *A*, nucleus anterioris thalami; *Dl*, lateral zone of area dorsalis telencephali; *Dm*, medial zone of area dorsalis telencephali; *DP*, nucleus dorsalis posterioris thalami; *Ha*, habenula; *I*, nucleus intermedius thalami; *LI*, lobus inferior; *ON*, optic nerve; *PG*, preglomerular nuclear complex; *PPd*, nucleus pretectalis periventricularis pars dorsalis; *Te O*, tectum opticum; *Va*, valvula cerebelli; *VL*, nucleus ventrolateralis thalami; *VM*, nucleus ventromedialis thalami.

optic nucleus has been identified as the *nucleus of the ventral optic tract* in *Lepisosteus* (Northcutt and Butler 1976), the *area opticus pretectalis pars ventralis* and *nucleus corticalis* (Springer and Gaffney 1981), the *basal optic nucleus* (Braford and Northcutt 1983), a pretectal (P2) nucleus in *Carassius* (Finger and Karten 1978), the *anterior glomerular nucleus* in *Ictalurus* (Finger 1978a), the medial *ventral pretectal nuclei* in *Astronotus* (Springer and Mednick 1985a), and the *area pretectalis pars ventralis* in various other teleosts (Vanegas and Ito 1983). The ventral accessory optic nucleus has been identified as the *accessory optic nucleus* in *Acipenser* (Repérant et al. 1982), *Polypterus* (Repérant et al. 1981; Braford and Northcutt 1983), *Lepisosteus* (Northcutt and Butler 1976), and *Carassius* (Springer and Gaffney 1981; Braford and Northcutt 1983), and as the *area*

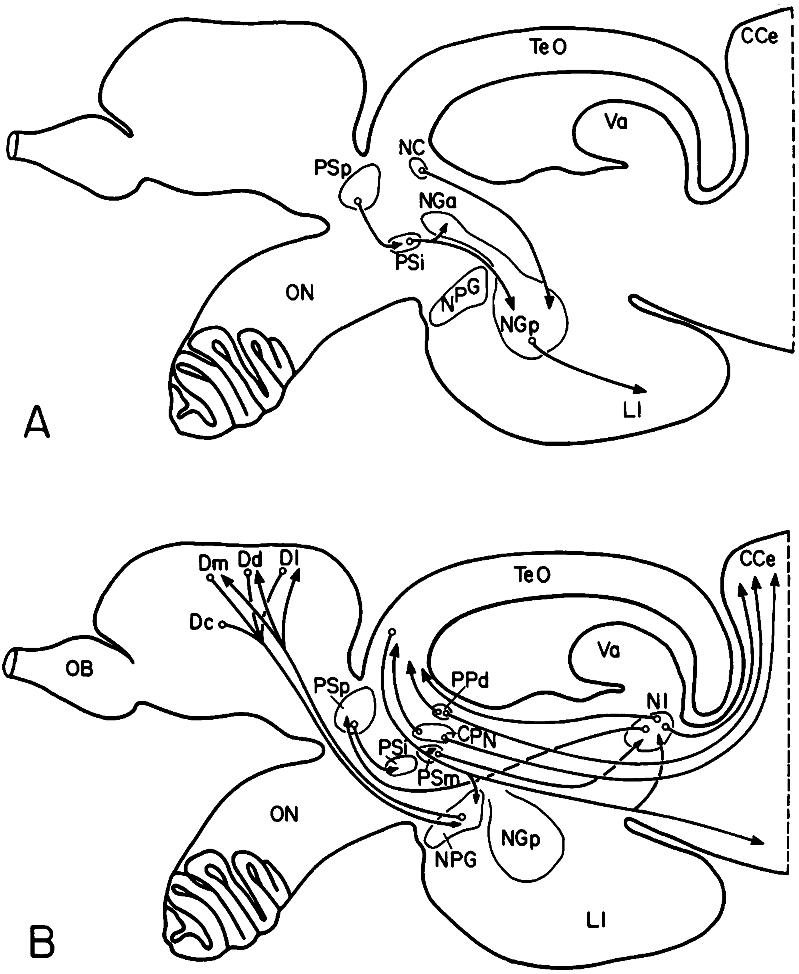

Figure 21.7. Diagram of some of the afferent and the efferent connections of nucleus glomerulosus (A) and pretectum (B) of *Lepomis* viewed in sagittal plane; *CCe*, corpus cerebelli; *CPN*, nucleus pretectalis centralis; *Dc*, central zone of area dorsalis telencephali; *Dd*, dorsal zone of area dorsalis telencephali; *Dl*, lateral zone of area dorsalis telencephali; *Dm*, medial zone of area dorsalis telencephali; *LI*, lobus inferior; *NC*, nucleus corticalis; *NGa*, nucleus glomerulosus pars anterior; *NGp*, nucleus glomerulosus pars posterior; *NI*, nucleus isthmi; *NPG*, nucleus preglomerulosus; *OB*, olfactory bulb; *ON*, optic nerve; *PPd*, nucleus pretectalis periventricularis pars dorsalis; *PSi*, nucleus pretectalis superficialis pars intermedius; *PSm*, nucleus pretectalis superficialis pars magnocellularis; *PSp*, nucleus pretectalis superficialis pars parvocellularis; *Te O*, tectum opticum; *Va*, valvula cerebelli.

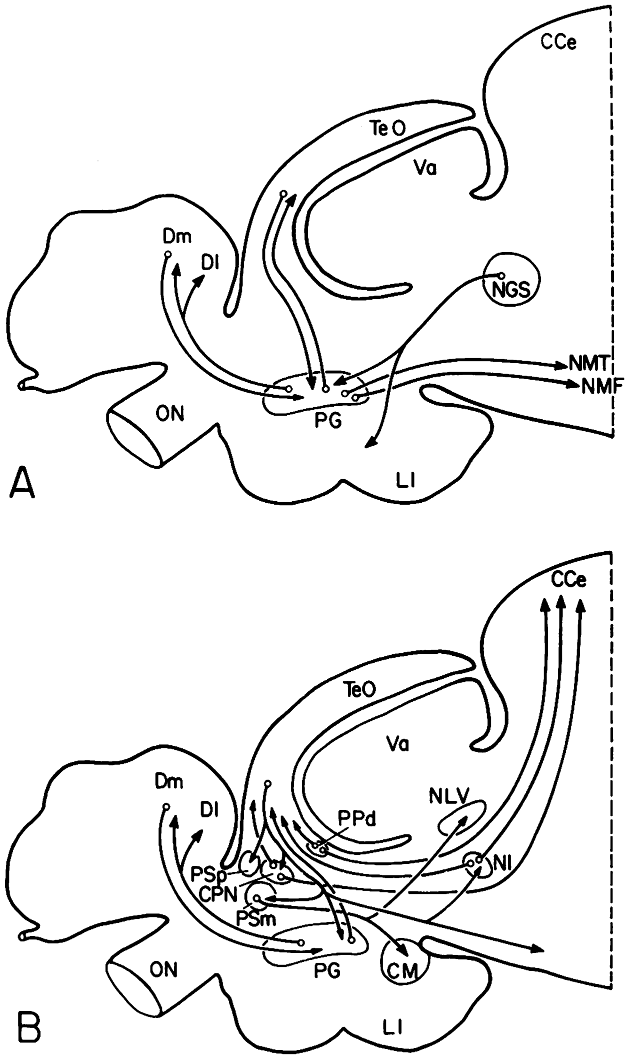

Figure 21.8. Diagram of some of the afferent and efferent connections of preglomerular complex (A) and pretectum (B) of *Carassius* viewed in sagittal plane; *CCe*, corpus cerebelli; *CM*, corpus mammillare; *CPN*, nucleus pretectalis centralis; *Dl*, lateral zone of area dorsalis telencephali; *Dm*, medial zone of area dorsalis telencephali; *LI*, lobus inferior; *NGS*, nucleus gustatorius secundarius; *NI*, nucleus isthmi; *NLV*, nucleus lateralis valvulae; *NMF*, nucleus motorious nervi facialis; *NMT*, nucleus motorius nervi trigemini; *ON*, optic nerve; *PG*, preglomerular nuclear complex; *PPd*, nucleus pretectalis periventricularis pars dorsalis; *PSm*, nucleus pretectalis superficialis pars magnocellularis; *PSp*, nucleus pretectalis superficialis pars parvocellularis; *Te O*, tectum opticum; *Va*, valvula cerebelli.

ventrolateralis in various other teleost species (Vanegas and Ito 1983). Only the dorsal accessory optic nucleus of *Ictalurus* has been shown to project to the corpus of the cerebellum and to the oculomotor nucleus (Finger and Karten 1978), but both dorsal and ventral accessory optic nuclei project to the cerebellar corpus in *Lepisosteus* (Northcutt 1982c) and *Lepomis* (Wullimann and Northcutt 1985), but apparently not in *Carassius* (Finger and Karten 1978; Grover and Sharma 1981) or *Cyprinus* (Luiten 1981).

Dorsal and ventral accessory optic nuclei appear to occur in all radiations of ray-finned fishes except, perhaps, for a dorsal accessory optic nucleus in cladistians. The ventral accessory optic nucleus is well developed in highly visual percomorphs, such as *Astronotus* (Springer and Mednick 1985a) and *Navodon* (Ito et al. 1984), but too few species have been examined to determine whether a well-developed ventral accessory optic nucleus is a percomorph or euteleost apomorphy. However, other highly visual teleosts (elopomorphs and clupeomorphs) do not exhibit a well-developed ventral accessory optic nucleus (Ekström 1982; Wullimann and Northcutt unpubl. obs.).

Acanthopterygian teleosts exhibit a distinct large-celled pretectal nucleus termed nucleus corticalis (Figs. 21.2B and C, 21.4A, and 21.7A) that probably receives retinal projections. The somata of nucleus corticalis are among the largest in the pretectum and can easily be confused with the somata of the mesencephalic trigeminal nucleus, particularly in osteoglossomorphs and elopomorphs. The cell bodies of nucleus corticalis form a mediolaterally elongated plate adjacent to the dorsolateral border of the central pretectal nucleus and pars magnocellularis of the superficial pretectal nucleus (Figs. 21.2C and 21.4A), and the dendrites of the corticalis cells extend into the superficial and central gray zone of the optic tectum, where they may form synapses with the entering retinotectal fibers (Sakamoto and Ito 1982). Retinofugal projections are claimed to terminate on the cell bodies of nucleus corticalis in *Carassius* (Sharma 1972; Springer and Gaffney 1981) and other cyprinids (Repérant and Lemire 1976; Repérant et al. 1976); but Springer and Mednick (1985a) and Presson, Fernald, and Max (1985) reported that retinofugal fibers pass through nucleus corticalis without forming synapses in *Astronotus* and *Haplochromis*, respectively. These results are rather surprising, as there is no question in the literature that percomorphs exhibit a distinct nucleus corticalis, whereas Sharma (1972) identified nucleus corticalis in *Carassius* as an indistinct population dorsal to the central pretectal nucleus, and Springer and Gaffney (1981) and, more recently, Fraley and Sharma (1984) identified the nucleus as caudal and ventral to pars magnocellularis of the superficial pretectal nucleus. Braford and Northcutt (1983) failed to identify a nucleus corticalis in *Carassius*, and the present survey (Table 21.2) suggests that a nucleus comparable to the nucleus corticalis of acanthopterygian teleosts does not exist in cypriniform and gymnotoid teleosts. Horseradish peroxidase injections into the optic tectum of the percomorphs *Navodon* (Sakamoto and Ito 1982) and *Lepomis* (Northcutt 1982b) label dendrites of nucleus corticalis, whose axons project ipsilaterally, in association with fibers of the horizontal commissure, before terminating in nucleus glomerulosus (Fig. 21.7A). Tectal injections in ostariophysans (Sligar and Voneida 1976; Grover and Sharma 1981; Luiten 1981), including

Carassius, fail to demonstrate a projection to the "glomerular nucleus," but tectal efferents do project via another tract (transverse commissure) to the preglomerular complex, as in many other species (Ebbesson and Vanegas 1976; Northcutt and Butler 1980; Luiten 1981). In fact, a distinct nucleus glomerulosus has not been identified in cyprinids (Braford and Northcutt 1983; Vanegas and Ito 1983). These observations and a cladistic analysis of the distribution of a recognizable nucleus corticalis and nucleus glomerulosus (Table 21.2) suggest that both nuclei are clearly synapomorphic for paracanthopterygians, atherinomorphs, and percomorphs. This conclusion is consistent with Mazzi's observation (1953) that other neoteleosts, in addition to those listed in Table 21.2, exhibit a well-developed nucleus glomerulosus. The possibility that these nuclei may also occur in characiforms suggests that two additional hypotheses must be considered: (1) nucleus corticalis and nucleus glomerulosus may have arisen with euteleosts and may subsequently have been lost in some ostariophysans; or (2) similar nuclei have evolved independently in some ostariophysans and neoteleosts. These hypotheses can be evaluated only after extensive descriptive and experimental examination of the various euteleost clades.

Nucleus glomerulosus (*nucleus rotundus* of Ito and Kishida 1975, 1977) of many percomorph teleosts, such as *Lepomis* and *Navodon,* is one of the most distinct diencephalic nuclei and can be recognized as a bilobed neural aggregate oriented obliquely in the caudal plane (Fig. 21.7). This nucleus exhibits rostral and caudal subdivisions (Brickner 1929; Sakamoto and Ito 1982; Wullimann 1985), which we term pars anterior and pars posterior. The phyletic distribution of a bilobed nucleus glomerulosus is unclear. It may characterize only acanthopterygians, or it may be a neoteleostean apomorphy. In *Navodon* the nucleus glomerulosus consists of four laminae arranged concentrically around a central core of fibers in the following centripetal order: peripheral capsule of fibers and large neurons, small-celled layer, fibrous layer, and glomerular layer (Sakamoto and Ito 1982). Nucleus glomerulosus receives a bilateral input from nucleus corticalis and an ipsilateral input from pars intermedius of the superfical pretectal nucleus; the axons of corticalis neurons terminate exclusively in glomeruli, whereas the axons of intermedius neurons terminate in the small-celled layer of pars anterior or the fibrous layer of pars posterior (Sakamoto and Ito 1982). Both the large and small cells of nucleus glomerulosus are efferent neurons and project to the ipsilateral nucleus diffusus of the inferior lobe (Fig. 21.7A) of the hypothalamus (Sakamoto and Ito 1982). Given these connections of nucleus glomerulosus, it is very likely that it is an important link in visually related circuits from the pretectum and optic tectum to the hypothalamus (Wullimann in press).

Optic Tectum, Preglomerular Complex, and Nucleus Isthmi

The course of entering retinotectal fibers and their termination in the various tectal laminae have been reviewed in detail for teleosts (Meek 1983; Vanegas 1983; Vanegas and Ito 1983), as well as nonteleost ray-finned fishes (Northcutt 1983). The plesiomorphic pattern of lamination of retinotectal fibers in ray-finned fishes appears to consist of a dorsal lamina located deep in the marginal zone, a central lamina spanning the superficial white and gray zone and extending down into the central zone, and a deep lamina at or immediately below the dorsal border of the deep white zone (Northcutt 1983). Both cyprinids (Repérant and Lemire 1976; Schmidt 1979; Springer and Gaffney 1981) and percomorph teleosts (Vanegas and Ebbesson 1973; Anders and Hibbard 1974; Landreth et al. 1975; Fernald 1982; Springer and Mednick 1985a) exhibit an additional retinotectal terminal lamina located immediately above the periventricular gray zone. It is presently uncertain whether the deep terminal lamina of nonteleost ray-finned fishes is the homologue of the same-named lamina in teleosts or the deeper periventricular lamina or is a field homologue of both. Clearly, teleosts exhibit an apomorphic pattern of retinotectal termination in comparison to other ray-finned fishes, but additional studies are needed to explain its functional significance.

Efferent projections of the optic tectum in ray-finned fishes are known for *Lepisosteus* (Northcutt and Butler 1980), three genera of ostariophysan teleosts (*Astyanax,* Sligar and Voneida 1976; *Carassius,* Grover and Sharma 1979a; *Cyprinus,* Luiten 1981), and two genera of percomorph teleosts (*Eugerres* and *Holocentrus,* Ebbesson and Vanegas 1976). All these studies report ascending projections to the pretectum and diencephalon, projections from one tectal lobe to the other (intertectal), and descending projections to the brain stem. The details of these studies have been reviewed elsewhere (Vanegas and Ito 1983; Northcutt 1983) and will not be repeated here. Instead, we shall focus on the details of two visually related circuits that involve the optic tectum and which may be apomorphic for ray-finned fishes.

In some percomorph teleosts the optic tectum projects ipsilaterally to a large kidney-shaped nucleus located in the rostral diencephalon, sandwiched between the marginal optic tract and the lateral forebrain bundle (Ebbesson and Vanegas 1976; Ito and Vanegas 1983). This nucleus, identified as *nucleus prethalamicus* (Meader 1934), does not receive retinofugal projections in *Holocentrus* (Campbell and Ebbesson 1969) and has been shown to project ipsilaterally to the telencephalon in *Adioryx* (Ito and Vanegas 1984), *Holocentrus* (Ebbesson 1980a; Ito et al. 1980), and *Myripristis* (Ito et al. 1980) and specifically to the lateral zone of area dorsalis telencephali in *Holocentrus* (Ito and Vanegas 1983) and *Sebastiscus* (Murakami, Morita, and Ito 1983). All these studies have noted the similarity in the afferent and efferent connections of *nucleus prethalamicus* of percomorphs and nucleus rotundus of amniotes. *Nucleus prethalamicus,* like nucleus rotundus, does not receive retinofugal projections, but does receive tectal input and projects to the telencephalon. Basing their conclusion on these similarities in connections, but failing to note or comment on the differences in topographical position of *nucleus prethalamicus* and nucleus rotundus (nucleus rotundus is located in the dorsal thalamus of birds and reptiles, whereas *nucleus prethalamicus* is located in the preoptic area of the hypothalamus of percomorphs) Ebbesson (1980a), Ito et al. (1980), and Ito and Vanegas (1983) proposed that *nucleus prethalamicus* of percomorphs is homologous to nucleus rotundus of amniotes. Interpreting the homology of *nucleus prethalamicus,* however, appears to be a small part of a larger problem. The diencephalon of most neopterygians is characterized by a series of nuclei termed the *preglomerular complex* (Braford and Northcutt 1983) that extends through most of the length of the basal diencephalon (Fig. 21.7 and 21.8). Various subdivisions of the preglomerular complex receive higher-order gustatory (Finger 1978b; Morita, Ito, and Masai 1980), lateral line (Finger 1980; Echteler 1984; Murakami, Fukuoka, and Ito 1986), and tectal (Ebbesson and Vanegas 1976; Northcutt and Butler 1980) inputs (Figs. 21.7B and 21.8) and project to the telencephalon (Ito and Kishida 1978; Finger 1980; Echteler and Saidel 1981) and optic tectum (Luiten 1981). Given the close association of *nucleus prethalamicus* to the preglomerular nuclei and the histological properties of *nucleus prethalamicus* (Ito and Vanegas 1983), it may be an apomorphic character of the preglomerular complex of beryciform and scorpaeniform percomorphs. Clearly, additional species among these percomorph categories should be examined for the distribution of a distinct *nucleus prethalamicus,* as well as possible transitional stages.

There are obviously two schools of thought concerning *nucleus prethalamicus* and the preglomerular complex. Members of one school (Ebbesson 1980a; Murakami, Morita, and Ito 1983; Vanegas and Ito 1983) interpret these nuclei as dorsal thalamic, primarily or solely on the basis of connections, and they have not addressed a topography that is peculiar to dorsal thalamic nuclei nor how the dorsal thalamus can be recognized when other diencephalic nuclei receive ascending sensory inputs and project to the telencephalon (Riley and Moore 1981; Ricardo 1981; Köhler, Haglund, and Swanson 1984; Shammah-Lagnado, Negrao, and Ricardo 1985). For example, the zona incerta in mammals, a subthalamic nucleus, receives tectal input (Shammah-Lagnado, Negrao, and Ricardo 1985) and projects to the globus pallidus (Ricardo 1981). The argument would be equally reasonable, based solely on connections, that *nucleus prethalamicus* of teleosts or nucleus rotundus of birds is homologous to the zona incerta of mammals. Proponents of the second school (Northcutt 1981b; Echteler and Saidel 1981; Braford and Northcutt 1983) interpret the nuclei of the preglomerular complex as possible derivatives of the posterior tuberculum, a more ventrally located major division of the diencephalon, which also receives ascending sensory inputs and projects to the telencephalon in other vertebrates. This interpretation is based on (1) the topographical position of the preglomerular complex; (2) the occurrence of other nuclei in the topographical position usually interpreted to be dorsal thalamus in other vertebrates (Braford and Northcutt 1983); (3) the projection of these more dorsally located nuclei, like dorsal thalamic nuclei in other vertebrates, to the telencephalon (Echteler and Saidel 1981; Northcutt 1981a; Murakami, Fukuoka and Ito, 1986); and (4) revealed by examination of cladistians, chondrosteans, and neopterygians, a morphocline from an unmigrated periventricular posterior tuberculum to a posterior tuberculum with complexly migrated nuclei (Braford and Northcutt 1983). The differing views of these two schools can be tested by further hodological and immunohistochemical studies of the nuclei identified as anterior, posterior dorsal, and posterior central thalamic by Braford and Northcutt (1983), as well as hodological experiments on the nucleus of the torus lateralis of cladistians and chondrosteans. The nucleus of the torus lateralis may be a field homologue of both the preglomerular complex and torus lateralis of neopterygians, as cladistians and chondrosteans do not exhibit any migrated nuclei in the rostral basal diencephalon. If experiments on the connections of the nucleus of the torus lateralis do not reveal similarities to those of the preglomerular complex of neopterygians, the simplest interpretation is that the preglomerular complex of neopterygians is an autapomorphy.

There may be similar problems concerning nucleus isthmi, a visually related nucleus of the caudal tegmentum in many teleosts. Nucleus isthmi is a spherical structure consisting of an outer shell of medium-sized neurons surrounding an inner noncellular neuropil (Sakamoto, Ito, and Ueda 1981). In the cyprinids *Carassius* and *Cyprinus*, nucleus isthmi (Fig. 21.8B) receives input from the ipsilateral optic tectum (Grover and Sharma 1979a; Luiten 1981) and projects back onto the same tectal lobe (Grover and Sharma 1981; Luiten 1981), as well as ipsilaterally to the corpus of the cerebellum (Luiten 1981). Identical reciprocal connections between the optic tectum and nucleus isthmi (Fig. 21.7B) have been reported in the percomorph *Navodon* (Sakamoto, Ito and Ueda 1981), and an additional input from pars magnocellularis of the superficial pretectal nucleus is reported in *Navodon* and in another percomorph, *Lepomis* (Striedter and Northcutt 1986), but does not appear to exist in *Carassius* (Northcutt and Braford 1984). Efferents to the ipsilateral corpus of the cerebellum also exist in *Lepomis* (Wullimann and Northcutt 1985). Nucleus isthmi, at least in percomorphs, receives a direct tectal input and an indirect input via pars magnocellularis and projects to the cerebellum, as back onto the optic tectum. At present it is impossible to determine whether the indirect pathway in percomorphs is plesiomorphic or apomorphic.

A similarly named tegmental nucleus occurs in tetrapods, with reciprocal connections to the optic tectum, but additional pretectal or cerebellar connections have not been reported (Gruberg and Udin 1978; Northcutt 1984b). Nucleus isthmi does not appear to exist in cartilaginous fishes (Smeets, Nieuwenhuys, and Roberts 1983), and a distinct nucleus isthmi has not been described in cladistians (Nieuwenhuys 1983; Nieuwenhuys and Oey 1983); chondrosteans have not been examined. It is thus possible that nucleus isthmi arose with the origin of bony fishes and that the same-named nuclei in teleosts and tetrapods are homologous; it is also possible that these nuclei are homoplasous and have evolved independently in actinopterygians and sarcopterygians.

Retinopetal Projections

Although numerous studies document retinopetal projecting nuclei in various piscine radiations, no clear picture of the plesiomorphic pattern of retinopetal cell groups or their phylogeny has emerged. In *Lampetra* bilateral retinopetal projections with a heavier contralateral component arise from the *medial M5 cell group of Schober*, and a more laterally located *mesencephalic reticular cell group* also projects to the contralateral retina (Vesselkin et al. 1980, 1984). Similar bilateral retinopetal projections are reported from medial and lateral tegmental cell groups termed the *pars superficialis* and *profunda*, respectively, of the isthmo-optic nucleus of the cladistian *Polypterus* (Meyer et al. 1983). Although an isthmo-optic nucleus has not been described in teleosts, it is possible that a retinopetally projecting tegmental nucleus is the plesiomorphic condition for anamniotes; but the phyletic distribution of this nucleus is unknown, as cartilaginous, chondrostean, ginglymodian, and halecomorph fishes have not been examined.

Retinopetal projections have been described for a number of teleosts (Ebbesson and Meyer 1981; Münz and Claas 1981; Münz, Stumpf, and Jennes 1981; Münz et al. 1982; Meyer and Ebbesson 1981; Meyer, Fiebig, and Ebbesson 1981; Uchiyama, Sakamoto, and Ito 1981; Gerwerzhagen et al. 1982; Stell et al. 1982, 1984; Crapon de Caprona and Fritzsch 1983; Demski and Northcutt 1983; Springer 1983; Finck 1984; Ekström 1984; Ito et al. 1984; Uchiyama and Ito 1984; Springer and Mednick 1985a), but the reported projections include a highly variable number of nuclei, ranging from cells in the olfactory bulb to cells in the optic tectum, and no obvious phyletic pattern has been discerned.

In cyprinids and silurids, fibers of the nervus terminalis whose cell bodies are located ventral to or among the axons of the olfactory nerve course through the ventral wall of the forebrain to enter the optic nerve and terminate within the retina (Bass 1981; Demski and Northcutt 1983; Springer 1983). In *Carassius* many of the ganglion cells and retinopetal fibers of the nervus terminalis are luteinizing hormone–releasing hormone (LHRH)–immunoreactive. Similar LHRH-positive cells, termed the *nucleus olfactoretinalis* (Münz, Stumpf, and Jennes 1981; Münz et al. 1982), occur in the olfactory bulb and area ventralis of the telencephalon of many poecilid, centrarchid, and cichlid species, and many of these cells possess axons that terminate in the retina (Ebbesson and Meyer 1981; Ekström 1984; Ito et al. 1984; Springer and Mednick 1985a). The neurons of the ganglion of the nervus terminalis are believed to arise ontogenetically from the olfactory placode (Locy 1899, 1903) and to migrate centrally along the course of the axons of the olfactory nerve. It is thus possible that the cells of *nucleus olfactoretinalis* and nervus terminalis are homologous and have been identified as different populations because of differences in the degree of their central migration.

Retinopetally projecting neurons have also been identified at the level of the optic chiasm as *nucleus intrachiasmaticus* in *Pantodon* (Gerwerzhagen et al. 1982) and the *preoptic retinopetal nucleus* in *Navodon* (Uchiyama, Sakamoto, and Ito 1981; Ito et al. 1984; Uchiyama and Ito 1984), as well as in thalamic and pretectal nuclei (Ebbesson and Meyer 1981; Meyer and Ebbesson 1981; Meyer, Fiebig, and Ebbesson 1981; Ekström 1984; Ito et al. 1984; Springer and Mednick 1985a) and in the optic tectum (Schmidt 1979; Ebbesson and Meyer 1981; Meyer and Ebbesson 1981; Meyer, Fiebig, and Ebbesson 1981). All retinopetal projections in teleosts reportedly terminate in the contralateral retina, and—as in nonteleost fishes—ipsilateral terminations have been reported also in *Astronotus* (Springer and Mednick 1985a) and in *Navodon* and *Sebastiscus* (Ito et al. 1984).

Most of the retinopetally projecting neurons of the thalamus and pretectum are located adjacent to various divisions of the optic tract and have been identified as components of an assortment of nuclei (Ebbesson and Meyer 1981; Meyer and Ebbesson 1981; Ekström 1984) or as a single *nucleus thalamoretinalis* (Springer and Mednick 1985a). Furthermore, there is considerable controversy regarding the sites of some retinopetally projecting neurons in the diencephalon and tectum, as most studies have utilized the retrograde transport of horseradish peroxidase (HRP) to visualize these neurons, and interpretations may be confounded by gliosis following optic nerve transection or transynaptic transport of HRP. The latter is particularly likely when lysolecithin, dimethyl sulfoxide, or both are used to facilitate the uptake of HRP (Ebbesson and Meyer 1981; Meyer and Ebbesson 1981). However, the existence of retinopetally projecting neurons located in the ganglion of nervus terminalis in *Astronotus* and *Carassius* and *nucleus thalamoretinalis* in *Astronotus* has been corroborated by use of the cobaltous lysine technique.

Although the data on the location of retinopetally projecting neurons are scanty, the broad phylogenetic distribution of a nervus terminalis (Demski and Northcutt 1983; Bullock and Northcutt 1984) allows us to pose several hypotheses regarding the phylogeny of these projections: (1) the plesiomorphic pattern for jawed fishes comprised only a retinopetally projecting nervus terminalis; (2) the plesiomorphic pattern comprised a retinopetally projecting nervus terminalis and a more caudally situated isthmo-optic nucleus, as in lampreys and *Polypterus;* or (3) the plesiomorphic pattern comprised a retinopetally projecting nervus terminalis, one or more diencephalic and pretectal nuclei, such as the so-called thalamoretinal nucleus, and an isthmo-optic nucleus. The first hypothesis assumes that the nervus terminalis projects to the retina in members of other gnathostome radiations, as it does in teleosts, that the retinopetally projecting cells of the diencephalon and pretectum are migrated ganglion cells of the nervus terminalis, and that an isthmo-optic nucleus is not homologous in lampreys, cladistians, and tetrapods. The second hypothesis depends on the same assumptions regarding the nervus terminalis and thalamoretinal nucleus and further assumes that an isthmo-optic nucleus is widespread phyletically and homologous. The third hypothesis again assumes that the nervus terminalis projects to the retina in many gnathostome radiations, but also assumes that the thalamoretinal and isthmo-optic nuclei are distinct and homologous phyletic characters across many gnathostome radiations. These hypotheses can be tested only when additional data exist on the embryology and immunohistochemistry of the nervus terminalis and thalamoretinal nucleus, as well as additional experimental studies of retinopetal projections in more phyletically diverse gnathostome species.

In this context, it is surprising that Ebbesson and collaborators cite the distribution of retinopetal projections as evidence supporting the phyletic hypothesis of parcellation (Ebbesson 1980b). Ebbesson and Meyer (1981) suggest that the presence of multiple retinopetal centers in teleosts is a plesiomorphic pattern for vertebrates and that reduction or loss characterizes the so-called advanced vertebrates. However, Meyer et al. (1983) note the occurrence of a single retinopetal center in the cladistian *Polypterus,* as in lampreys (Vesselkin et al. 1980). Unless Ebbesson and collaborators wish to argue that both lampreys and *Polypterus* exhibit degenerate retinopetal projections, they would logically conclude that a single isthmal retinopetal center is plesiomorphic for gnathostomes and that teleosts exhibit an "advanced" condition owing to parcellation. Even this conclusion requires the assumption that all retinopetal projections are homologous among different gnathostome radiations, an assumption clearly not substantiated at present. This example, however, demonstrates the futility of attempts to discern evolutionary processes when the homology and polarity of characters are unknown and when taxa, rather than characters, are assumed to be plesiomorphic or apomorphic.

Conclusions

Although a considerable number of neurobiologists have focused on the visual system of ray-finned fishes during the past twenty years, it is clear that most of our attention has been directed towards a very few species. Most frequently, cyprinids or cichlids have been examined, and their visual circuitry has been used as a general model for the analysis of axon guidance and other developmental problems, or details of their visual pathways and centers have been compared to those for members of other vertebrate radiations to support contentions regarding the origin and subsequent evolution of these neural characters, without regard for evolutionary diversity and its basis within radiations. These trends are clearly reflected by the paucity of data on numerous groups of ray-finned fishes. There are no descriptive or experimental studies for one of the teleost clades (clupeomorphs) and only one and two experimental studies, respectively, of species in two of the other three clades (osteoglossomorphs and elopomorphs). In each case the species chosen exhibits large numbers of apomorphic characters, which increase the probability that many of the visual characters are also apomorphic. In the case of euteleosts, the largest single clade, less than half of the sister groups have been examined (Fig. 21.1B), and it is difficult or impossible to evaluate the polarity of the visual characters reported in the other euteleost groups.

The literature on visual centers and pathways would support the contention that there are two basic patterns of visual organization among teleosts: a percomorph pattern (Fig. 21.2A–C) and a cyprinid pattern (Fig. 21.2D–F). The percomorph pattern can be characterized by a complexly pleated optic nerve and pars parvocellularis of the superficial pretectal nucleus, an extensive and highly differentiated pars intermedius and magnocellularis of the superfical pretectal nucleus, a distinct nucleus corticalis and bilobed nucleus glomerulosus, and a highly differentiated ventral accessory optic nucleus and nucleus isthmi. In contrast, the cyprinid pattern can be characterized by a simple fasciculated optic nerve and an nonfolded or simply folded pars parvocellularis of the superficial pretectal nucleus, a small or nonexistent pars intermedius of the superficial pretectal nucleus, a small or absent nucleus corticalis and nucleus glomerulosus, and a poorly developed ventral accessory optic nucleus and nucleus isthmi. Given the usual propensity for believing that simple characters are plesiomorphic, one might conclude that the cyprinid pattern is plesiomorphic and the percomorph pattern apomorphic. In fact, neither pattern is plesiomorphic, and a cladistic analysis indicates that both patterns exhibit a mixture of plesiomorphic and apomorphic characters.

As noted earlier, a complexly pleated optic nerve and folded pars parvocellularis of the superficial pretectal nucleus are most parsimoniously interpreted as plesiomorphic characters for actinopterygians and teleosts, respectively, and a fasciculated optic nerve and nonfolded or simply folded pars parvocellularis would then be considered apomorphic characters for cypriniforms, if not ostariophysans. A conclusion regarding ostariophysans is presently impossible, as the visual characters of anotophysans, the sister group of all ostariophysans examined, have not been described. Similarly, the presence of a distinct pars intermedius of the superficial pretectal nucleus is most parsimoniously interpreted as a plesiomorphic character for clupeomorphs and euteleosts, if not teleosts, and its reduction or loss is apomorphic for cyprinids.

The absence or presence of only an indistinct nucleus corticalis and nucleus glomerulosus cannot be evaluated because of the difficulty of recognizing such poorly differentiated nuclei without experimental evidence. In this case, a phyletic analysis reveals gaps in our knowledge and the necessity for new studies of a number of neglected groups of ostariophysans, as well as other teleosts.

The presence of a small ventral accessory optic nucleus in cyprinids is most parsimoniously interpreted as the retention of an actinopterygian plesiomorphic character, whereas the presence of a small, poorly differentiated nucleus isthmi in cyprinids is most parsimoniously interpreted as an apomorphic character, and a well-developed nucleus isthmi appears to be a plesiomorphic character of teleosts. However, there is insufficient evidence to decide whether a nucleus isthmi occurs in other ray-finned fishes; thus it is presently impossible to determine whether the nucleus isthmi of teleosts is homologous to the same-named nucleus in tetrapods. Consideration of many of the apomorphic visual characters of the cyprinid pattern (fasciculated optic nerve, simply folded pars parvocellularis, indistinct or absent pars intermedius, and a poorly developed nucleus isthmi) suggests that cyprinids arose from a more visual ancestor. It is of interest whether reduction in vision occurred with the origin of ostariophysans, the origin of otophysans (was reduction in vision correlated with increase in acoustical abilities?) or with the origin of cypriniforms. Many gymnotoids and siluroids are characterized by relatively small eyes, although some siluroids possess relatively large eyes, so that reduction in vision may characterize the origin of otophysans or may have occurred a number of times independently. Thus the ostariophysan fishes may be an appropriate group in which to examine the effects of reduction and the constraints on redevelopment of this particular sensory system.

Although the present cladistic analysis is hampered by the lack of information on visual characters in a large number of groups of teleosts, it is clear that more than two patterns of visual organization occur (Table 21.2). A complexly folded pars parvocellularis of the superficial pretectal nucleus is not always correlated with a pleated optic nerve. The optic nerves of *Esox* (Schilling and Northcutt 1986) and *Umbra* are fasciculated, but each possesses a complexly folded pars parvocellularis. Conversely, the optic nerves of *Amia, Brevoortia,* and *Gymnothorax* are pleated but each possesses an nonfolded or simply folded pars parvocellularis. In percomorph teleosts, both nucleus intermedius and nucleus corticalis project to a large, well-differentiated nucleus glomerulosus (Fig. 21.7A); on the other hand, clupeomorph teleosts appear to possess a well-developed nucleus intermedius, but a nucleus corticalis and nucleus glomerulosus cannot be recognized (Table 21.2). The efferents of nucleus intermedius presently known are based on HRP injections into nucleus glomerulosus (Sakamoto and Ito 1982). Thus a phyletic analysis would suggest that nucleus intermedius may possess additional efferents that are presently unknown, but it is also possible that we have misidentified this superficial pretectal nucleus in clupeomorphs. Similarly, *Ictalurus* may possess a nucleus corticalis (Table 21.2) but there is no recognizable nucleus intermedius or nucleus glomerulosus. Again, it is possible that nucleus corticalis has additional efferents in many teleosts, that efferents have evolved *de novo* in *Ictalurus*, or that we have misidentified the nucleus. Another notable exception to the suspected distribution of nucleus corticalis occurs in *Osteoglossum*. This genus exhibits a strikingly extensive population of large neurons in the pretectum in a position comparable to that of nucleus corticalis. If this population does represent nucleus corticalis, it would clearly alter our understanding of the origin and evolution of nucleus corticalis. However, it is also possible that this population in *Osteoglossum* is an expanded mesencephalic trigeminal nucleus associated with the spectacular feeding behavior of these animals. It is equally interesting that our survey reveals large ''pretectal'' nuclei of uncertain identity in *Osteoglossum*, clupeomorphs, esocids, and salmonids. In each case, a well-differentiated nucleus occurs in a position comparable to a pars intermedius, a pars magnocellularis, or an anterolateral portion of the preglomerular complex. In each case, the histology of the mysterious nucleus is sufficiently different from that of the structures described in most euteleosts that it cannot be identified with any certainty. In fact, the histology varies sufficiently among the above taxa to make it unlikely that these nuclei are homologous. We therefore suspect that additional nuclei, of which we are unaware, may exist in this region or that other pretectal nuclei that do not receive retinofugal fibers in percomorphs, such as the posterior pretectal nucleus (Fig. 21.2F), may be more extensive in other teleost groups. In each of the above cases, the accuracy of our interpretations regarding connections and of our speculations regarding homology is really secondary to the realization that phyletic analysis reveals correlations among neural characters, as well as new characters not previously recognized. Regardless of the final details regarding these nuclei and their distribution, it is clear that the pretectum in ray-finned fishes results from, and likely continues to reflect, a series of unique natural experiments in the processing of visual information.

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