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**Cover illustration.** Photomicrographs of transverse sections through comparable midtectal levels in cases following injection of the contralateral ventral (A) and dorsal (B) hemiretinas with tritiated proline. Saidel and Butler (p. 162).

## Comparative Cytoarchitectonic Analysis of Some Visual Pretectal Nuclei in Teleosts

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**Abstract.** The posterior prepectal nucleus, which in *Osteoglossum* receives second order visual input and projects to the inferior lobe of the hypothalamus, was identified and characterized in species from all major groups of non-neoteleost teleosts. The hypothesis that the posterior prepectal nucleus in these species is homologous to both the pars intermedius of the superficial prepectal nucleus and nucleus glomerulosus in acanthopterygians is supported by multiple similarities in relative position and cytoarchitecture. Nucleus corticalis, which receives retinal input and projects to the posterior prepectal nucleus (or to nucleus glomerulosus), was identified in species belonging to three of the four major teleost radiations. Both the posterior prepectal nucleus and nucleus corticalis are plesiomorphic for teleosts. The presence of glomeruli in the posterior prepectal nucleus and nucleus glomerulosus in esocids and acanthopterygians, respectively, and the presence of two nuclei, the pars intermedius and nucleus glomerulosus, in acanthopterygians, as opposed to one nucleus, the posterior prepectal nucleus, are apomorphies.

### Introduction

Marked variation occurs in the organization of the prepectum among teleost fishes. Northcutt and Wullimann [1988] found strikingly different patterns of organization in the presence or absence of certain nuclei or in their degree of development in representatives of the various teleost radiations. One example of this diversity is the large, complexly organized nucleus glomerulosus which has been described in neoteleosts [Franz, 1912; Mazzi, 1953; Northcutt and Wullimann, 1988]. Although this nucleus is an obvious and striking feature of the prepectum in percomorph teleosts, a homologue is not readily identifiable in species belonging to a number of other teleost lineages. This paper will examine a number of species drawn from diverse teleost lineages in an attempt to clarify the common and derived traits relating to the organization of visual prepectal nuclei.

Extant teleost fishes can be divided into four major radiations – Osteoglossomorpha (including arawanas, the freshwater butterfly fish, notoapterids, mormyrids, and mooneyes), Elopomorpha (including tenpounders, tarpons, and eels), Clupeomorpha (herrings and anchovies), and Euteleostei (fig. 1). The Euteleostei comprise Esocae (pikes and pickerels), Ostariophysi (cyprinids, characins, silurids, and gymnotids), Osmeroidei and Argentinoidei (smelts and deep sea fishes), Salmonidae (trouts and salmons), and the Neoteleostei – Stomiiformes (middle depth, marine fishes, including lightfishes and hatchetfishes), Aulopiformes (small, marine fishes including thread-sail fishes), Myctophiformes (pelagic, marine fishes including lantern fishes and pearleyes), Paracanthopterygii (including cods, hakes, toadfishes, goosefishes, and anglerfishes), Atherinomorpha (including killifishes, livebearers, four-eye fishes, and flying fishes), and Percomorpha (comprising 12 orders) [Migdalski and

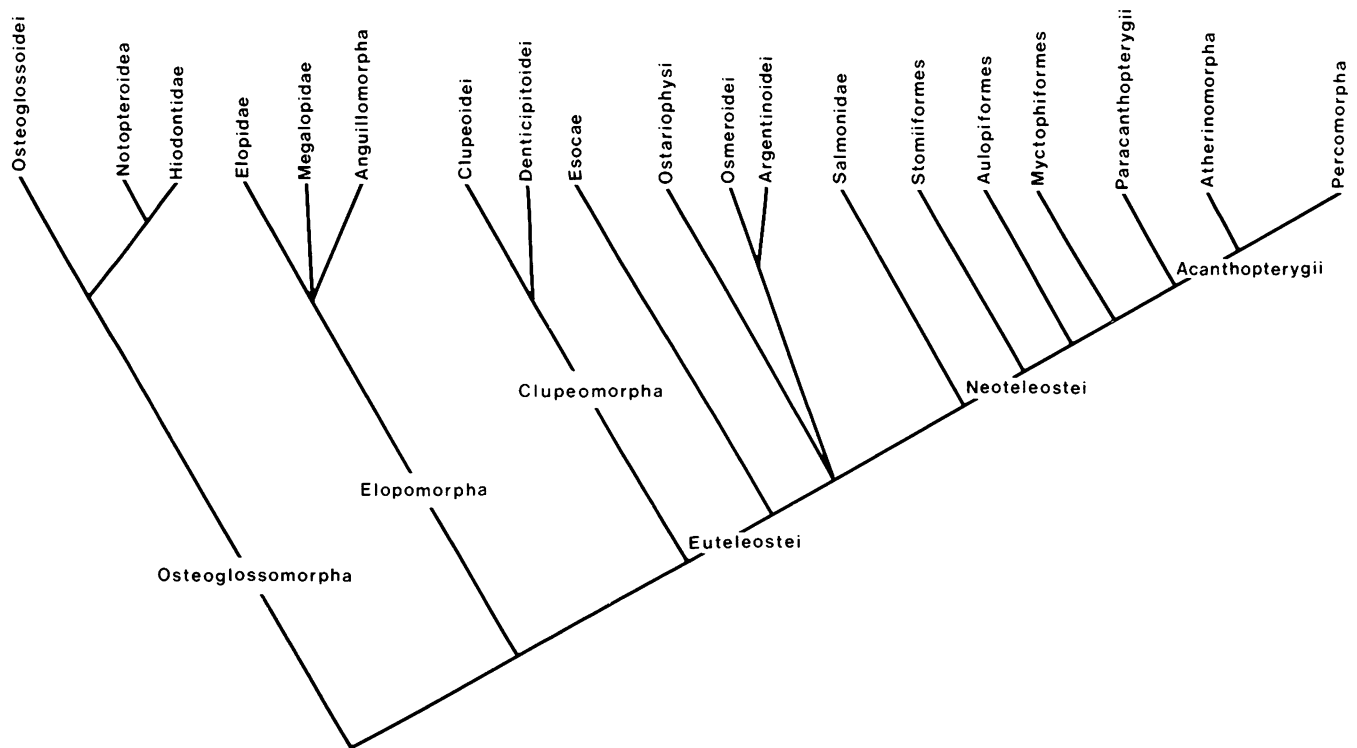


Fig. 1. Dendrogram modified from Lauder and Liem [1983] of extant teleost radiations.

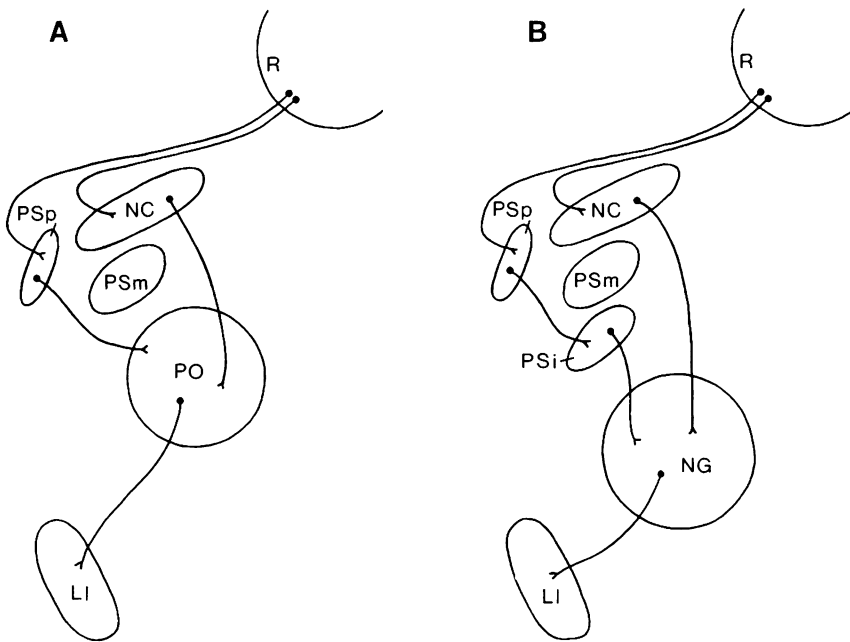
### List of Abbreviations

AP	Accessory pretectal nucleus
C	Central zone of tectum
FR	Fasciculus retroflexus
H	Habenula
LI	Inferior lobe of hypothalamus
NC	Nucleus corticalis
NG	Nucleus glomerulosus
NGa	Anterior lobe of nucleus glomerulosus
NGp	Posterior lobe of nucleus glomerulosus
M	Mesencephalic nucleus of the trigeminal nerve
OT	Optic tract
P	Periventricular and deep white zones of tectum
PC	Posterior commissure
PG	Preglomerular complex
PO	Posterior pretectal nucleus
PSi	Pars intermedialis of superficial pretectal nucleus
PSm	Pars magnocellularis of superficial pretectal nucleus
PSP	Pars parvocellularis of superficial pretectal nucleus
R	Retina
S	Superficial zone of tectum
TL	Torus longitudinalis
TLa	Torus lateralis
V	Tectal ventricle
Vh	Hypothalamic ventricle

Fichter, 1976; Lauder and Liem, 1983). Surveys analyzing the morphology of central nervous system structures in various species representing these radiations are needed in order to generate and test hypotheses regarding evolutionary trends.

In *Navodon*, a percomorph acanthopterygian, nucleus glomerulosus receives input from two visually related pretectal nuclei – pretectalis superficialis pars intermedialis and corticalis – and projects to the inferior lobe of the hypothalamus (fig. 2) [Sakamoto and Ito, 1982]. Nucleus glomerulosus consists of glomeruli which surround a central core of fibers. The glomeruli are, in turn, surrounded by three more concentric layers – a fibrous layer, a small-celled layer, and most peripherally a capsule of large cells and fibers [Sakamoto and Ito, 1982]. Projections from nucleus corticalis terminate in the glomeruli, while projections from the pars intermedialis of the superficial pretectal nucleus terminate in the small-celled layer anteriorly and in the fibrous layer posteriorly [Sakamoto and Ito, 1982].

In percomorph fishes, the pars intermedialis of the



**Fig. 2.** Schematic summary diagram of the known connections of some of the visually related pretectal nuclei in (A) osteoglossomorph and (B) euteleost fishes. See text for explanation and references.

superficial pretectal nucleus and nucleus corticalis both lie rostral and dorsolateral to nucleus glomerulosus. Nucleus corticalis is a large-celled nucleus at the base of the central zone of the tectum and has been found to receive a direct retinal projection in a variety of percomorphs [Campbell and Ebbesson, 1969; Vanegas and Ebbesson, 1973; Anders and Hibbard, 1974; Gulley et al., 1975; Butler and Northcutt, 1981; Fernald, 1982; Ekström, 1984; Northcutt and Butler, 1991]. The pars intermedius of the superficial pretectal nucleus lies ventromedial to the magnocellular superficial pretectal nucleus [Northcutt and Wullimann, 1988] and receives projections from the parvocellular superficial pretectal nucleus [Murakami et al., 1986b; Striedter and Northcutt, 1989], which is the 'lateral geniculate nucleus' of many other authors and a retinofugal target [Campbell and Ebbesson, 1969; Vanegas and Ebbesson, 1973; Anders and Hibbard, 1974; Gulley et al., 1975; Repérant et al., 1976; Butler and Northcutt, 1981; Fernald, 1982; Ekström, 1984; Ito et al., 1984; Springer and Mednick, 1985a; von Bartheld and Meyer, 1988].

Northcutt and Wullimann [1988] could identify the distinctive nucleus glomerulosus on the basis of cytoarchitecture alone only in paracanthopterygians and acanthopterygians. They recognized a nucleus corticalis in these advanced euteleosts and possibly in osteoglossomorphs and some ostariophysans, and connective studies, subsequently carried out [Wulli-

mann and Northcutt, 1989], have verified the identity of this nucleus in *Osteoglossum*. A large pretectal nucleus in a position similar to that of the pars intermedius of nucleus pretectalis superficialis and the rostral pole of nucleus glomerulosus was found in osteoglossomorphs, clupeomorphs, esocids and salmonids, but the differences in its histology as compared with nucleus glomerulosus in paracanthopterygians and acanthopterygians precluded any certainty as to its identity [Northcutt and Wullimann, 1988]. However, because of the relative smallness of this nucleus and its position ventral to the magnocellular superficial pretectal nucleus in clupeomorphs, Northcutt and Wullimann [1988] identified it as the pars intermedius in this clade.

This pretectal nucleus has subsequently been identified in *Osteoglossum* and *Carassius* and has been named the posterior pretectal nucleus [Wullimann and Northcutt, 1989; Wullimann and Meyer, 1990]. It lies ventromedial to nucleus pretectalis superficialis pars magnocellularis and ventrolateral to the central pretectal nucleus. In some osteoglossomorphs, the posterior pretectal nucleus is a very large, histologically homogeneous nucleus. Its connections and those of the parvocellular superficial pretectal nucleus were recently studied by Wullimann and Northcutt [1989], and their results allowed for the present reinterpretation of the evolution of this part of the pretectum in teleosts.

In the arawana, *Osteoglossum bicirrhosum*, it was found that the rostral portion of the posterior prepectal nucleus receives direct input from the parvocellular superficial prepectal nucleus and that the caudomedial, main portion of the posterior prepectal nucleus receives input from nucleus corticalis (fig. 2). The posterior prepectal nucleus in turn projects to nucleus centralis and parts of nucleus diffusus of the inferior lobe, suggesting that the posterior prepectal nucleus is homologous to both the pars intermedialis of the superficial prepectal nucleus and nucleus glomerulosus of acanthopterygians [Wullimann and Northcutt, 1989]. Further recent work on the distribution of acetylcholinesterase (AChE) in the prepectum of *Osteoglossum* and species of euteleosts [Wullimann and Meyer, 1990], demonstrating similarities in AChE activity, supports this hypothesis.

These new connectional and histochemical results provide a basis for reexamining the cytoarchitecture of this region of the prepectum in the four radiations of teleosts – the osteoglossomorphs, elopomorphs, clupeomorphs, and various euteleosts. In order to study evolutionary trends, it is sometimes important to conduct a broad survey of selected species, as has been done here employing cytoarchitectural analysis. Hypotheses generated or supported by studies such as the present one can then subsequently be further tested using hodological methods.

The present work has revealed a common organizational pattern among all groups of teleosts examined which suggests that both the posterior prepectal nucleus and nucleus corticalis are plesiomorphic features of teleosts. Our results also strongly support the hypothesis that the posterior prepectal nucleus is homologous to both the pars intermedialis of the superficial prepectal nucleus and nucleus glomerulosus in acanthopterygians.

## Materials and Methods

The original research reported herein was performed under guidelines established by the University of California, San Diego. Brains used in this study are from a variety of species of teleosts, representing all four major clades, as follows: *Osteoglossum bicirrhosum*, *Pantodon buchholzi* (Osteoglossomorpha); *Elops saurus*, *Anguilla anguilla* (Elopomorpha); *Clupea harengus*, *Brevoortia tyrannus* (Clupeomorpha); and *Esox lucius*, *Carassius auratus*, *Salmo gairdneri*, *Lepomis cyanellus*, and *Balistoides conspicillum* (Euteleostei). Specimens were deeply anesthetized with tricaine methanesulphonate (MS 222, Sigma) and transcardially perfused with either 0.1 M phosphate buffer (pH 7.4) or 1% heparin in teleost

Ringer's solution, followed by either AFA (90 ml 80% ethanol, 5 ml formalin, and 5 ml glacial acetic acid) or 4% paraformaldehyde in 0.1 M phosphate buffer. The brains were then removed from the crania and postfixed for at least one month in the same fixative.

For histology, the brains were embedded in paraffin and sectioned in the transverse plane at 15  $\mu$ m. Sections were serially mounted on glass slides, silver-stained with Protargol (Rogues chimie, St. Ouen, France, or Merck, Darmstadt, Germany) according to the Bodian method [Romeis, 1989], and, in most cases, counterstained with cresyl violet.

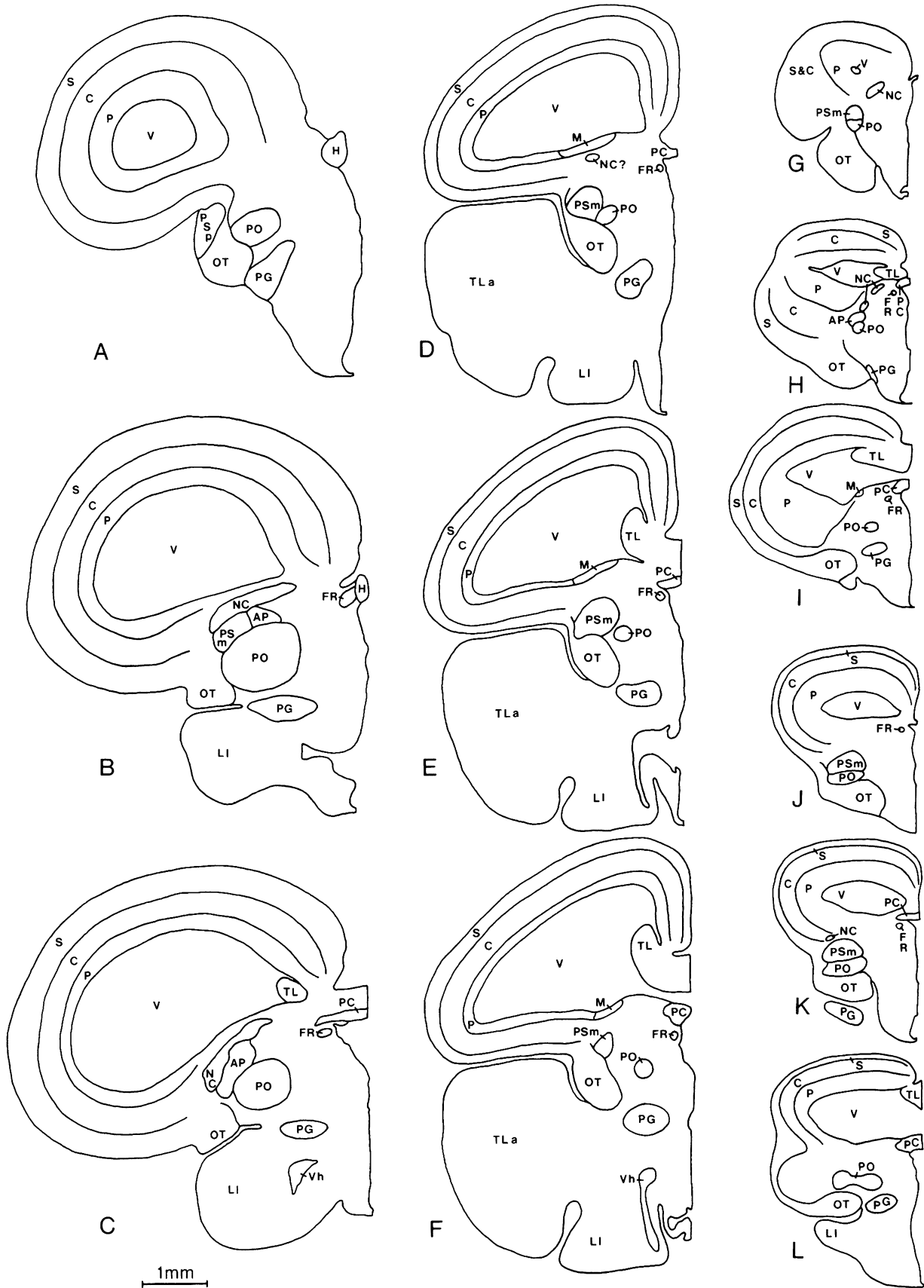
## Results

We will first describe the cytoarchitecture of the posterior prepectal nucleus and nucleus corticalis in osteoglossomorphs and then consider the nuclei in the same area in elopomorphs, clupeomorphs, primitive euteleosts – esocids and salmonids – and advanced euteleosts. Thalamic nuclei are omitted from the drawings and observations, as a sufficiently detailed analysis of them has not yet been completed in all species examined here. Nomenclature is based on that of Braford and Northcutt [1983], Northcutt and Wullimann [1988], and Wullimann and Northcutt [1989]. Our phyletic analysis is predicated on the hypotheses regarding the evolutionary relationships of ray-finned fishes proposed by Lauder and Liem [1983].

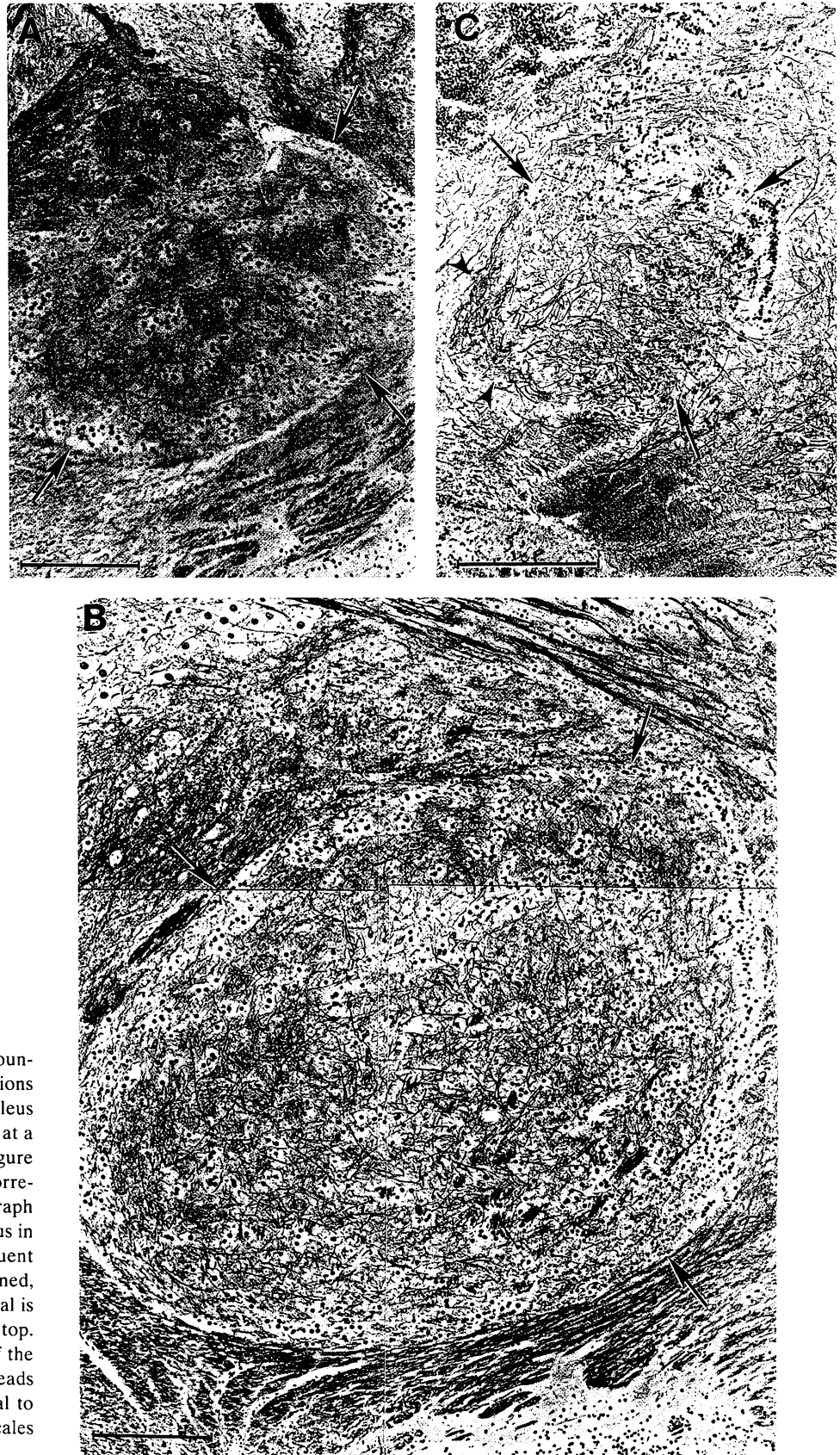
### *Osteoglossomorphs*

In the arawana *Osteoglossum bicirrhosum*, at a level through the habenula (H), the pars parvocellularis of the superficial prepectal nucleus (PSP) and the rostral pole of the posterior prepectal nucleus (PO) appear embedded among the fibers of the optic tract, with the posterior prepectal nucleus lying medial to the pars parvocellularis (fig. 3A). At its rostral pole, the posterior prepectal nucleus is relatively small and composed of a neuropil, with small and medium sized cells scattered in it (fig. 4A). The cells are aggregated into small rows and clusters within the neuropil.

The posterior prepectal nucleus continues much farther caudally than the parvocellular portion of the superficial prepectal nucleus, and at mid-prepectal levels it forms a large, ovoid shape in transverse section, with a mixture of medium and small cells, which tend to be grouped in clusters, and small patches of fiber bundles dispersed within it. Around parts of the perimeter, particularly its medial portion, is a thin lami-



**Fig. 3.** Camera lucida drawings of the left sides of rostral to caudal transverse sections through the pretectum in *Osteoglossum bicirrhosum* (A-C), *Elops saurus* (D-F), *Brevoortia tyrannus* (G-I), and *Clupea harengus* (J-L).



**Fig. 4.** Photomicrographs of uncounterstained, Bodian, transverse sections through the posterior pretectal nucleus (PO) on the left side in *Osteoglossum* at a rostral level (A) corresponding to figure 3A and a mid-pretectal level (B) corresponding to figure 3B. Photomicrograph through the posterior pretectal nucleus in *Pantodon* (C). The latter and subsequent photomicrographs are of counterstained, Bodian, transverse sections, and lateral is toward the left and dorsal toward the top. Arrows in A–C indicate the border of the posterior pretectal nucleus. Arrowheads in C indicate nucleus corticalis lateral to the posterior pretectal nucleus. Bar scales represent 200  $\mu\text{m}$ .

na of small cells (fig. 4B). No subdivisions of this nucleus could be distinguished on cytoarchitectural grounds. At this level (fig. 3B), the magnocellular superficial pretectal nucleus (PSm) lies immediately dorsolateral to the posterior pretectal nucleus. The accessory pretectal nucleus (AP), first described by Wullimann and Meyer [1990], lies dorsal to the posterior pretectal nucleus.

The large cells which form nucleus corticalis (NC, fig. 3B, 4B, 5A) lie dorsal to the magnocellular portion of the superficial pretectal nucleus and the accessory pretectal nucleus at a level through the rostral part of the tectum. Additional criteria used to identify nucleus corticalis are that its cells (1) are in a position clearly continuous with the central zone of the tectum, (2) are randomly oriented and multipolar, and (3) have eccentric nuclei which do not show a preferential orientation. Cells of the mesencephalic nucleus of the trigeminal nerve, which will be discussed in detail below vis à vis nucleus corticalis, lie farther caudally within the periventricular zone of the tectum. The preglomerular complex (PG) is ventromedial to the posterior pretectal nucleus (fig. 3B).

Farther caudally in the pretectum, the posterior pretectal nucleus is less large although still very prominent. The histology is the same as farther rostrally, but the peripheral lamina of small cells is not clearly discernible at this level. The accessory pretectal nucleus has replaced the caudal pole of the magnocellular portion of the superficial pretectal nucleus and lies dorsolateral to the posterior pretectal nucleus, and nucleus corticalis lies dorsolateral to the accessory pretectal nucleus (fig. 3C). The preglomerular complex is still present ventromedially.

In the freshwater butterfly fish *Pantodon buchholzi*, the posterior pretectal nucleus is relatively small at its rostral pole as in *Osteoglossum*, but it contains mostly small cells scattered in a neuropil. Farther caudally the nucleus is quite large and lies ventromedial to the magnocellular portion of the superficial pretectal nucleus and the cell plate of nucleus corticalis. Throughout most of the extent of the posterior pretectal nucleus, the small cells are located predominantly in its medial and dorsomedial part, and many are grouped into clusters (fig. 4C). The ventrolateral part of the nucleus is more fibrous in appearance and also contains a large number of medium sized cells. The smaller caudal pole of the nucleus likewise contains a predominance of fibers lateroventrally and fibers with medium and small cells, many of which are in clusters,

as in the rest of the nucleus. The posterior pretectal nucleus remains dorsal to the preglomerular complex. The mesencephalic nucleus of the trigeminal nerve lies caudal to nucleus corticalis in the periventricular tectal zone.

#### *Elopomorphs*

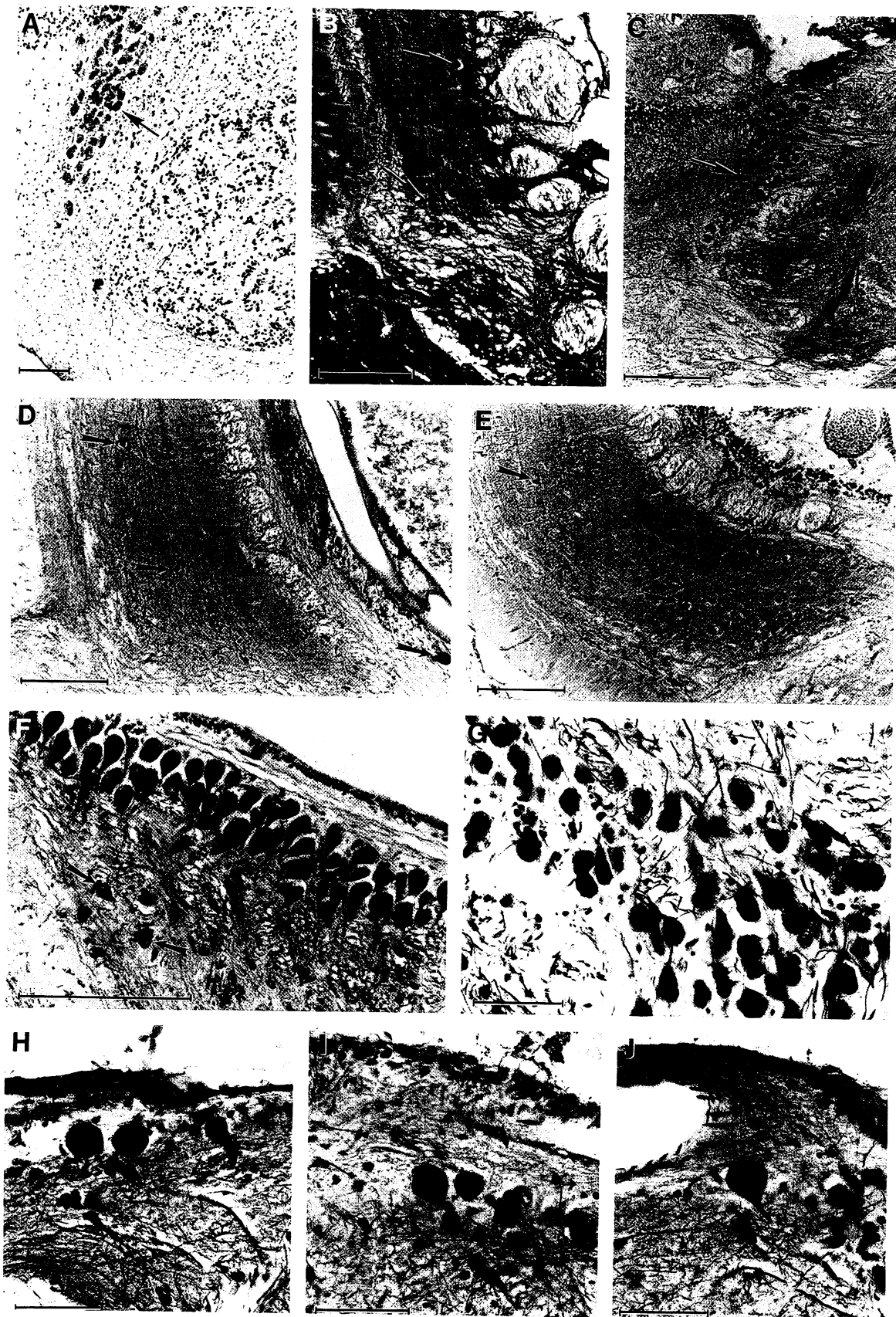
In the ladyfish *Elops saurus*, the posterior pretectal nucleus is a relatively much smaller nucleus than that seen in *Osteoglossum*. Its rostral pole lies caudal to the parvocellular portion of the superficial pretectal nucleus at a mid-pretectal level. It contains a mixture of medium and small cells scattered in a neuropil. The magnocellular portion of the superficial pretectal nucleus is juxtaposed to the posterior pretectal nucleus dorsolaterally (fig. 3D). *Elops* appears to have an unusually large mesencephalic trigeminal nucleus (Mes V), close to the position where nucleus corticalis would be expected to lie and forming a compact cell plate similar to nucleus corticalis. It is identified as Mes V here due to (1) its position within the periventricular layer of the tectum, (2) the characteristic spherical or tear-drop shape of its cells with the enlarged portion oriented uniformly towards the ventricular surface of the tectum, and (3) the typically eccentric position of the cell nuclei, usually displaced towards the ends of the cells nearest the ventricular surface (fig. 5F). Additionally, the cells of Mes V are larger than cells of nucleus corticalis seen in other species. Ventral to Mes V lie a few scattered, medium to large cells of more variable shape which might possibly comprise a very small nucleus corticalis.

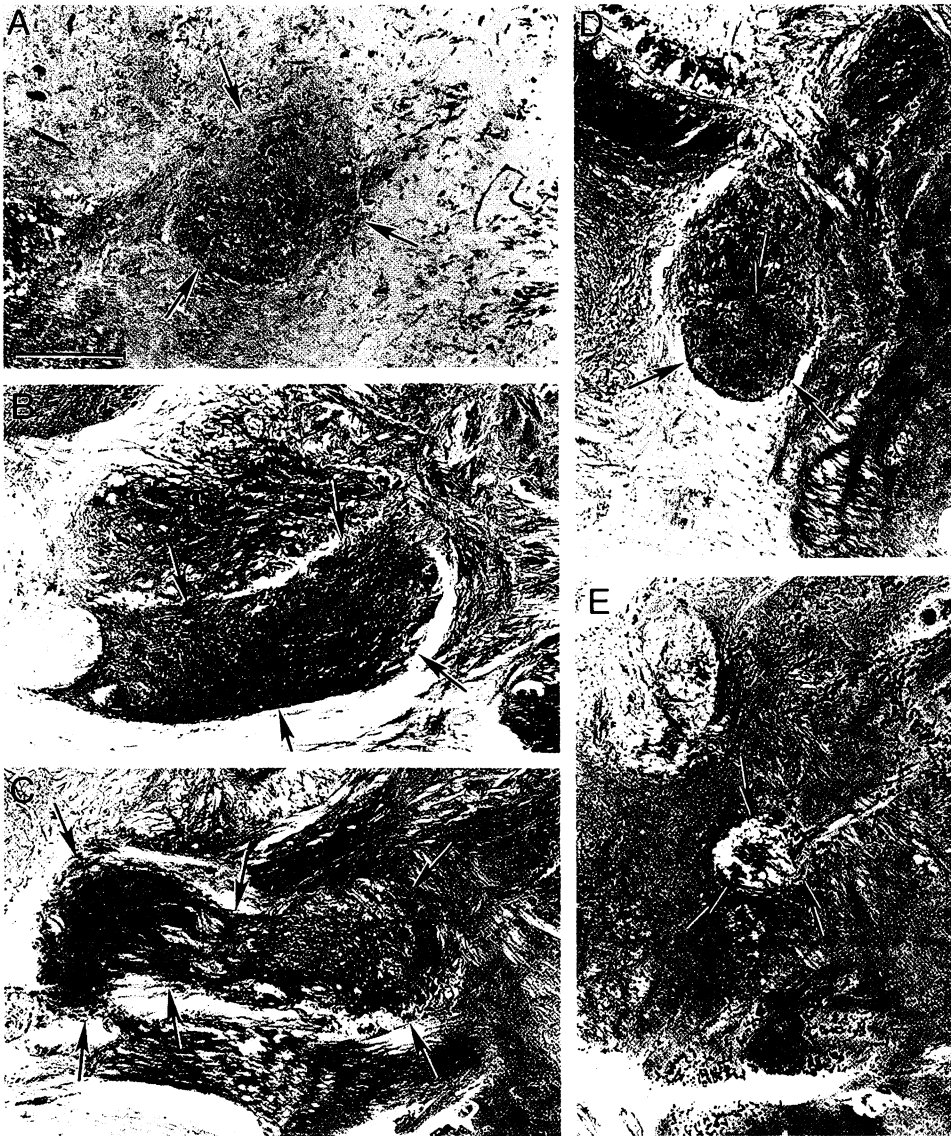
Slightly more caudally in the pretectum, the posterior pretectal nucleus maintains its position ventro-

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**Fig. 5.** Photomicrographs of nucleus corticalis (NC), indicated by arrow, in *Osteoglossum* (A), nucleus corticalis in *Clupea* with the cell plate and cells in tectum indicated by arrows (B), and nucleus corticalis in *Lepomis* indicated by arrow (C). D Putative nucleus corticalis cells in the central zone of the tectum in *Esox*, indicated by the two arrows to the upper left, and a cell of the mesencephalic nucleus of the trigeminal nerve located in the periventricular zone of the tectum, indicated by arrow at lower right. E Putative nucleus corticalis cells in the central zone of the tectum in *Salmo*, indicated by arrows. F The mesencephalic nucleus of the trigeminal nerve (Mes V) in *Elops* formed by a plate of very large, darkly stained, tear-drop shaped cells. Ventral to Mes V are a few cells which might represent nucleus corticalis, indicated by arrows. G Cells of nucleus corticalis in *Lepomis*. H Mes V cells in *Clupea*. I, J Mes V cells in *Lepomis*. Bar scales represent 200  $\mu\text{m}$  in A-F and 50  $\mu\text{m}$  in G-J.







**Fig. 6.** Photomicrographs of the posterior pretectal nucleus in *Elops* (A) corresponding to figure 3E, in *Clupea* (B, C) corresponding to figures 3K and L, respectively, and in *Brevoortia* (D, E) corresponding to figures 3G and I, respectively. Arrows indicate the border of the posterior pretectal nucleus. The magnocellular portion of the superficial pretectal nucleus lies dorsolateral to the posterior pretectal nucleus in A and dorsal to it in B and D. Bar scale in A represents 200  $\mu$ m and is the same for B-E.

medial to the well developed and relatively large magnocellular portion of the superficial pretectal nucleus (fig. 3E) and contains small and medium sized cells. The majority of cells lie in the medial half of the nucleus and form clusters (fig. 6A). A few medium sized cells are scattered in the lateral portion. Farther caudally, at a level through the posterior commissure (fig. 3F), the position of the posterior pretectal nucleus is slightly more medial. The preglomerular complex is ventral to the posterior pretectal nucleus. At this caudal level, the posterior pretectal nucleus is composed only of a few small and medium sized cells scattered in its neuropil.

In the eel, *Anguilla anguilla*, another elopomorph, the posterior pretectal nucleus is also relatively small.

At mid-pretectal levels it is composed of a neuropil with only a few small and medium sized, scattered cells, lying ventromedial to the magnocellular and parvocellular portions of the superficial pretectal nucleus. More caudally, the posterior pretectal nucleus becomes smaller in size, consisting of a neuropil with a few cells. Throughout its extent, it maintains a position dorsal to the relatively large preglomerular complex. A nucleus corticalis could not be identified in *Anguilla*. There are two cell plates formed by moderately large and relatively loosely scattered cells which lie across the base of the rostral tectum in an area continuous with the tectum's central zone. The more ventrally located cell plate appears to be the central pretectal nucleus. The identity of the other plate is

uncertain. The larger, spherical cells of the mesencephalic nucleus of the trigeminal nerve are present farther caudally and fully embedded within the ventral part of the periventricular tectal zone, and this nucleus in *Anguilla* is not developed to the extreme degree that it is in *Elops*.

#### *Clupeomorphs*

In the menhaden *Brevoortia tyrannus*, the posterior prepectal nucleus appears to be relatively small compared with that seen in other teleosts. It lies immediately ventral to the magnocellular portion of the superficial prepectal nucleus at a mid-prepectal level (fig. 3G), and both nuclei lie ventrolateral to nucleus corticalis, the lateral part of which is traversed by fibers of the optic tract coursing into the tectum. The posterior prepectal nucleus contains almost exclusively small cells, which are loosely aggregated into clusters within the neuropil, and is bordered by a clearly defined peripheral lamina of small cells (fig. 6D). Somewhat more caudally, at a level through the posterior commissure (fig. 3H), the posterior prepectal nucleus is formed by a small neuropil with a few scattered small cells and a modest condensation of small cells along its medial edge. The magnocellular portion of the superficial prepectal nucleus has been replaced dorsal to the posterior prepectal nucleus by the accessory prepectal nucleus, and the cell plate of nucleus corticalis lies dorsomedially, ventral to the base of the tectum. Farther caudally, the posterior prepectal nucleus shifts medially in position and continues to lie dorsal to the preglomerular complex (fig. 3I). The posterior prepectal nucleus does not extend far caudally beyond this level, although the preglomerular complex does. At this level, a few cells forming the mesencephalic nucleus of the trigeminal nerve (Mes V) lie periventricularly and have the diagnostic teardrop shape and large size. The caudal portion of the posterior prepectal nucleus consists of a lateral fibrous region and a medial aggregation of small cells (fig. 6E).

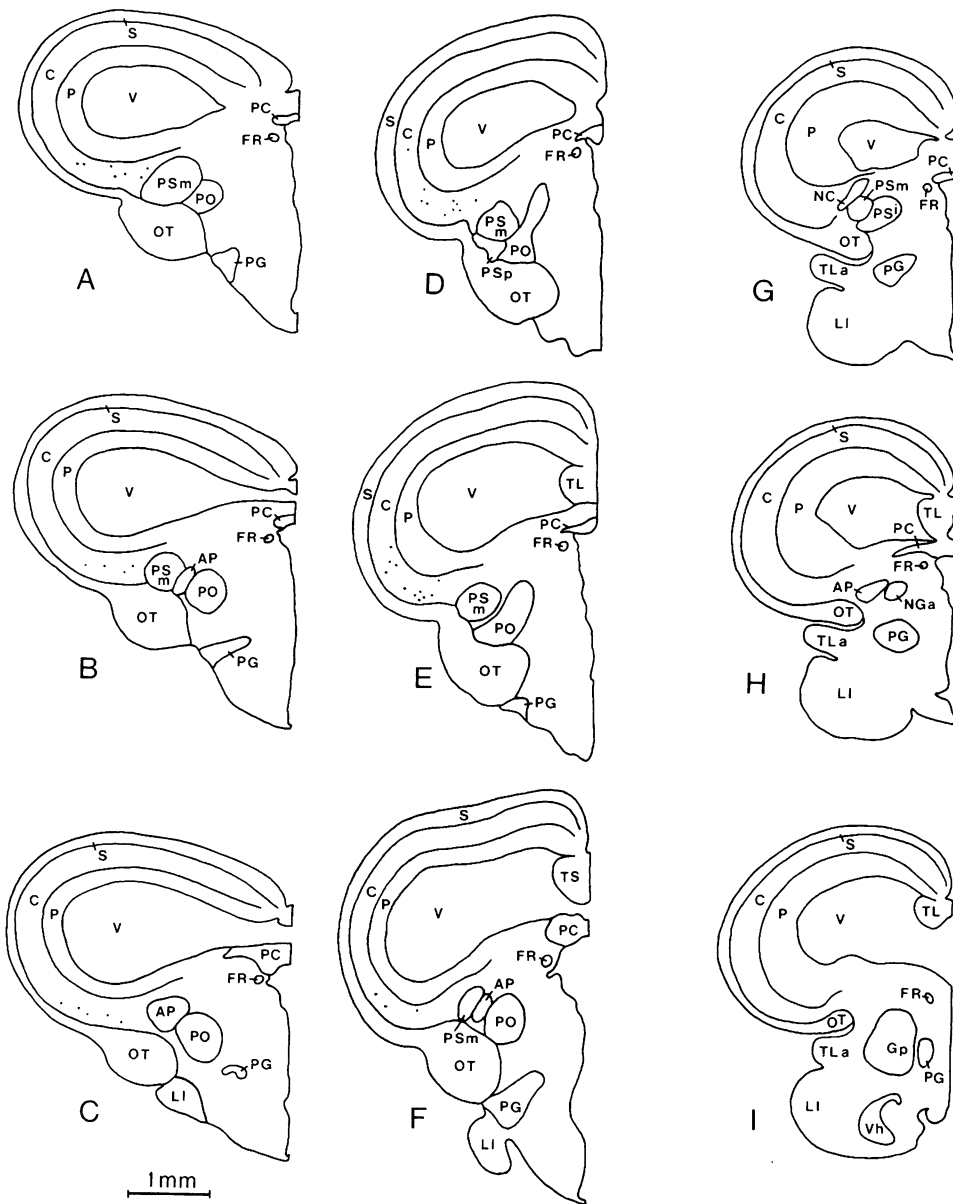
In the herring *Clupea harengus*, both the magnocellular portion of the superficial prepectal nucleus and the posterior prepectal nucleus are relatively much larger than in *Brevoortia*, and the magnocellular portion of the superficial prepectal nucleus is also exceptionally large in comparison with other teleosts. The magnocellular portion of the superficial prepectal nucleus has its typically rounded shape and contains large, scattered cells. The posterior prepectal nucleus

forms a large nucleus ventral to the magnocellular portion of the superficial prepectal nucleus, elongated mediolaterally such that its dorsal border forms the shape of a saucer around the ventral half of the magnocellular portion of the superficial prepectal nucleus (fig. 3J, K). The posterior prepectal nucleus in *Clupea* contains numerous scattered small cells, some of which are aggregated in clusters in the neuropil, and also has a few medium sized cells (fig. 6B). A higher proportion of cells is present in the medial than in the lateral part of the nucleus. Farther caudally, the posterior prepectal nucleus becomes dumb-bell shaped in transverse section, similar to a mammalian red blood cell in profile, with areas of small cells in clusters and neuropil at its medial and lateral ends and a more fibrous appearing area in the thinner center (figs. 3L, 6C). The more lateral area does not continue as far caudally as the central and medial areas; the position of the latter two areas shifts somewhat medially at more caudal levels, and the nucleus closely resembles the caudal pole of the posterior prepectal nucleus in *Brevoortia*, composed of a lateral fibrous area with a medial area of small cells and in a position dorsal to the preglomerular nuclear complex.

In addition to the difference in size of the magnocellular portion of the superficial prepectal nucleus and the posterior prepectal nucleus between *Brevoortia* and *Clupea*, there is also a difference in the position of some of the neurons of nucleus corticalis. In *Clupea*, this nucleus lies across the base of the central zone of the tectum, as it does in *Brevoortia* and in many other teleosts. However, in *Clupea*, some of the corticalis neurons are scattered for a short distance dorsal to the main cell plate so that they lie fully within the central tectal zone (fig. 5B). Typical cells of the mesencephalic nucleus of the trigeminal nerve lie farther caudally in a periventricular position (fig. 5H). We believe that there are two other, more extreme examples of corticalis neurons lying within rather than immediately ventral to the central tectal zone which are described below.

#### *Euteleosts: Esocids*

In the pike *Esox lucius*, the magnocellular portion of the superficial prepectal nucleus is about twice the size of the posterior prepectal nucleus in diameter at mid-prepectal levels (fig. 7A). The rostral part of the posterior prepectal nucleus contains medium and small cells which are aggregated into clusters of different degrees of density and are predominantly lo-



**Fig. 7.** Camera lucida drawings of the left sides of rostral to caudal transverse sections through the pretectum in *Esox lucius* (A–C), *Salmo gairdneri* (D–F), and *Lepomis cyanellus* (G–I). Small dots in tectum in A–F represent putative nucleus corticalis cells.

cated in the medial half of the neuropil. Among the cell clusters are glomeruli of varying size (fig. 8A). The posterior pretectal nucleus lies ventromedial to the magnocellular portion of the superficial pretectal nucleus, but dorsal to the latter there is no collection of large cells forming a nucleus corticalis. There is, however, a modest population of large cells (figs. 5D, 7A) scattered in and confined to the most ventrolateral portion of the central zone of the tectum, a region which abuts the magnocellular portion of the superficial pretectal nucleus. Based on the observation that some of the corticalis neurons in *Clupea* are scattered

in this same location, dorsolateral to the main cell plate of the nucleus, we believe that these scattered cells in this location in *Esox* are corticalis neurons.

Somewhat more caudally in the pretectum, the accessory pretectal nucleus is interposed between the posterior pretectal nucleus and the magnocellular portion of the superficial pretectal nucleus (fig. 7B). Only a few putative corticalis cells are still present in the ventrolateral region of the central tectal zone at this level. In the posterior pretectal nucleus, the major proportion of the cells, most of which are in clusters, lie in the medial half of the nucleus (fig. 8B), and

small glomeruli are present throughout the nucleus (fig. 10A). Farther caudally, the diameter of the posterior pretectal nucleus in transverse sections becomes larger, and the clusters of cells are more evenly distributed within the nucleus, interspersed with numerous glomeruli in a fibrous neuropil (fig. 8C). Through its more caudal levels, the posterior pretectal nucleus lies ventromedial to the accessory pretectal nucleus, which has replaced in position the caudal pole of the magnocellular portion of the superficial pretectal nucleus, and a few putative corticalis neurons are also still present in the tectum (fig. 7C). The preglomerular complex is present ventral to the posterior pretectal nucleus through this region (fig. 7A–C). The majority of the large, tear-drop shaped cells of the mesencephalic nucleus of the trigeminal nerve are present farther caudally, scattered along the ventral portion of the periventricular gray of the tectum.

#### *Euteleosts: Salmonids*

In the rainbow trout *Salmo gairdneri*, the rostral portion of the posterior pretectal nucleus lies ventromedial to the magnocellular portion of the superficial pretectal nucleus and medial to the caudal part of the parvocellular superficial pretectal nucleus (PSP, fig. 7D). All three nuclei are relatively large in *Salmo*. At this mid-pretectal level, the posterior pretectal nucleus is composed of small and medium sized cells scattered in a neuropil, with the greater number of cells in the dorsomedial three quarters of the nucleus and only a few cells in a fibrous portion in the lateroventral quadrant (fig. 9A). There is no trace of a discrete corticalis cell plate in *Salmo*, but, as is the case to a lesser degree in the pike *Esox*, there are scattered, large neurons in the ventrolateral quadrant of the central tectal zone which we believe to be corticalis neurons (figs. 5E, 7D).

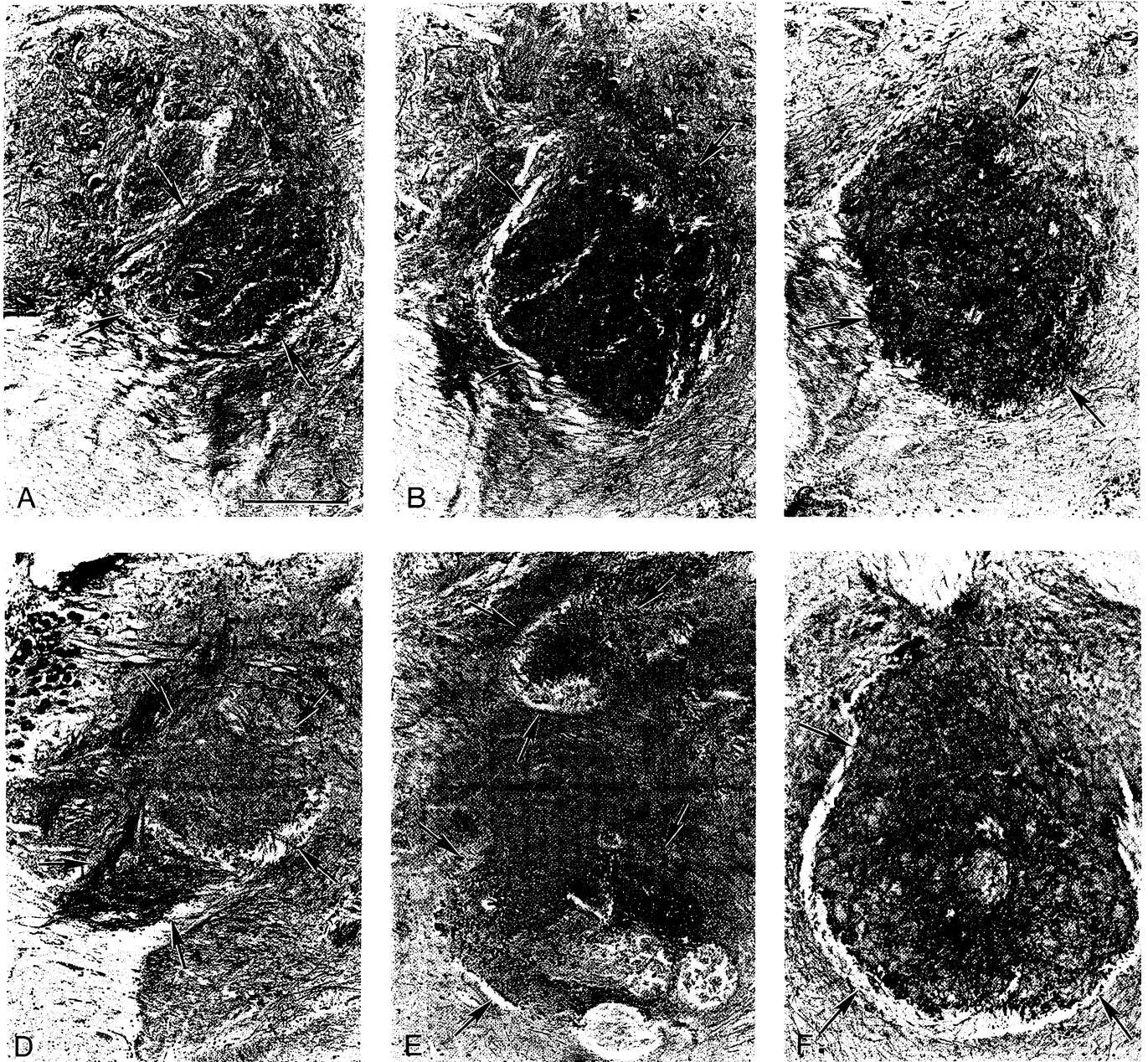
At a level caudal to the parvocellular portion of the superficial pretectal nucleus and at the rostralmost level of the preglomerular complex (PG, fig. 7E), the posterior pretectal nucleus has an elongated, ovoid shape, curving slightly around the ventral and medial borders of the magnocellular portion of the superficial pretectal nucleus, similar in shape to the posterior pretectal nucleus in the clupeomorph *Clupea*. The cells in the posterior pretectal nucleus are scattered throughout most of the nucleus, with only the ventrolateral-most portion having a sparser density of cells in its neuropil (fig. 9B). The cells are in loose aggregations. Putative corticalis neurons con-

tinue to be present in the tectum at this level (fig. 7E). Farther caudally, the posterior pretectal nucleus assumes an almost circular shape in transverse section and lies ventromedial to the magnocellular portion of the superficial pretectal nucleus, with the rostral pole of the accessory pretectal nucleus interposed between (fig. 7F). The preglomerular complex lies ventrally. The neuropil of the posterior pretectal nucleus contains a number of small fascicles encircled by the small cells (fig. 9C). Discrete glomeruli do not appear to be present in the posterior pretectal nucleus in *Salmo*.

#### *Euteleosts: Acanthopterygians*

To this point, we have described the posterior pretectal nucleus and nucleus corticalis in three of the four major clades of teleosts and in some primitive euteleosts. In advanced euteleosts (acanthopterygians), two nuclei are present in positions similar in most regards to the position of the posterior pretectal nucleus in other teleosts. These nuclei have been identified as the pars intermedius of the superficial pretectal nucleus and nucleus glomerulosus, and both together have been proposed to be homologous to the posterior pretectal nucleus in other teleosts [Butler et al., 1989; Wullimann and Northcutt, 1989; Wullimann and Mayer, 1990].

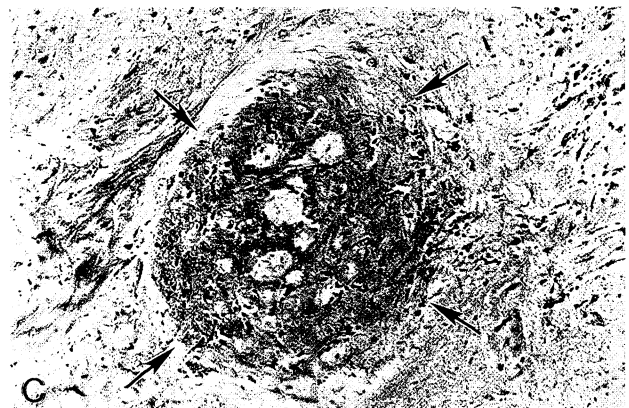
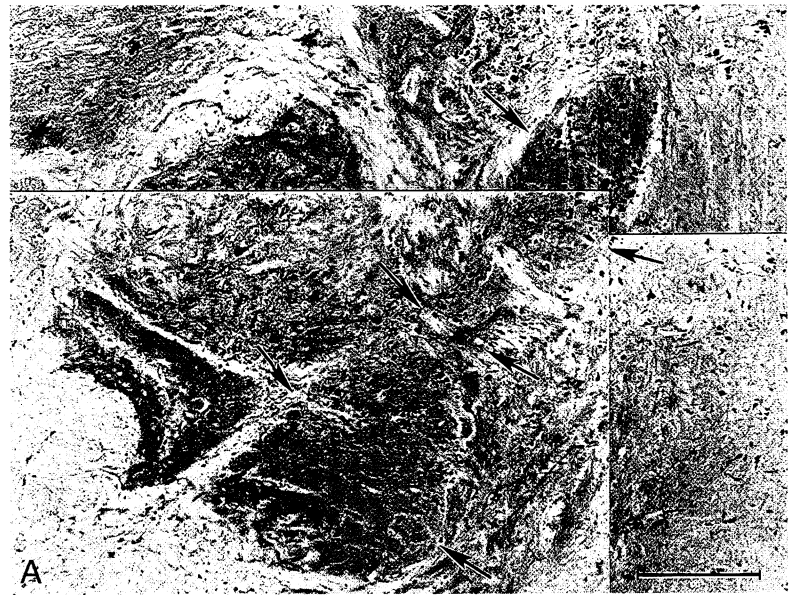
In the green sunfish *Lepomis cyanellus*, at a level through the posterior commissure, the pars intermedius of the superficial pretectal nucleus lies ventromedial to the magnocellular portion of the superficial pretectal nucleus, slightly curving around the ventral and medial borders of the magnocellular portion of the superficial pretectal nucleus (fig. 7G). The intermediate portion of the superficial pretectal nucleus contains small cells scattered in a neuropil, with a large number of small cells condensed along its ventromedial border. A few, larger cells are also present. The ventrolateral portion of the nucleus is more fibrous than the larger, dorsomedial portion (fig. 8D). Dorsolateral to the magnocellular portion of the superficial pretectal nucleus at this same level is the easily recognizable cell plate of nucleus corticalis (figs. 5C, 8D). The corticalis cells are of variable shape – round or elongated (fig. 5G). They have eccentric nuclei, but unlike the cells of the mesencephalic nucleus of the trigeminal nerve, which can be observed more caudally (fig. 5I, J), there is no tendency for uniformity of the orientation of their nuclei towards the ventricle. Nucleus corticalis lies across the base of the central zone of the tectum (fig. 7G).



**Fig. 8.** Photomicrographs of the posterior pretectal nucleus in *Esox* (A–C) corresponding to figures 7A–C, respectively, the pars intermedius of the superficial pretectal nucleus in *Lepomis* (D) corresponding to figure 7G, the anterior lobe of nucleus glomerulosus (NGa) dorsal to the preglomerular complex (PG) in *Lepomis* (E) corresponding to figure 7H, and the posterior lobe of nucleus glomerulosus (NGp) in *Lepomis* (F) corresponding to figure 7I. Arrows indicate the border of the posterior pretectal nucleus in A–C, of the pars intermedius of nucleus superficialis pretectalis in D, of the anterior lobe of nucleus glomerulosus dorsally and the preglomerular complex ventrally in E, and of the posterior lobe of nucleus glomerulosus in F. Bar scale in A represents 200  $\mu\text{m}$  and is the same for B–F.

At the caudal end of the pars intermedius of the superficial pretectal nucleus, a few small cells in the ventromedial part of the nucleus can be traced in serial sections accompanying fibers exiting the nucleus.

These fibers appear to correspond to the efferent projections of the intermediate portion of the superficial pretectal nucleus to nucleus glomerulosus in *Navodon* [Sakamoto and Ito, 1982]. More caudally, the



**Fig. 9.** Photomicrographs of the posterior prepectal nucleus in *Salmo* corresponding to the levels shown in figures 7D–F. Arrows indicate the border of the nucleus. Bar scale in **A** represents 200  $\mu\text{m}$  and is the same for **B** and **C**.

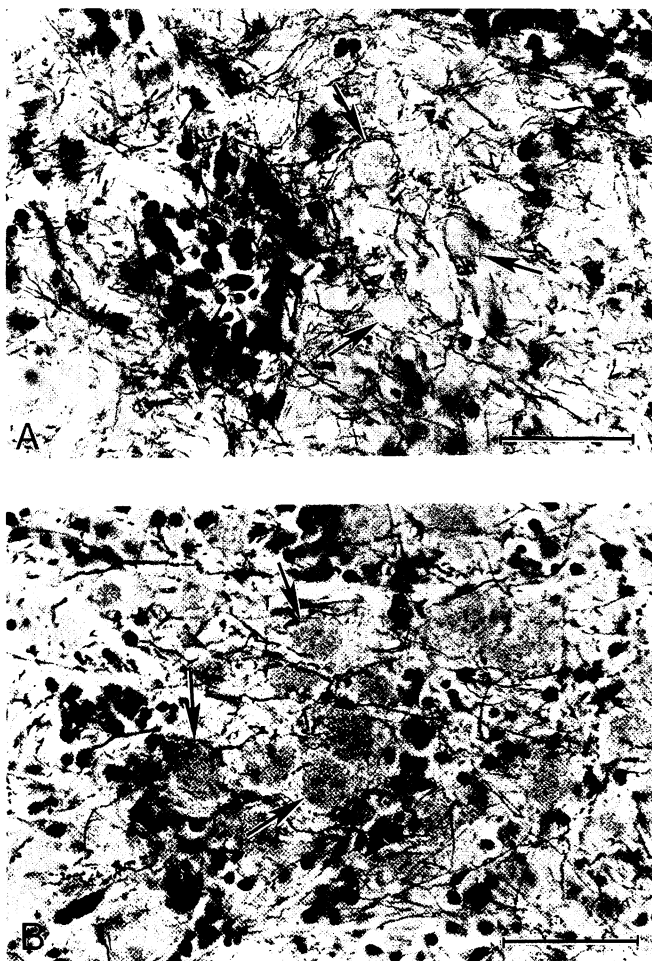


Fig. 10. Photomicrographs of glomeruli, indicated by arrows, in the posterior pretectal nucleus in *Esox* (A) and in the posterior lobe of nucleus glomerulosus in *Lepomis* (B). Bar scales represent 50  $\mu\text{m}$ .

tract, with a group of small cells on its ventromedial border, shifts medially, and at this level, a few glomeruli appear among the fibers. This is the rostral pole of the anterior lobe of nucleus glomerulosus (NGa, figs. 7H, 8E). Thus, there is actually a small transition zone present between these two nuclei. At this level, the cells of the preglomerular complex lie ventral to the anterior lobe of nucleus glomerulosus. Farther caudally, the preglomerular complex is much reduced in size and lies medial to the large posterior lobe of nucleus glomerulosus. The anterior lobe of nucleus glomerulosus merges into the dorsal aspect of the posterior lobe of nucleus glomerulosus (fig. 7I). The cells within this posterior lobe of nucleus glomerulo-

sus encircle numerous large glomeruli (fig. 10B), and centrally a fibrous core is present in the nucleus. There is a lamina of small cells around the periphery (fig. 8F).

### Discussion

The nomenclature used for pretectal nuclei related to nucleus corticalis, the posterior pretectal nucleus, and their putative homologues will be briefly considered first. The known connections and histochemistry of the pretectal nuclei analyzed here and the previous problems concerning their identification will then be considered. Thirdly, the present findings on nucleus corticalis and its distribution among teleosts will be discussed. Finally, the similarities and differences between the posterior pretectal nucleus in various teleosts on one hand and the pars intermedia of the superficial pretectal nucleus and nucleus glomerulosus in acanthopterygians on the other hand will be analyzed.

### Nomenclature

In their analysis of the organization of the diencephalon and pretectum in actinopterygian fishes, Braford and Northcutt [1983] discussed the current usage of nomenclature in relation to a number of previous studies. A more detailed comparison of terminology was later published by Northcutt and Wullimann [1988]. As the nomenclature used here is based on these latter two studies, it is beyond the scope of the present paper to undertake a detailed correlation of this nomenclature with that of previous workers. However, a brief overview of terms used for nuclei related to those described in detail here, particularly the pars parvocellularis and pars magnocellularis of nucleus pretectalis superficialis, the accessory pretectal nucleus, and the central pretectal nucleus, may be useful for orientation.

Nucleus pretectalis superficialis pars parvocellularis has previously been termed the lateral geniculate nucleus in a number of studies [e.g., Campbell and Ebbesson, 1969; Anders and Hibbard, 1974; Ito et al., 1984; Springer and Mednick, 1985a]. It has more recently been termed the pars parvocellularis of the superficial pretectal nucleus [e.g., Fernald and Shelton, 1985; Springer and Mednick, 1985b; Butler and Northcutt, 1991]. Nucleus pretectalis superficialis pars magnocellularis has previously been given a variety of



names, including nucleus rotundus [Schnitzlein, 1962], nucleus geniculatus posterior pars ventralis [Ebbesson and Vanegas, 1976], and nucleus pretectalis [Ito et al., 1981].

The accessory pretectal nucleus, a relatively cell-sparse area caudal to the pars magnocellularis of nucleus pretectalis superficialis, was first described by Wullimann and Meyer [1990]. The central pretectal nucleus [Northcutt and Butler, 1976; Braford and Northcutt, 1983; Presson et al., 1985], which lies more medially, has previously been given a variety of other names, including the P1 pretectal nucleus of Finger and Karten [1978]; nucleus pretectalis medialis [Springer and Mednick, 1985a], and pars dorsalis of area pretectalis [Vanegas and Ito, 1983].

The cytoarchitecture and the relationships of the above nuclei to each other and to nucleus corticalis, the posterior pretectal nucleus, the pars intermedius of nucleus pretectalis superficialis, and nucleus glomerulosus have been demonstrated with photomicrographs of Bodian stained, transverse sections and with line drawings in the recent paper by Wullimann and Meyer [1990].

#### *Review of Previous Findings*

Nucleus corticalis, composed of large cells arrayed across the base of the tectum, has been reported to receive retinal projections in a variety of acanthopterygians, as cited above, and also in the osteoglossomorphs *Gnathonemus* [Lázár et al., 1984] and *Pantodon* [Butler and Saidel, 1991]. The dendrites of the corticalis cells extend into the central zone of the tectum [Northcutt, 1982; Sakamoto and Ito, 1982]. Nucleus corticalis has been found to project bilaterally to nucleus glomerulosus in a percomorph [Sakamoto and Ito, 1982] and to the caudomedial portion of the posterior pretectal nucleus in an osteoglossomorph [Wullimann and Northcutt, 1989]. Cells of nucleus corticalis have also been found to be reactive for acetylcholinesterase [Wullimann and Meyer, 1990]. However, the phyletic distribution of nucleus corticalis among teleosts has remained uncertain.

The pars intermedius has been recognized as one of the divisions of the superficial pretectal nucleus in acanthopterygians, in addition to a pars parvocellularis and a pars magnocellularis [Brickner, 1929; Sakamoto and Ito, 1982; Northcutt and Wullimann, 1988; Striedter and Northcutt, 1989]. The retina projects heavily to the pars parvocellularis [e.g., Ebbesson, 1968; Repérant et al., 1976; Butler and Northcutt,

1981; Ekström, 1984; Springer and Mednick, 1985a; von Bartheld and Meyer, 1988; Northcutt and Butler, 1991], which in turn projects to the pars intermedius [Murakami et al., 1986b; Striedter and Northcutt, 1986; 1989]. The pars intermedius projects to nucleus glomerulosus in percomorphs [Sakamoto and Ito, 1982].

Northcutt and Wullimann [1988] noted the presence of large pretectal nuclei of variable size and histology, and therefore uncertain identity, in osteoglossomorphs, clupeomorphs, esocids and salmonids in regions comparable to or near that of pars intermedius in acanthopterygians. Subsequently, the findings of Wullimann and Northcutt [1989] that the pars parvocellularis in an osteoglossomorph projects to the rostrolateral part of the posterior pretectal nucleus suggested the possibility that this portion of the nucleus is homologous to the pars intermedius of the superficial pretectal nucleus of acanthopterygians.

Nucleus glomerulosus, sometimes also called nucleus rotundus, has long been recognized in advanced euteleosts [Fritsch, 1878; Franz, 1912] due to its strikingly large size and distinctive cytoarchitecture. It has an anterior lobe, elongated in the rostrocaudal plane, and a posterior lobe, much larger in diameter in transverse section and with concentrically organized laminae [Sakamoto and Ito, 1982; Wullimann, 1985]. In acanthopterygians, the caudal part of the pregglomerular complex surrounds the posterior lobe of nucleus glomerulosus. Therefore, the latter nucleus and portions of the pregglomerular complex have sometimes been confused. There is evidence that the pregglomerular complex is a separate, unrelated entity that represents a migrated group of the posterior tuberculum [Northcutt, 1981; Ehteler and Saidel, 1981; Braford and Northcutt, 1983], and subdivisions of it, unlike nucleus glomerulosus, receive ascending gustatory [Wullimann, 1988], lateral line mechanosensory [McCormick, 1989], and acousticolateral projections [Murakami et al., 1986a].

The fine structure and connections of nucleus glomerulosus have been studied with both electron and light microscopy [Ito and Kishida, 1975; 1977; Sakamoto and Ito, 1982], and the glomeruli which are present within it are formed by the axons of corticalis cells with their terminal endings and the dendritic tips of the post-synaptic neurons [Sakamoto and Ito, 1982]. Cells of nucleus glomerulosus surround the glomeruli. This nucleus also receives projections from the pars intermedius of the superficial pretectal nu-

cleus which are distributed to the small celled layer of its pars anterior and the fibrous layer of the pars posterior [Sakamoto and Ito, 1982]. Nucleus glomerulosus projects to the inferior lobe of the hypothalamus in percomorphs [Sakamoto and Ito, 1982].

The findings of Wullimann and Northcutt [1989] that the large posterior pretectal nucleus in *Osteoglossum* receives projections from both nucleus corticalis and the pars parvocellularis, as discussed above, and, further, that the posterior pretectal nucleus projects to the inferior lobe of the hypothalamus thus strongly suggest that the posterior pretectal nucleus is homologous to both the pars intermedius and nucleus glomerulosus of acanthopterygians. Lending further support to this possibility, histochemical work has shown that in a percomorph, cells and neuropil in both nucleus corticalis and the pars intermedius, as well as glomeruli in nucleus glomerulosus, are acetylcholinesterase positive and that in *Osteoglossum*, cells and neuropil in nucleus corticalis and the posterior pretectal nucleus are, likewise, acetylcholinesterase positive [Wullimann and Meyer, 1990].

The diversity of the cytoarchitecture of nuclei in teleosts in regions comparable to that of the pars intermedius, the difficulty in clearly recognizing a nucleus corticalis in various teleosts, and the absence in many teleosts of a large, morphologically typical nucleus glomerulosus precluded gaining a clear understanding of the evolution of the pretectum in teleosts until the more recent connectional [Wullimann and Northcutt, 1989] and histochemical [Wullimann and Meyer, 1990] work was done. In light of findings that sets of nuclei in both osteoglossomorphs and acanthopterygians have similarities of connections, histochemistry, and approximate location but seemingly marked differences in cytoarchitectonics and size, we felt it worthwhile to reexamine in detail the cytoarchitecture of the previously noted nuclei in other radiations of teleosts.

#### *Nucleus Corticalis*

Nucleus corticalis forms a clearly recognizable, large, discrete cell plate across the base of the rostral part of the tectum in advanced euteleosts (paracanthopterygians and acanthopterygians), such as *Lepomis*. Similar plates of large cells at the base of the rostral tectum have also been seen in *Osteoglossum* and in the elopomorph *Elops* [Northcutt and Wullimann, 1988]. We believe that the prominent nucleus of large cells in *Elops* is not nucleus corticalis but

rather the mesencephalic nucleus of the trigeminal nerve for several reasons. It is situated in the periventricular gray layer of the tectum. Its cells have a characteristic tear-drop shape with the enlarged ends oriented toward the ventricle. The nuclei in its cells are eccentric and tend to be oriented in the ends of the cells toward the ventricular surface. A location in the periventricular gray zone of the tectum and cells which are unipolar are two of the characteristics of the mesencephalic nucleus of the trigeminal nerve in a wide variety of vertebrate species noted by Ariëns Kappers et al. [1967]. They illustrate large, tear-drop shaped cells in this nucleus in fishes, amphibians, reptiles, and mammals.

In contrast, the large cell plate present in *Osteoglossum* and the smaller but distinct cell plate in *Pantodon* are situated in a region continuous with the central tectal zone, have randomly oriented, multipolar cells, and have eccentric nuclei in the cells which do not show a preferential orientation toward the ventricle. Furthermore, a small mesencephalic nucleus of the trigeminal nerve can be recognized in these two fishes farther caudally. Nucleus corticalis of paracanthopterygians and acanthopterygians also meets most of our criteria for identifying it. In *Lepomis*, the cells are more rounded in shape, and in some percomorphs, such as balistids, nucleus corticalis is so large that it may extend beyond the area continuous with the central tectal zone and thus invade a portion of the periventricular zone. The mesencephalic nucleus of the trigeminal nerve, on the other hand, has never been observed to extend into the area continuous with the central tectal zone. We thus believe that the cell plates observed in *Osteoglossum* and *Pantodon* are nucleus corticalis, as previous work has indicated [Northcutt and Wullimann, 1988; Wullimann and Northcutt, 1989].

The same criteria were used in evaluating the presence or absence of a nucleus corticalis in the other fish examined. The clupeomorph *Clupea* has the most discrete corticalis cell plate of these other species, but it is relatively small and compact in comparison to the nucleus corticalis in *Osteoglossum* and *Lepomis*. More diffuse scattering of the large nucleus corticalis cells over a greater area occurs in the clupeomorph *Brevoortia*. The presence of this nucleus in the elopomorphs *Elops* and *Anguilla* remains questionable. No corticalis cell plate is present in the two primitive euteleosts studied – *Esox* and *Salmo*.

Pinganaud and Clairambault [1979] discussed the

difficulty of identifying a nucleus corticalis in *Salmo irideus* on the basis of topography or cytoarchitecture; they tentatively identified a possible candidate for nucleus corticalis in the caudal pretectum on the basis of a retinal projection to the area visualized with autoradiography. This area appears to correspond to the caudal part of the subsequently described central pretectal nucleus [Braford and Northcutt, 1983] or to the caudal continuation of the accessory optic tract [Northcutt and Butler, 1991]. It is certainly much farther caudal than the site of nucleus corticalis in other species studied. Our observations in *Clupea* that some of the cells of nucleus corticalis are not confined to the cell plate but are scattered dorsal to it within, rather than next to, the central tectal zone suggests that scattered large neurons in the ventrolateral quadrant of the central tectal zone in *Esox* and *Salmo* comprise a homologue of nucleus corticalis in these teleosts. Bazer and Ebbesson [1987] noted this possibility in the esocid *Esox niger*. The presence of glomeruli in the posterior pretectal nucleus in *Esox* (fig. 10A) strongly supports the contention that cells homologous to nucleus corticalis are present in this species, as the glomeruli in nucleus glomerulosus in acanthopterygians are formed by corticalis axons [Sakamoto and Ito, 1982], as discussed above.

The cytoarchitecture of nucleus corticalis is thus quite variable among different teleosts. We can, however, make several conclusions concerning it. Nucleus corticalis is present in various species in three of the four major teleost radiations, i.e., in *Osteoglossum* and *Pantodon* among osteoglossomorphs, in both clupeomorphs examined, and in advanced euteleosts. Its presence in elopomorphs is open to question. Only a few corticalis-like cells are present in *Elops*; loosely scattered cells dorsal to the central pretectal nucleus in *Anguilla* are negative for acetylcholinesterase [Wullimann, unpublished observations], in contrast to the presence of AChE in nucleus corticalis in other fishes studied [Wullimann and Meyer, 1990]. Cells homologous to nucleus corticalis appear to be present in the primitive euteleosts – esocids and salmonids – albeit not in the form of a discrete cell plate.

Among ostariophysans, the presence of a nucleus corticalis is still a matter of dispute. Braford and Northcutt [1983] found that nucleus corticalis is absent in the goldfish *Carassius auratus*, as did Northcutt and Wullimann [1988] and Wullimann and Meyer [1990], although Sharma [1972] and Springer and Gaffney [1981] have previously claimed its presence in

this species based on experimentally determined retinofugal projections but disregarding histological appearance. Its presence has been noted in some other ostariophysans [e.g., Ebbesson and Ito, 1980; Sas and Maler, 1986], including one siluriform, the catfish *Ictalurus* [Prasada Rao and Sharma, 1982]. However, Striedter [1990] has not found it to be present in *Ictalurus*. The ostariophysans may represent a special situation, as they appear to have undergone a period of reduced vision during their evolution [Northcutt and Wullimann, 1988].

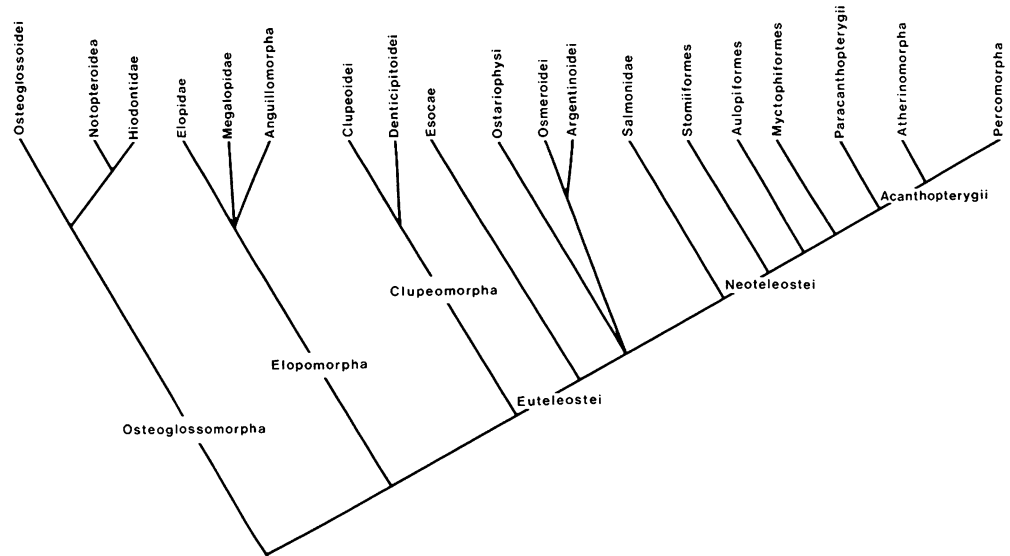
On the basis of its distribution, we can conclude that the presence of a nucleus corticalis is a plesiomorphic condition of teleosts. Its loss or reduction, as in elopomorphs and some ostariophysans, would thus be apomorphic. Nucleus corticalis forms a cell plate, albeit of varying degrees of compactness. Such a plate can be seen in *Osteoglossum*, *Pantodon*, *Clupea*, *Brevoortia*, some ostariophysans, and *Lepomis*, representing three of the four major teleost radiations (fig. 11). The scattered cells in the restricted portion of the central tectal zone in *Esox* and *Salmo*, which we believe represent cells homologous to nucleus corticalis, thus appear to be an apomorphy and possibly represent a neotenic condition. This possibility is based on (1) the observation that the dendrites of corticalis neurons ramify within the central tectal zone [Northcutt, 1982; Sakamoto and Ito, 1982] and may thus represent a subpopulation of migrated tectal neurons and (2) the condition in *Clupea* of some corticalis neurons positioned dorsal to rather than within the nucleus corticalis cell plate which could represent an intermediate condition for this grade of organization.

*Posterior Pretectal Nucleus, Nucleus Pretectalis Superficialis Pars Intermedius, and Nucleus Glomerulosus*

One of the persistent problems in studying nucleus glomerulosus has been the pitfall of confusing it with portions of the preglomerular complex. This problem has been reviewed in detail by Braford and Northcutt [1983] and by Northcutt and Wullimann [1988], so it will only be considered briefly here. Another problem has been that the existence of nucleus glomerulosus in various orders of teleosts has been questionable, as outside of paracanthopterygians and acanthopterygians possible homologues of nucleus glomerulosus show significant differences in cytoarchitectonics and position.

In paracanthopterygians and acanthopterygians,

Nuclei Present	PO	-	PO	PO	PO	PO	PO	PO/-	PO	PSi & NG
Ventromedial to PSm Rostrally	+		+	+	+	+	+	+	+	+ +
Dorsal to Preglomerular Complex	+		+	+	+	+	+	+	+	- -
Medium + Small Cells	+		+	+	+/-	+	-	+	+	- +
Irregular Cell Distribution	+/-		+	-	+	+	-	+	+	+ -
Cell Clusters	+		+	-	+	+	-	+	+	- +
Glomeruli	-		-	-	-	+	-	-	-	- +
Nucleus/ei Size: Large (L), Small (S)	L	L	S	S	L/S	L	S/-	L	L	L L
NC Cells: Plate (P), in Tectum (T)	P		?	?	P/(T)	T	P/-	T	T	P



**Fig. 11.** Dendrogram modified from Lauder and Liem [1983] of teleost phylogeny and table showing distribution of characters of the posterior pretectal nucleus (PO) in non-neoteleosts in the first eight lines and the distribution of a cell plate of nucleus corticalis versus the presence of putative nucleus corticalis cells in the tectum in the last line. Characters given in the two columns for Percomorpha in the first eight lines are for the pars intermedius of nucleus superficialis pretectalis (PSi) and nucleus glomerulosus (NG). In all columns, '+' indicates the presence of the feature, and '-' indicates that the feature was not observable. Data in this table are primarily from the present findings and additionally from Wullmann [unpublished observations] in Notopteroideae and Hiodontidae, from Braford and Northcutt [1983], Northcutt and Wullmann [1988], Striedter [1990], Wullmann and Meyer [1990], and Wullmann [unpublished observations] regarding the posterior pretectal nucleus in Ostariophysi, and from the above references and other authors including Ebbesson and Ito [1980] and Sas and Maler [1986] regarding nucleus corticalis in Ostariophysi.

the caudal portions of the preglomerular complex surround a substantial portion of the posterior lobe of nucleus glomerulosus. The latter can be recognized by its unique cytoarchitecture [Ito and Kishida, 1975, 1977; Sakamoto and Ito, 1982], however. In the present study, it was found that in all non-neoteleosts examined, while the caudal pole of the posterior pretectal nucleus (the putative homologue of nucleus glomerulosus) is in some cases near the preglomerular complex, the two nuclei are never difficult to distinguish. The posterior pretectal nucleus is dorsal to

the preglomerular complex in all these cases (figs. 3, 7A-F). Thus, while the caudal pole of the posterior pretectal nucleus is of varying morphology, it cannot be confused with the preglomerular complex which is easily identified by following it caudally from its distinctive, lateroventrally situated rostral pole in the rostral diencephalon.

While the study of the cytoarchitecture of the posterior pretectal nucleus in teleosts revealed marked variations, some common features were also identified which are diagnostic for this nucleus across spe-

cies. The posterior prepectal nucleus is present in most non-neoteleosts studied to date. This distribution indicates that it is plesiomorphic for teleosts. Where present in non-neoteleosts, the posterior prepectal nucleus appears to be a single nucleus. Its rostral part lies ventromedial or ventral to the pars magnocellularis of the superficial prepectal nucleus. Throughout its extent, this nucleus lies dorsal to the preglomerular complex and is clearly distinguishable from it. The nucleus contains cells ranging in size from small to medium in all species except for the ostariophysan *Carassius* and the clupeomorph *Brevoortia*, in which the posterior prepectal nucleus contains only small cells. In most species the distribution of cells within the nucleus is variable; often a higher density of cells is present in the medial part of the nucleus than in the lateral part through its rostral and middle levels. This variable cell distribution is present in the osteoglossomorph *Pantodon*, although in *Osteoglossum*, the distribution is much more uniform. It is also uniform in *Carassius* and *Anguilla*, where the nucleus is very small and contains very few cells. Regardless of cell distribution within the nucleus, many of the cells are arranged in clusters within the neuropil of the nucleus, the only exception to this being in the small posterior prepectal nucleus in *Carassius* and *Anguilla*. In all non-neoteleosts except the pike *Esox*, the nucleus does not appear to contain glomeruli, although electron microscopic studies are needed to check this observation. The size of the nucleus relative to the rest of the diencephalon is variable. Among osteoglossomorphs, it is very large in *Osteoglossum* and *Pantodon*. It is also large in *Hiodon* but appears to be absent in notopterids [Wullimann, unpublished observations]. In elopomorphs and in the clupeomorph *Brevoortia*, the posterior prepectal nucleus is small. It is also small or absent in various ostariophysans [Northcutt and Wullimann, 1988; Wullimann and Meyer, 1990; Striedter, 1990]. However, in the clupeomorph *Clupea* and in *Esox* and *Salmo*, the posterior prepectal nucleus is large.

From the distribution of these identified features among the species examined, we conclude that those features which are plesiomorphic for the posterior prepectal nucleus in teleosts are (1) its being a single nucleus, (2) location of the rostral part of the nucleus ventromedial to nucleus superficialis prepectalis pars magnocellularis, (3) location of the entire nucleus dorsal to the preglomerular complex, (4) the presence of a range of cell sizes, (5) a variable distribution of

cells within the nucleus, with a greater number of cells in the more medial part of the nucleus at its rostral and middle levels, (6) the aggregation of the cells into clusters, and (7) an absence of glomeruli. Whether the plesiomorphic condition of the nucleus is large or small in size cannot be determined from the present data, as it is both large and small within two major radiations (osteoglossomorphs and clupeomorphs), small in another (elopomorphs) and large in the majority of species examined in the fourth (including nucleus glomerulosus in advanced euteleosts). The distribution of the presence or absence of the above features of the posterior prepectal nucleus in teleosts is summarized in figure 11. The posterior prepectal nucleus has also been found to be AChE positive in the two divergent species studied to date – *Osteoglossum* and *Carassius* [Wullimann and Meyer, 1990] – and this feature may thus also be plesiomorphic. Among clearly apomorphic features are the uniformity of cell distribution throughout the posterior prepectal nucleus in *Osteoglossum*, the larger than usual population of medium sized cells in this nucleus in the osteoglossomorph *Pantodon*, the absence of medium sized cells in the nucleus in *Carassius* and the clupeomorph *Brevoortia*, and the presence of glomeruli in the nucleus in the pike *Esox*. The absence of a posterior prepectal nucleus in the silurid *Ictalurus* [Striedter, 1990] and in notopterids is also an apomorphy.

Of the above features of the posterior prepectal nucleus, several can be used as defining characteristics. The location of the nucleus ventromedial to nucleus prepectalis superficialis pars magnocellularis and dorsal to the preglomerular complex is very constant. The presence of a range of cell sizes and an uneven distribution of the cells within the nucleus are also frequently observed features. Aggregation of the cells into small clusters is diagnostic. In addition to these features, hodological studies demonstrating afferent projections from nucleus prepectalis superficialis pars parvocellularis and nucleus corticalis, efferent projections to the inferior lobe of the hypothalamus, and strong AChE reactivity would also be diagnostic.

An examination of the pars intermedius of the superficial prepectal nucleus and nucleus glomerulosus in the perciform *Lepomis*, and in other acanthopterygians studied to date [Sakamoto and Ito, 1982; Northcutt and Wullimann, 1988; Wullimann and Meyer, 1990], with regard to the identified features of the posterior prepectal nucleus reveals both differences and similarities (fig. 11). The pars intermedius

of the superficial pretectal nucleus and nucleus glomerulosus are two separate nuclei with distinctively different histology, albeit that there is a small transition zone of small cells which continue with a fiber tract between them. Similar to the rostral part of the posterior pretectal nucleus, the pars intermedius lies ventromedial to the pars magnocellularis of the superficial pretectal nucleus. In contrast to the posterior pretectal nucleus, the posterior lobe of nucleus glomerulosus is so expanded caudally that part of it is surrounded by the preglomerular complex. Similar to the posterior pretectal nucleus, there is a range of cell sizes in both the pars intermedius and nucleus glomerulosus, and within the pars intermedius, the cells are unevenly distributed, the greater density of cells being within its medial portion. In *Lepomis*, the cells within nucleus glomerulosus form clusters. Whereas the posterior pretectal nucleus does not appear from light microscopic observations, except in *Esox*, to contain glomeruli, the hallmark of nucleus glomerulosus is that it does so in profusion. The presence of glomeruli in the posterior pretectal nucleus in *Esox* raises the question as to whether glomeruli are a plesiomorphic feature of the posterior pretectal nucleus/nucleus glomerulosus in euteleosts. Discrete, identifiable glomeruli could not be found in our material in the large posterior pretectal nucleus in *Salmo* nor in the small posterior pretectal nucleus in *Carassius*. Electron microscopic studies need to be done, and additional neoteleosts, ostariophysans, osmeroids and argentinoids need to be examined to resolve this question. As regards size, the pars intermedius of the superficial pretectal nucleus and particularly nucleus glomerulosus are very large in acanthopterygians, as is the posterior pretectal nucleus in some osteoglossomorphs, some clupeomorphs, and in esocids and salmonids.

In conclusion, the number of cytoarchitectonic features which the pars intermedius of the superficial pretectal nucleus and nucleus glomerulosus together have in common with the posterior pretectal nucleus lend strong support to the hypothesis, based on similarities of connections and histochemistry [Sakamoto and Ito, 1982; Wullimann and Northcutt, 1988; Wullimann and Meyer, 1990], that the posterior pretectal nucleus is homologous to both the pars intermedius and nucleus glomerulosus. The presence of a posterior pretectal nucleus is plesiomorphic for teleosts. The presence of two distinct nuclei, the pars intermedius and nucleus glomerulosus, is apomorphic in

acanthopterygians, and perhaps even in neoteleosts. A number of features of the posterior pretectal nucleus can be recognized as plesiomorphic and used in characterizing and identifying the nucleus in various extant species. Nucleus corticalis, which projects to the posterior pretectal nucleus and to nucleus glomerulosus, is also plesiomorphic for teleosts. Whether the ramifications of the axons of corticalis neurons within the posterior pretectal nucleus/nucleus glomerulosus were modified to form glomeruli in ancestral euteleosts or were independently modified in esocids and acanthopterygians still remains to be determined.

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