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## Connections of the Corpus Cerebelli in the Green Sunfish and the Common Goldfish: A Comparison of Perciform and Cypriniform Teleosts

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**Key Words.** Cerebellar afferents · Cerebellar efferents · Fish · Phyletic analysis · Evolution

**Abstract.** Examination of the connections of the corpus cerebelli in one perciform (*Lepomis cyanellus*) and one cypriniform teleost (*Carassius auratus*) reveal that ipsilateral afferent connections in both species arise from an anterior group of nuclei in the diencephalon and mesencephalon, and a posterior group of nuclei in the rhombencephalon. Some nuclei of the anterior group and all those of the posterior group have in addition a weaker, and the medial octavolateralis nucleus a stronger, contralateral component. The inferior olivary nucleus in both species projects solely contralaterally. Nucleus paracommissuralis, the ventral accessory optic nucleus and nucleus isthmi are minute in *Carassius* compared to *Lepomis*. The latter species has in addition a bilateral corpopetal projection (ipsilaterally stronger) from the lateral cuneate nucleus. Efferent fibers in both species reach the contralateral nucleus ruber, oculomotor nucleus, nucleus of the medial longitudinal fasciculus, torus semicircularis, ventromedial and ventrolateral thalamic nuclei, optic tectum and superior and inferior reticular formation. An additional weaker ipsilateral terminal field could be observed in all nuclei except in the ventrolateral and ventromedial thalamic nuclei, the dorsal periventricular pretectal nucleus and the optic tectum. *Lepomis* in addition has a bilateral terminal field in the ventral accessory optic nucleus (contralaterally stronger). In both species, stronger ipsilateral and weaker contralateral terminal fields were present in the torus longitudinalis and the valvula cerebelli. The two patterns of corpopetal connections in *Lepomis* and *Carassius* were used as models for perciforms and cypriniforms in the analysis of the existing information in the literature on teleosts. While most discrepancies in the literature on percomorphs and ostariophysines could be interpreted consistently, the available information on mormyrids revealed a very different pattern of corpopetal organization: presence of additional connections (from a division of the nucleus preglomerulosus) and absence of otherwise well-established corpopetal connections in teleosts. In a second step, a phyletic analysis of teleostean corpopetal organization revealed that while teleosts share with all other vertebrates a group of corpopetal connections from the rhombencephalon, they evolved many new, more anteriorly located afferent inputs to the corpus cerebelli. Furthermore, electroreceptive mormyrids in addition evolved newly at least one corpopetal connection and lost many others.

### Introduction

Comparative vertebrate neuroanatomists seek to understand the evolutionary history of morphological variation in the nervous system. Ray-finned fishes (actinopterygians), the overwhelming majority of which are teleosts, comprise close to 30,000 species – more than half of all vertebrates – and show unparalleled diversity in the development of the cerebellum

[Ariens Kappers et al., 1936; Larsell, 1967; Nieuwenhuys, 1967; Kuhlenbeck, 1975]. In spite of this variation, there have been few experimental investigations of the cerebellar connections in teleosts [Finger, 1978a, b; Ito et al., 1982; Meek et al., 1986a, b], and the majority of these have focused exclusively on electrosensory teleosts. For example, both ictalurids [Finger, 1978a, b] and the weakly electric mormyrids [Meek et al., 1986a, b] are electroreceptive. Some of

their cerebellar connections, therefore, may be autapomorphic, i.e. they may represent uniquely derived characters for electroreceptive teleosts. In order to document and understand the existing morphological variation, and recognize different patterns of cerebellar organization, *some* nonelectrosensory teleosts must be examined. Only then will it be possible to determine which connections are derived (apomorphic) and which are primitive (plesiomorphic) for teleosts, i.e. to determine the evolutionary polarity of different features of cerebellar connectivity in teleosts and in turn in all vertebrates. Such analysis requires the application of cladistic methodology [Northcutt, 1984, 1985, 1986; Northcutt and Wullimann, 1988].

Three main approaches or strategies have been used in studying brain evolution: opportunistic, modeling, and phyletic analysis [Northcutt, 1986]. These approaches, each with specific advantages and disadvantages, need not be mutually exclusive, but, rather, can be applied complementarily. Thus, the present paper comprises two parts. The first part describes two patterns of cerebellar connectivity based on experimental information, one for *Lepomis cyanellus* (Perciformes, Percormorpha) and one for *Carassius auratus* (Cypriniformes, Ostariophysinae). We chose these two species for investigation because a great deal of information is available on the extracerebellar neuronal circuitry both in percormorphs and in ostariophysines [Wullimann, 1985; Northcutt and Wullimann, 1988]. The two connectivity patterns will then be used as models for perciform and cypriniform cerebellar organization in analyzing the existing literature. The second part of the paper constitutes a phyletic analysis, i.e. is an interpretation of the evolutionary polarity of the recognized anatomical patterns.

The existing confusion regarding teleostean cerebellar afferent connections arising in the diencephalon (including the accessory optic system) and pretectum [for a review, see Wullimann, 1985] illustrates the necessity of this two-step approach. Varying numbers of retino- and tectorecipient cell groups in this region have been reported to project to the cerebellum in various species of different teleost clades [Karten and Finger, 1976; Finger, 1978a; Finger and Karten, 1978; Luiten, 1981; Grover and Sharma, 1981; Ito et al., 1982]. In the modeling part of this study we attempt to clarify the patterns of anatomical connections between these visually related nuclei and the cerebellum in perciform and in cypriniform teleosts and to provide a basis for deciding which differences in the liter-

ature are due to methodology or interpretation and which are real species differences. In the second step, this information will be used to analyze patterns of cerebellar organization in ray-finned fishes and – as far as possible – in other vertebrates.

The cerebellum of actinopterygians is generally considered to comprise three main subdivisions: (1) a vestibulolateral lobe (including a medial caudal lobe and the paired, lateral eminentiae granulares), (2) a corpus cerebelli and (3) a valvula cerebelli. This last division is an autapomorphy for ray-finned fishes, and a second paper reporting its connections is in preparation. The present paper is exclusively concerned with the afferent and efferent connections of the cerebellar corpus. One abstract reporting the afferent connections of the corpus in *Lepomis*, and one reporting the afferent connections of the valvula in *Carassius* have appeared previously [Wullimann and Northcutt, 1985; Wullimann and Northcutt, in press].

Unless otherwise indicated, the neuronanatomical nomenclature follows Braford and Northcutt [1983] and Northcutt and Wullimann [1988].

## Materials and Methods

### Animals

Green sunfish, *L. cyanellus* (standard length: 5–10 cm) and common goldfish, *C. auratus* (standard length: 6–15 cm), were obtained from local dealers. Animals were kept in filtered group tanks at temperatures of 22–24°C and fed twice a week.

### Experimental Procedures

Before surgery, the animals were anesthetized in a dilute solution of MS222 (tricaine methanesulfonate, Sigma). In *Lepomis*, a midsagittal incision into the most rostral epaxial musculature was made and the cranium above the corpus cerebelli removed using a dental drill. In *Carassius*, a unilateral hemispherical incision through the skin and cranium was drilled. The resulting skin-bone flap was folded back towards the opposite body side with forceps. Although the roof of the cranium was broken, the skin above it remained intact. Absorbent tissue (Kimwipes) was used to remove suprameningeal fat tissue above the corpus cerebelli. Care was taken not to damage blood vessels in this process. Horseradish peroxidase (HRP, Sigma VI) paste was applied uni- or bilaterally to the cerebellar corpus with insect pins (size 000) (*Lepomis*: 20 cases, *Carassius*: 8 cases). Saline-soaked gelfoam (Upjohn) was placed on the brain and the skin-bone flap folded back over the wound and closed with histoacryl (Braun Melsungen, FRG) in the case of *Carassius*; in *Lepomis* the musculature and skin were sutured and also closed with histoacryl. Tetracycline (1 mg/100 g body weight) was injected intraperitoneally before the animals were revived and isolated in plastic containers within the home tank.

After survival times of 2–9 days, the animals were reanesthetized with MS222 and perfused transcardially with cold 0.04 M

phosphate buffer (pH 7.4), followed by 4% glutaraldehyde in phosphate buffer. The brains were removed, postfixed for 1 h in the same fixative plus 30% sucrose, embedded in a gelatin(10%)-sucrose(30%) medium and again postfixed for 4 h in fixative-sucrose before being frozen sectioned at 35  $\mu$ m in the transverse plane. Subsequently, sections were reacted according to the Hanker-Yates protocol [Hanker et al., 1977], or processed with the tetramethyl benzidine method of Mesulam [1978] or the heavy-metal intensified diaminobenzidine method [Adams, 1981] and mounted on chrome-alum-coated slides. Sections were then counterstained with either a 0.5% cresyl violet or 1% methyl green solution.

#### Normal Anatomy

For normal series (including specimens used in table I), animals of both species were anesthetized with MS222 and perfused with 0.04 M cold phosphate buffer followed by AFA (90 ml 80% ethanol, 5 ml formalin, 5 ml glacial acetic acid). The brains were removed from the skull and postfixed for at least 1 month in AFA before they were embedded in paraffin and cut transversely at 15  $\mu$ m. The mounted sections were then reacted with Bodian silver and counterstained with cresyl violet.

## Results

### Gross Morphology

The three parts traditionally recognized in the cerebellum of actinopterygians – vestibulolateral lobe, corpus, and valvula cerebelli – are present to a varying extent in both species (fig. 1) investigated. The vestibulolateral lobe includes the paired eminentiae granulares and the transverse plate (or caudal lobe), which borders the rhomboid fossa rostrally. The caudal lobe includes, from ventral to dorsal, paired periventricular granular cell masses [called auricles in much of the older literature, see Larsell, 1967] and their interconnecting granular cell band, a fibromolecular layer above it, and a layer of granule cells that interconnects medially the granular cell masses of the eminentiae granulares.

The corpus cerebelli, superficially delimited from the caudal lobe by the posterolateral fissure (fig. 1A), is centrally a dorsocaudal extension of the median granular mass of the caudal lobe, surrounded by a molecular layer. Similarly, the valvula cerebelli arises as a rostral continuation of the caudal lobe, protruding into the tectal ventricle. The cerebellar valvula displays complex folding in *L. cyanellus*, especially in its lateral part (fig. 2–4), whereas in *Carassius* it is separated by a longitudinal fissure into a medial and a lateral part (fig. 5–7). The granular and molecular masses of all three cerebellar subdivisions are continuous, with the exception of the periventricular granu-

**Table I.** Suspected distribution of two corporeal nuclei in teleosts based on normal histological material

	NI	NP
Osteoglossomorpha		
<i>Osteoglossum bicirrhosum</i>	+	–
Elopomorpha		
<i>Elops saurus</i>	+	–
Clupeomorpha		
<i>Clupea harengus</i>	+	–
Euteleostei		
Esocae		
<i>Esox lucius</i>	+	–
<i>Umbra limi</i>	+	–
Ostariophysi		
Cypriniformes		
<i>Carassius auratus</i>	(+)	(+)
Characiformes		
<i>Crenuchus spilurus</i>	+	+
<i>Serrasalmus nattereri</i>	+	+
Siluriformes		
<i>Ictalurus melas</i>	–	+
<i>Sorubim lima</i>	–	+
Salmonidae		
<i>Salmo gairdneri</i>	+	–
Atherinomorpha		
<i>Strongylura notata</i>	+	–
<i>Leurestes tenuis</i>	+	–
Percomorpha		
<i>Lepomis cyanellus</i>	+	+
<i>Toxotes jaculatrix</i>	+	+
<i>Balistoides conspicillum</i>	+	+

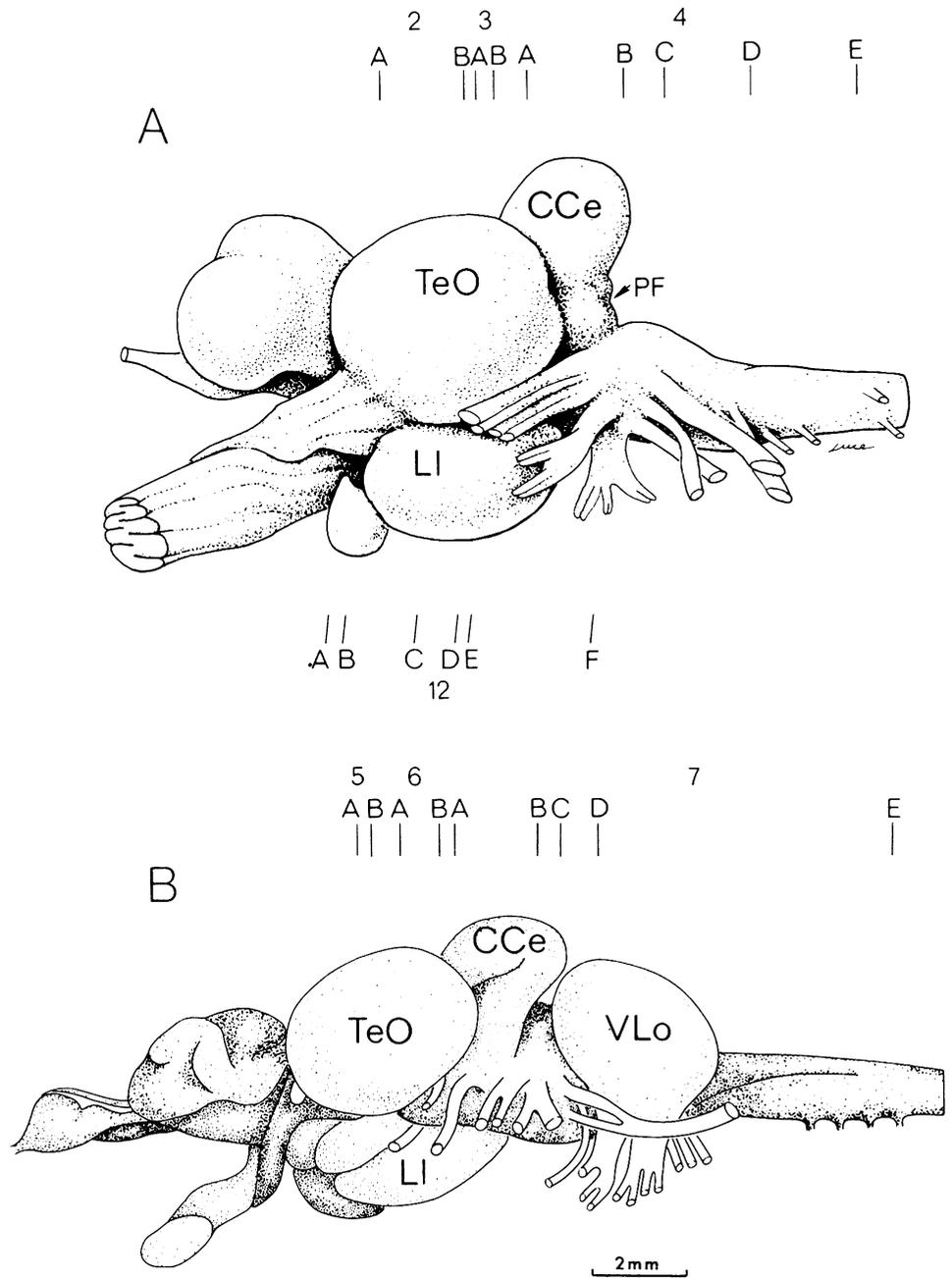
+ = Big nucleus; (+) = minute nucleus; – = nucleus not observable.

lar cell masses and their interconnecting granular cell band.

The morphological position of the corpus cerebelli requires brief clarification. In both *Lepomis* and *Carassius* the dorsal tip of the corpus is bent caudally (fig. 1), resulting in a morphological distortion: the dorsal surface of the corpus actually corresponds to its topologically rostral surface, the caudal tip of the corpus to its topologically dorsal surface and the ventral part of the corpus to its topologically caudal part.

*List of abbreviations*

A	Nucleus anterior thalami	NGa	Nucleus glomerulosus pars anterior
AC	Anterior cerebellar tract	NGp	Nucleus glomerulosus pars posterior
BC	Brachium conjunctivum	NGS	Nucleus gustatorius secundarius
CC	Crista cerebellaris	NI	Nucleus isthmi
CCa	Central canal	NIIn	Nucleus interpeduncularis
CCe	Corpus cerebelli	NLV	Nucleus lateralis valvulae
CH	Commissura horizontalis	NMF	Nucleus motorius nervi facialis
CM	Corpus mamillare	NMT	Nucleus motorius nervi trigemini
CN	Lateral cuneate nucleus	NMV	Nucleus motorius nervi vagi
CP	Nucleus centralis posterior thalami	NOc	Nucleus nervi oculomotorius
CPN	Nucleus pretectalis centralis	NP	Nucleus paracommissuralis
CPo	Commissura posterior	NPG	Nucleus pregglomerulosus
CW	Commissure of Wallenberg	NPLI	Nucleus periventricularis recessus lateralis of the inferior lobe
DH	Dorsal horn of spinal cord	NR	Nucleus ruber
DMON	Decussation of the octavolateralis area	NRL	Nucleus reticularis lateralis
DO	Nucleus octavus descendens	NTr	Nucleus nervi trochlearis
DP	Nucleus dorsalis posterior thalami	ON	Nervus opticus
DT	Nucleus tegmentalis dorsalis	PE	Nucleus praeemientialis
DTr	Descending trigeminal tract	PF	Posterolateral fissure
EG	Eminentia granularis	PG	Periventricular granular cell mass of the caudal lobe
EW	Perinuclear neurons of the nucleus of Edinger-Westphal	PGI	Preglomerular complex
FLL	Fasciculus longitudinalis lateralis	PL	Nucleus perilemmisularis
FLM	Fasciculus longitudinalis medialis	PPd	Nucleus pretectalis periventricularis pars dorsalis
FLo	Facial lobe	PPv	Nucleus pretectalis periventricularis pars ventralis
FR	Fasciculus retroflexus	PSm	Nucleus pretectalis superficialis pars magnocellularis
G	Granular layer of cerebellum	s	Sensory root of nervus facialis
GLo	Glossopharyngeal lobe	SC	Spinal cord
H	Habenula	sg	Sensory root of nervus glossopharyngeus
Hc	Hypothalamus ventralis, pars caudalis	SR	Superior raphe
Hy	Hypophysis	SRF	Superior reticular formation
I	Nucleus intermedius thalami	STN	Isthmic sensory trigeminal nucleus
IO	Inferior olive	TA	Nucleus tuberos anterior
IR	Inferior raphe	Tel	Telencephalon
IRF	Inferior reticular formation	TeO	Tectum opticum
LC	Nucleus of the locus coeruleus	TGL	Tractus gomerulolobaris
LFB	Lateral forebrain bundle	TGS	Tractus gustatorius secundarius
LH	Nucleus lateralis hypothalami	TL	Torus longitudinalis
LI	Lobus inferior hypothalami	TLa	Nucleus of the torus lateralis
M	Molecular layer of cerebellum	TMCa	Tractus mesencephalocerebellaris anterior
MF	Nucleus funicularis medialis	TMCP	Tractus mesencephalocerebellaris posterior
MON	Nucleus octavolateralis medialis	TO	Tractus opticus
NAOD	Nucleus accessorius opticus dorsalis	TPI	Tractus pretectoisthmicus
NAOV	Nucleus accessorius opticus ventralis	TS	Torus semicircularis
NC	Nucleus corticalis	TTB	Tractus tectobulbaris
NCLI	Nucleus centralis of the inferior lobe	Va	Valvula cerebelli
NCW	Nucleus of the commissure of Wallenberg	VH	Ventral horn of spinal cord
NDLc	Nucleus diffusus of the inferior lobe, pars caudalis	VL	Nucleus ventrolateralis thalami
NDLl	Nucleus diffusus of the inferior lobe, pars lateralis	VLo	Vagal lobe
NDLm	Nucleus diffusus of the inferior lobe, pars medialis	VM	Nucleus ventromedialis thalami
NDT	Nucleus of the descending trigeminal tract	VT	Nucleus tegmentalis ventralis
NeV	Nervus vagus		
NF	Nucleus of the fasciculus longitudinalis medialis		



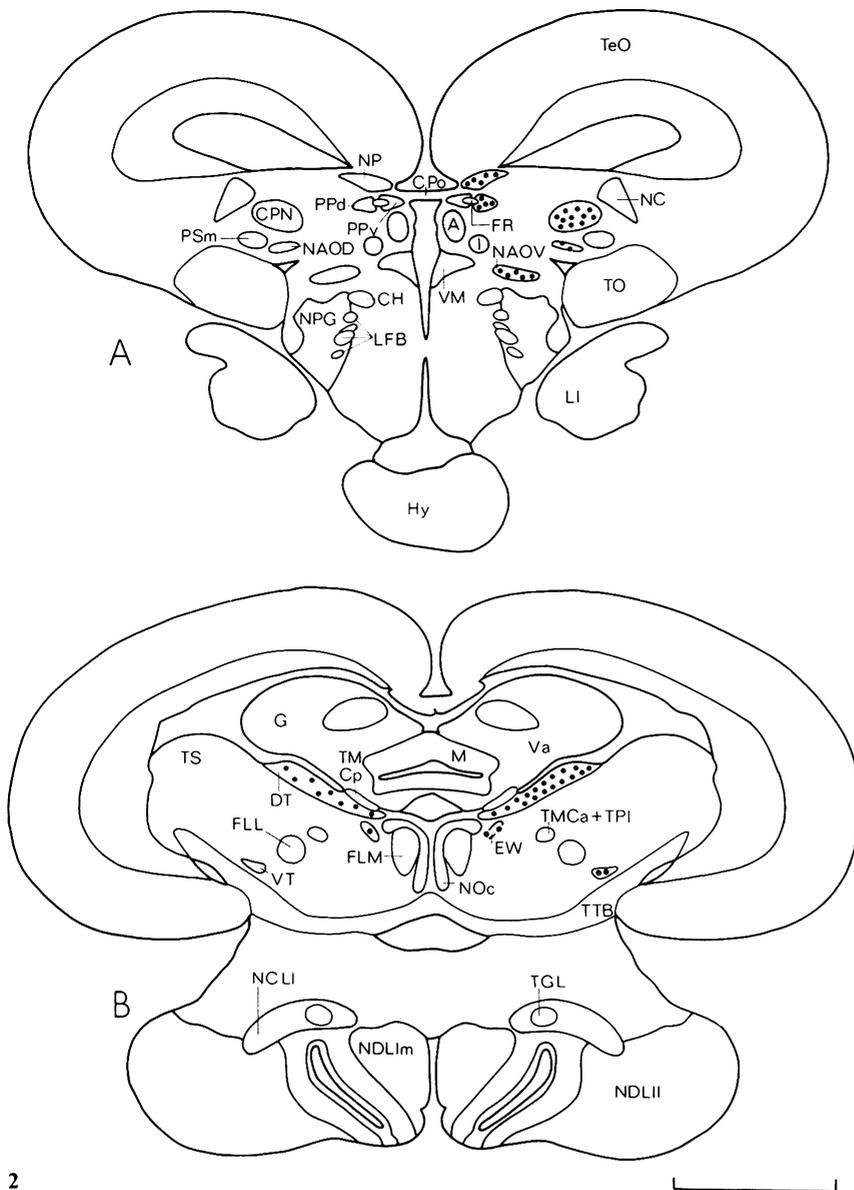
**Fig. 1.** Brains of *L. cyanellus* (A) and *C. auratus* (B) in lateral view. Levels of charted afferent (fig. 2-7) and efferent (fig. 12) connections of the corpus cerebelli are indicated.

Consequently, although our HRP injections cover all parts of the cerebellar corpus in the rostrocaudal axis, these injections were positioned mainly in the topologically rostral and dorsal part, and to a lesser degree in the topologically caudal part of the corpus. To avoid confusion we will refer to positions within the cerebellar corpus conventionally with respect to the

rest of the brain and - when necessary - refer to the topologically correct locations.

*Afferent Connections*

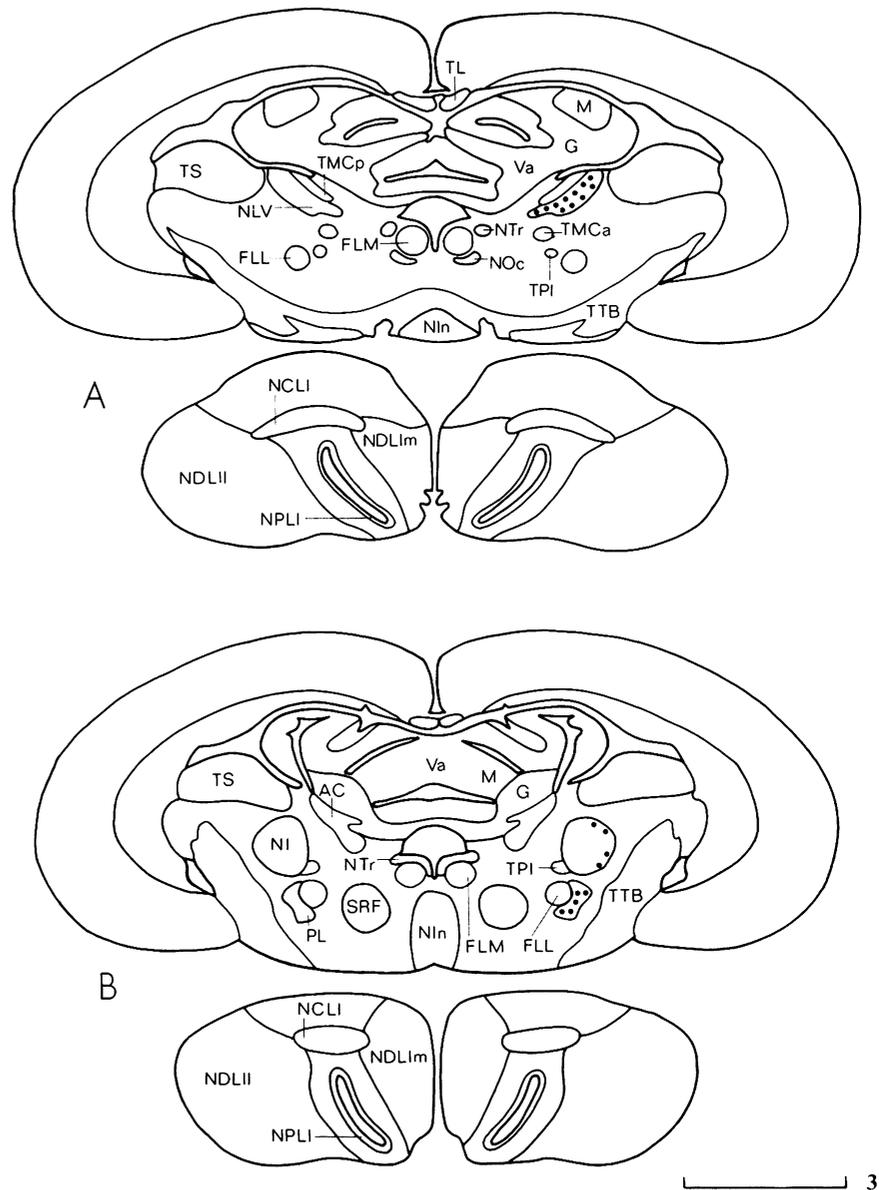
In *Lepomis*, we found retrogradely filled cells most rostrally at diencephalic and pretectal levels: the ipsilateral nucleus paracommissuralis (NP) [Ito et al.,



**Fig. 2-7.** Chartings of afferent connections of the corpus cerebelli in *Lepomis* (2-4) and *Carassius* (5-7). ● = Retrogradely filled cells. Black area in 4B and 7B indicates the injection site. Bar scales equal 1 mm.

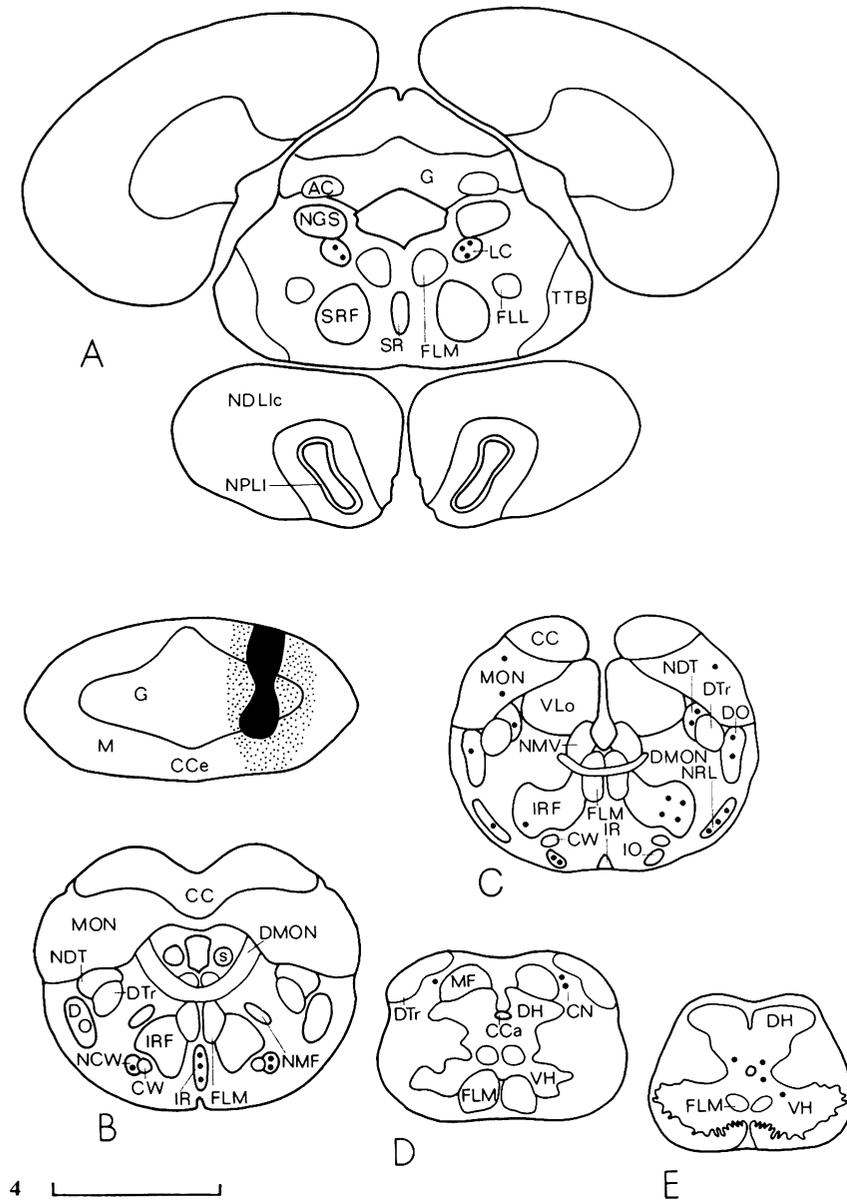
1982], dorsal periventricular pretectal (PPd), central pretectal (CPN), and dorsal (NAOD) [basal optic nucleus of Braford and Northcutt, 1983] and ventral (NAOV) [accessory optic nucleus of Braford and Northcutt, 1983] accessory optic nuclei (fig. 2A; 8A, C), all of which extensively contribute axons to a massively labeled tract that extends caudally. This tract is

the anterior part of the tractus mesencephalocerebellaris [Larsell, 1967]. As it is traced to the corpus cerebelli, it is joined by additional fibers from labeled neurons of the ipsilateral ventral tegmental nucleus (VT) (fig. 2B, 9A), perilemniscal nucleus (PL), and nucleus isthmi (NI) (fig. 3B, 9C). Many neurons of the ipsilateral nucleus lateralis valvulae (NLV) project to the



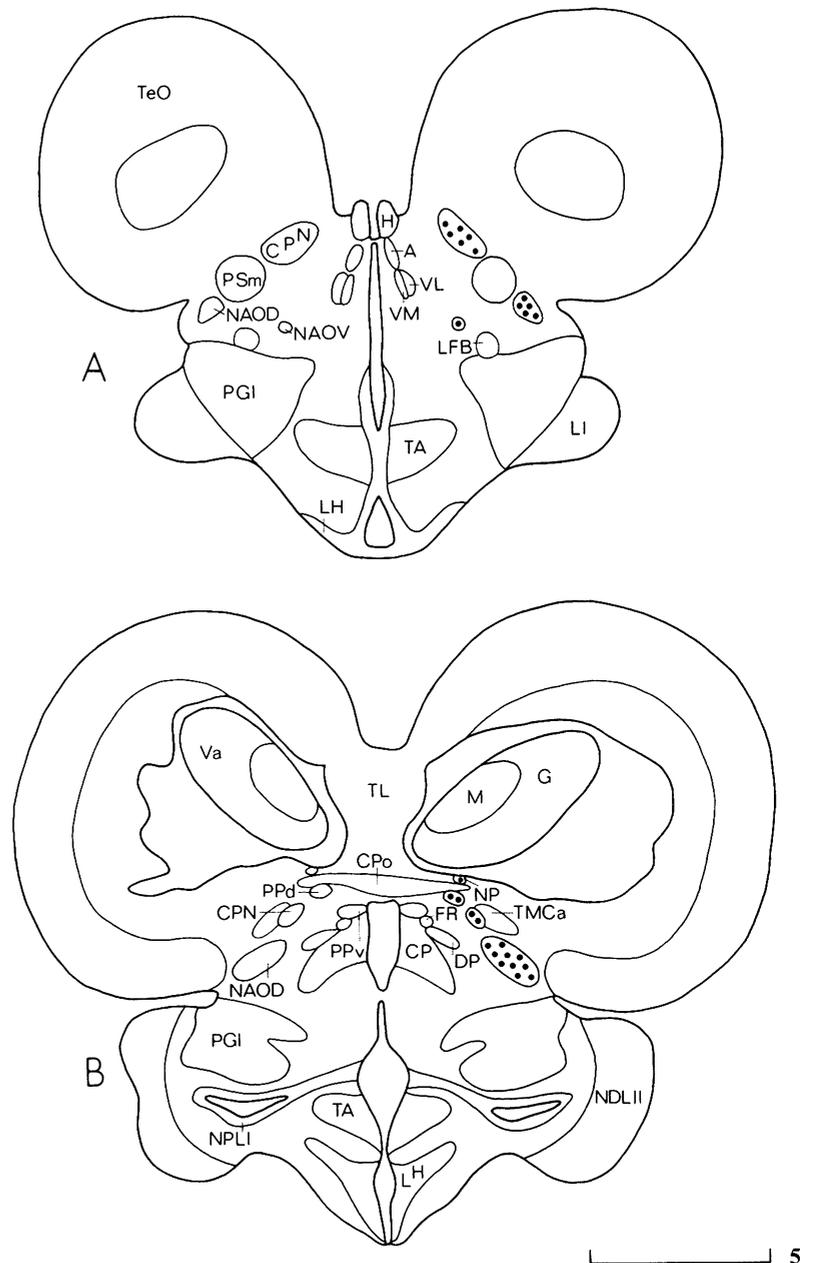
corpus cerebelli and form the posterior part of the mesencephalocerebellar tract (fig. 3A). This part of the tract probably includes axons also from the dorsal tegmental nucleus (DT) [lateral tegmental nucleus of Northcutt and Butler, 1980] and from a few large perinuclear neurons of the Edinger-Westphal nucleus (EW), both of which are retrogradely labeled bilaterally (fig. 2B). The labeled EW lie between the dorsal

tegmental and the (unlabeled) oculomotor nucleus, an area where also the Edinger-Westphal nucleus has recently been identified in a teleost [Wathey, 1988]. Anterior and posterior mesencephalocerebellar tracts join just caudal to the lateral nucleus of the valvula (fig. 3B) and can be traced along the ventral border of



the valvular granular layer before they enter the granular layer of the cerebellar corpus (fig. 4A). At this level, the fibers connecting the corpus cerebelli to the anterior part of the brain form a compact bundle, the anterior cerebellar tract (fig. 3B, 4A). We introduce this term to designate the intracerebellar portions of both the anterior and the posterior mesencephalocer-

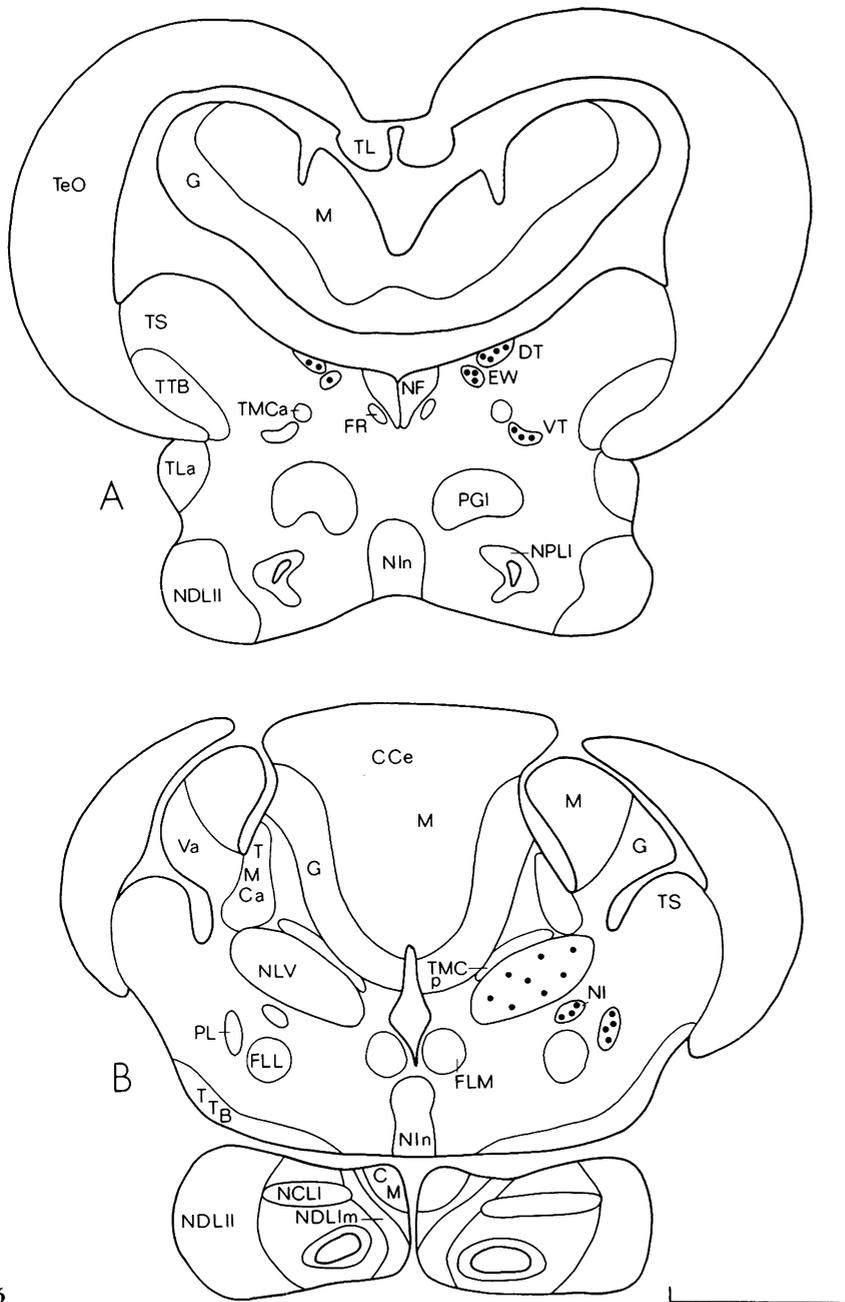
ebellar tracts and the (efferent) brachium conjunctivum (see Efferent Connections). Consequently, we term the fused intracerebellar portions of the fiber tracts, connecting the corpus cerebelli to the caudal parts of the brain, posterior cerebellar tract. Bilaterally labeled neurons of the nucleus of the locus coeruleus (LC) (fig. 4A, 10A) probably also contribute ax-



ons to the anterior cerebellar tract, but these fibers, unlike their labeled cell bodies, could not be identified unambiguously.

At more caudal levels (fig. 4B-E) we found retrogradely labeled neurons in the inferior raphe, bilaterally in the nucleus of the commissure of Wallenberg (fig. 4B), the medial octavolateral nucleus,

the nucleus of the descending trigeminal root, the descending octaval nucleus, the lateral reticular nucleus, the inferior reticular formation and, strictly contralaterally, in the inferior olivary nucleus (fig. 4C). Bilateral labeling was also observed in a nucleus lateral to the medial funicular nucleus [lateral cuneate nucleus of Finger, 1978a, fig. 4D] and, at spinal

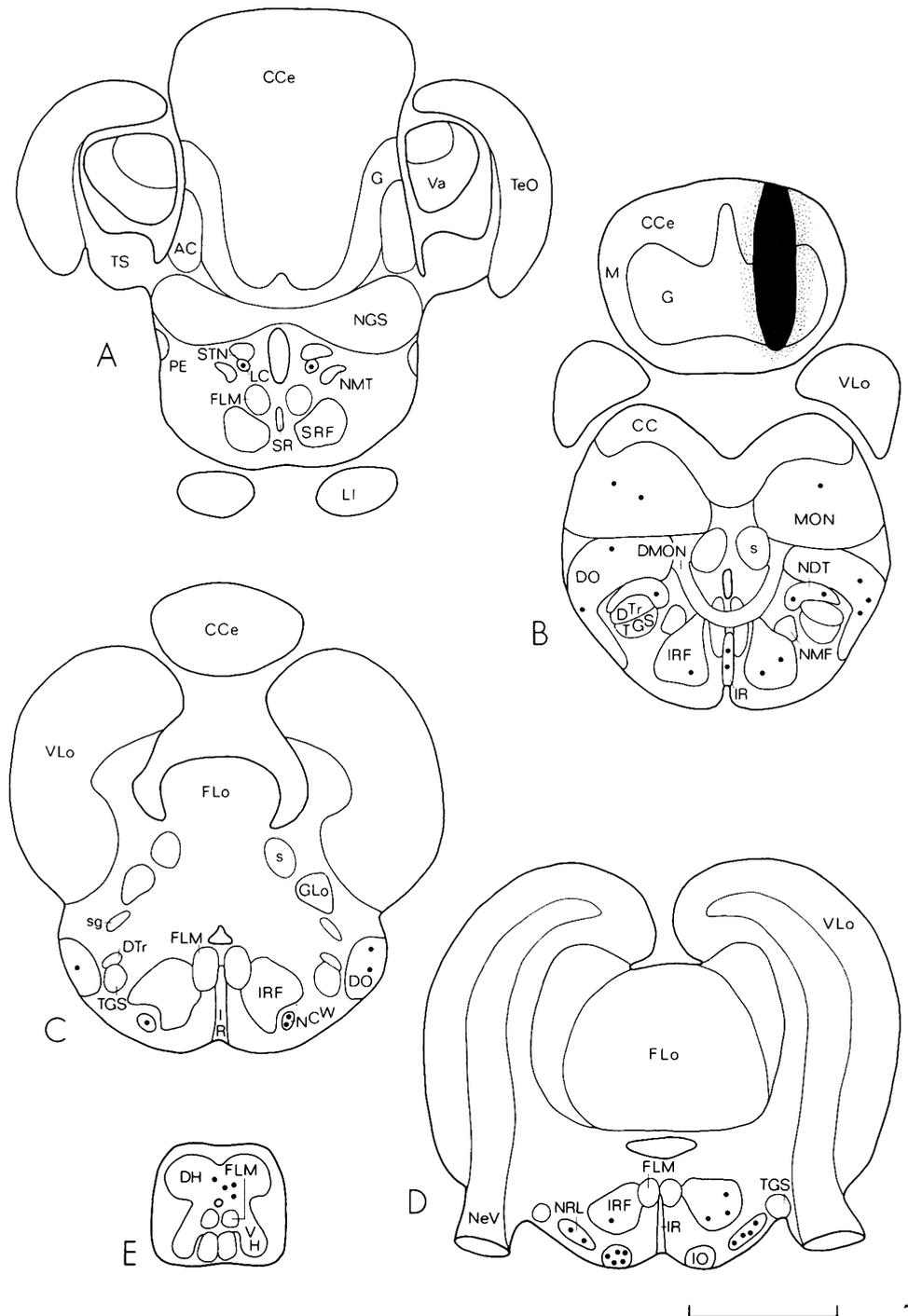


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levels, in the intermediate and ventral gray columns (fig. 4E).

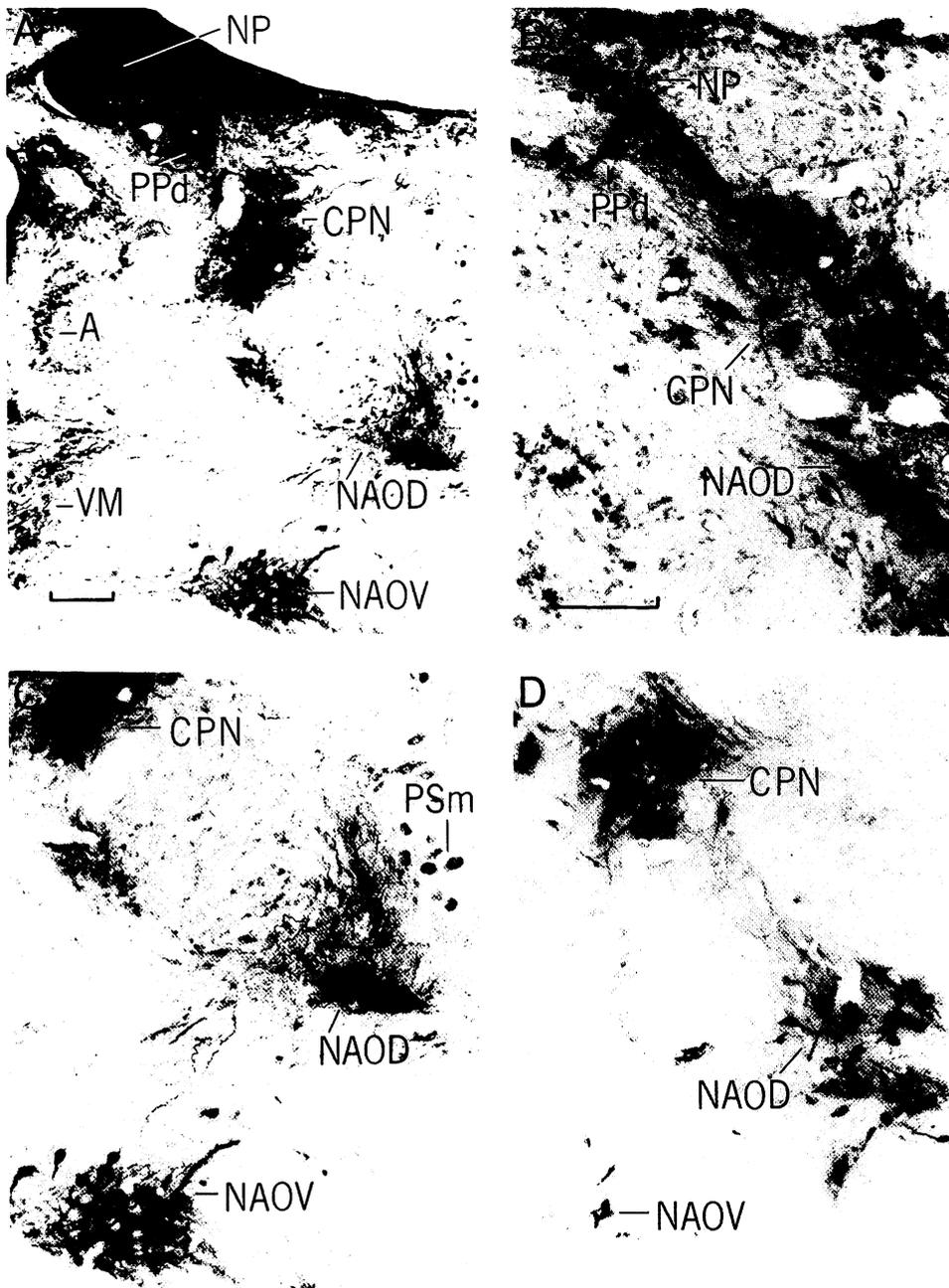
After injections into the corpus of *Carassius*, the following rostrally located cell groups were retrogradely labeled as in *Lepomis*: the ipsilateral nucleus paracommissuralis (NP), dorsal periventricular pre- tectal (PPd), central pretectal (CPN), dorsal (NAOD)

and ventral accessory optic nuclei (NAOV) (fig. 5A, B, 8B, D), VT (fig. 6A, 9B), PL, NI (fig. 6B, 9D), and, bilaterally, the LC (fig. 7A, 10B). The anterior mes- encephalocerebellar tract, which consists largely of axons arising from neurons of these anterior cell groups, can be traced as several fascicles through the NLV (fig. 11D) to join the posterior mesencephalo-



cerebellar tract (fig. 6B), which includes axons from retrogradely labeled neurons in the lateral nucleus of the valvula (fig. 6B, 11D), the DT and a few large neurons representing the EW (fig. 6A, 9B). In *Carassius*, as in *Lepomis*, retrograde labeling in all these rostrally located nuclei is ipsilateral, with the DT, the EW, and the LC also showing weaker contralateral labeling.

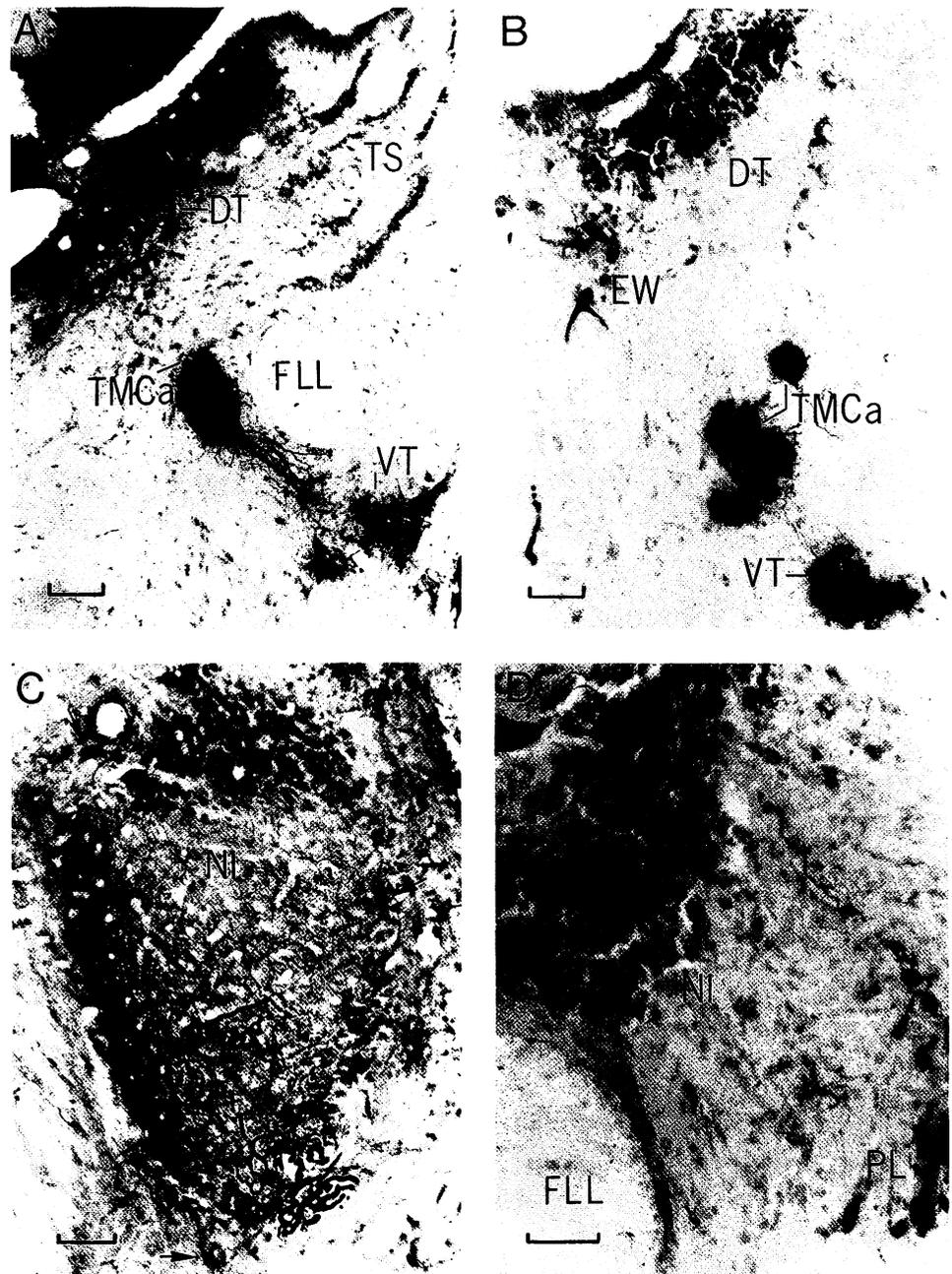
In *Carassius*, some cells in two additional nuclei were retrogradely labeled in cases where injections of the cerebellum included the rostral transitional region between the corpus and valvula cerebelli: the nucleus subeminalis of Finger [1978a] and nucleus praeeminalis. These two nuclei project extensively to the valvula cerebelli in *Carassius* [Wullmann and



**Fig. 8.** Afferent cell groups in the ipsilateral diencephalon and pretectum of *Lepomis* (A, C) and *Carassius* (B, D) as visualized in cross-sections after HRP injections into the corpus cerebelli. Note the drastic size difference of NP (A, B) and NAOV (C, D) in the two species. The ipsilateral terminal fibers in ventromedial thalamus in A result from a bilateral injection in this case. In figures 8–11 medial is to the left except in 10C and 11A, C, E where medial is to the right, and dorsal to the top. Bar scales equal 0.1 mm (C and D are the same magnification as B).

Northcutt, in press; unpubl. observations] and they cannot be recognized after injections of the corpus in *Lepomis*. Therefore, we conclude that these two nuclei have input to the valvula and not the corpus cerebelli in *Carassius* and that the sparse label after rostral corpus injections is due to spread of HRP into fibers of passage from the valvula. While a histologically dis-

tinct NP, as present in *Lepomis*, cannot be recognized in *Carassius*, there are some retrogradely filled cells dorsal to the posterior commissure, which may be the homologue of this nucleus in *Carassius* (fig. 5B, 8B). Similarly, the NAOV and NI are considerably smaller in *Carassius* compared to *Lepomis*, but they are nevertheless definitely retrogradely labeled

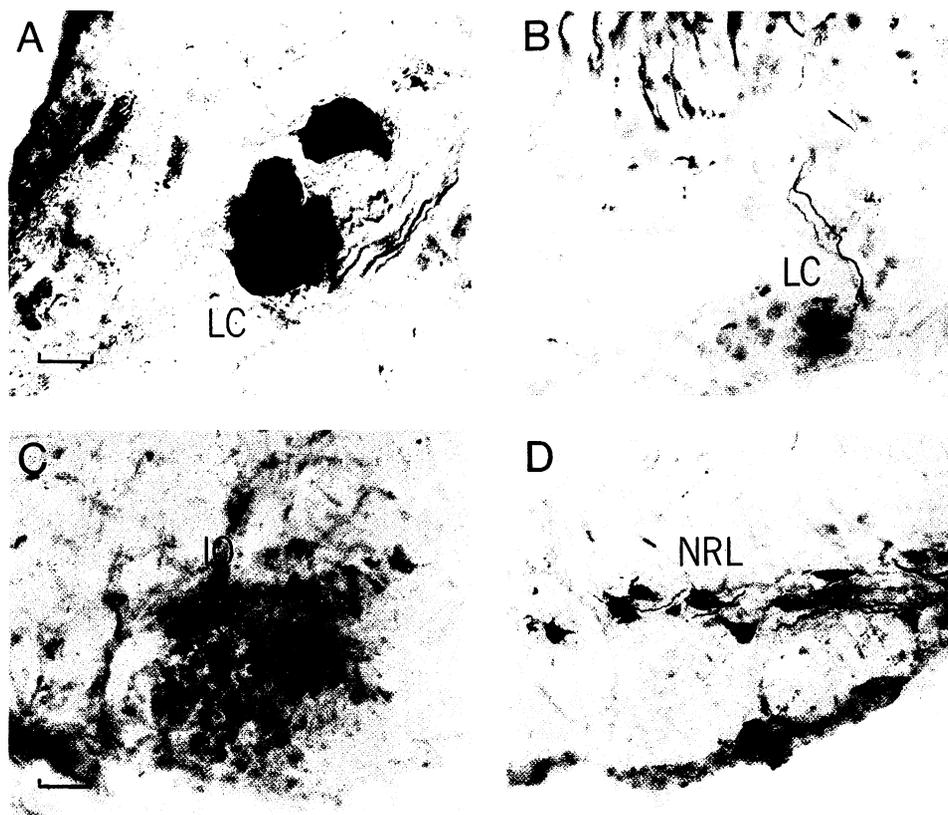


**Fig. 9.** Corpopetal cell groups in the ipsilateral mesencephalon (A, B) and isthmus region (C, D) of *Lepomis* (A, C) and *Carassius* (B, D) shown in cross-sections. Note the different neuron types of the EW and the DT (B) and the size difference of NI in *Lepomis* and *Carassius* (C, D). Arrows in C point to retrogradely filled cells. Bar scale equals 0.1 mm (A) and 0.05 mm (B-D).

(fig. 8D, 9D). A further difference with regard to *Lepomis* is that the fused anterior and posterior mesencephalocerebellar tracts enter the granular layer of the cerebellar corpus as several fascicles rather than as a compact anterior cerebellar tract.

Caudally located cell groups labeled after injections of the corpus in *Carassius* (fig. 7B-E, 10C, D)

were identical to those in *Lepomis*, with one exception: the lateral cuneate nucleus (CN) cannot be identified in *Carassius*. All bilateral labeling observed in the two investigated species was stronger on the ipsilateral side, except in the case of the medial octavolateral nucleus, where labeling was heavier contralaterally.



**Fig. 10.** Corporetal cell groups in the ipsilateral isthmic region (A, B) and the ipsilateral (D) and contralateral (C) brain stem of *Lepomis* (A) and *Carassius* (B-D) shown in cross-sections. Note the apparent difference in cell size and shape of the LC in the two species. Bar scale equals 0.025 mm (A) (same magnification in B) and 0.05 mm (C) (same magnification in D).

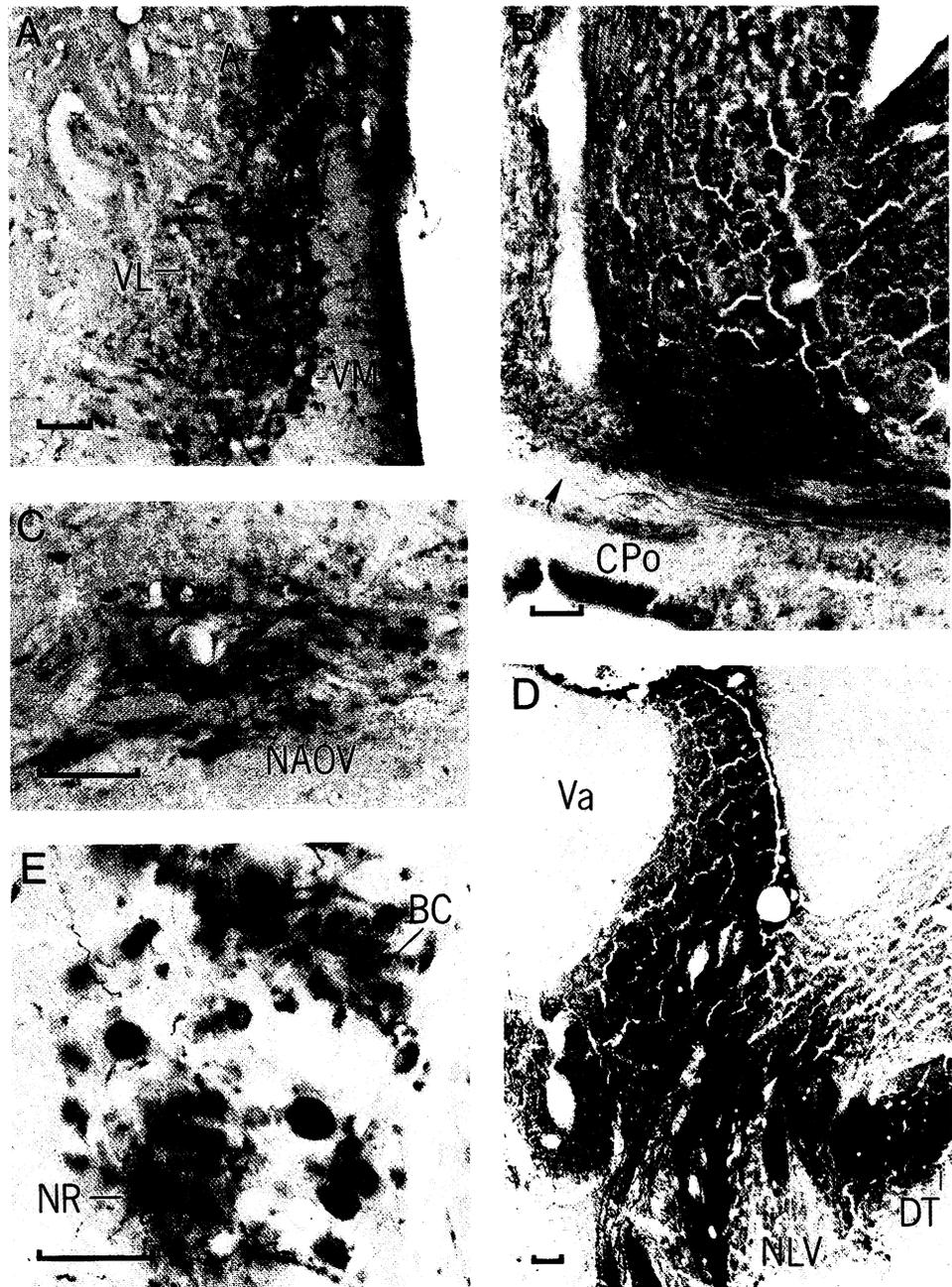
In both species, retrograde labeling of the caudal cell groups (fig. 4B-E, 7B-E) was considerably weaker than that of the more rostral ones (fig. 2-4A, 5-7A), except in the case of the inferior olive. As noted earlier, the dorsal part of the corpus in both species corresponds topologically to the rostral corpus. Our HRP injections were made dorsally and were therefore all located mainly in the topologically rostral portion of the corpus. Only injections that included ventral (topologically caudal) parts of the cerebellar corpus (as is the case in fig. 2-4 and 5-7) yielded retrograde labeling in caudal cell groups (fig. 4B-E, 7B-E), except for the inferior olive which was also labeled after dorsal injections. We will deal with this compartmentalization of cerebellar inputs in a subsequent paper. Due to the generally weaker labeling in the medulla oblongata and spinal cord, single afferent fibers were very difficult to follow to their cells of origin in our material. Close to and within the corpus cerebelli, however, in cases where caudal cell groups were labeled, a posterior cerebellar tract was labeled in addition to the anterior one (containing anterior and posterior mesencephalocerebellar tracts

and brachium conjunctivum). In contrast to the anterior cerebellar tract, the posterior tract was labeled bilaterally after unilateral injections, with the contralateral fibers entering the ipsilateral cerebellum. The posterior cerebellar tract, therefore, carries fibers from at least some of the caudally located labeled cell groups. It can be traced from a lateral position in the medulla oblongata mediorostrally along the ventral border of the eminentia granularis, through the latter into the granular layer of the corpus cerebelli.

In both species, the lateral nucleus of the valvula and the inferior olive project in topographical order onto the corpus and valvula cerebelli. All findings on topography, however, will be described in a subsequent paper.

#### *Efferent Connections*

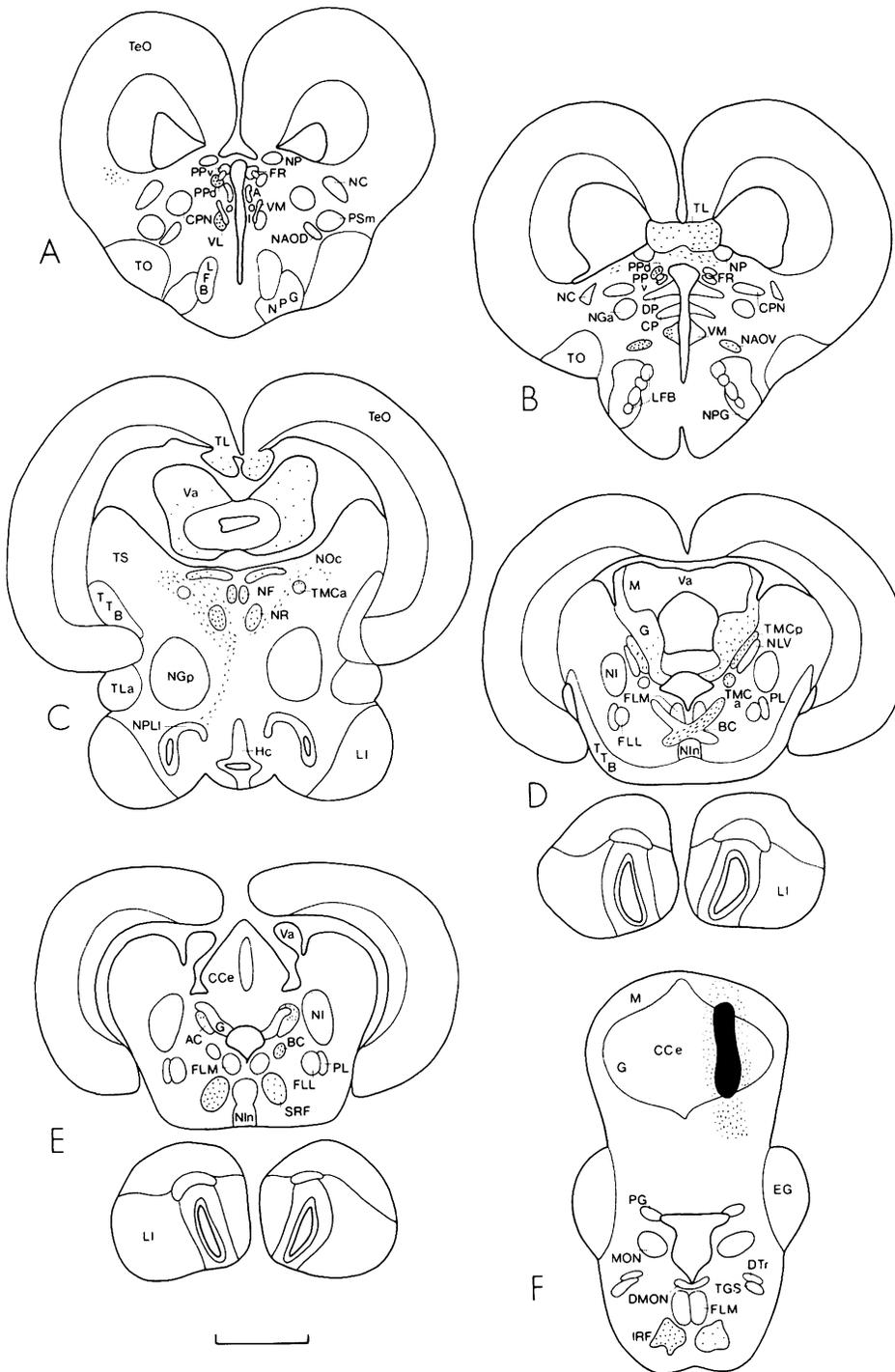
In *Lepomis*, most efferent fibers (fig. 12) exit the corpus cerebelli (fig. 12F), course first within the anterior cerebellar tract, then ventrally to it in a rostral direction (BC in fig. 12E) before decussating ventrally to, and partially within, the medial longitudinal fasciculus to reach the contralateral tegmentum (fig. 12D).



**Fig. 11.** Efferent targets of the corpus cerebelli in *Lepomis* (A, C, E) and *Carassius* (B, D). Note that the contralateral terminal field in the ventral thalamus does not extend into the dorsal thalamus (A). The contralateral terminal field in nucleus ruber seems to be located predominantly in a central neuropil surrounded by large, round cell bodies (E). The ipsilateral terminal field in the torus longitudinalis has a weak contralateral counterpart. Arrow (B) points to an efferent fiber crossing within the posterior commissure. D It is shown apart from the efferent fibers branching out in the granular layer of the valvula cerebelli, how the afferent fibers from the anteriorly located nuclei pass in several bundles through NLV, which itself is retrogradely labeled. Note the low density of labeled cells in NLV as compared to the more laterally located DT, in which almost all cells are labeled. Bar scales equal 0.05 mm.

This fiber tract has been referred to as the brachium conjunctivum [Larsell, 1967; Paul, 1982; Finger, 1983]. The ascending part of the brachium conjunctivum forms a diffuse terminal field in the contralateral mesencephalic tegmentum, and appears to terminate in a cell group which has been called the red nucleus (nucleus ruber) (fig. 11E, 12C). At this level, some fibers could be traced to the medial part of the contra-

lateral nucleus periventricularis recessus lateralis lobi inferiores (fig. 12C), but no terminals were observed. Ascending efferent fibers then extend dorsorostrally, terminating within the oculomotor nucleus, the nucleus of the medial longitudinal fasciculus and the medial aspect of the torus semicircularis (fig. 12C), before terminating in several diencephalic cell groups, such as the ventromedial and ventrolateral thalamus

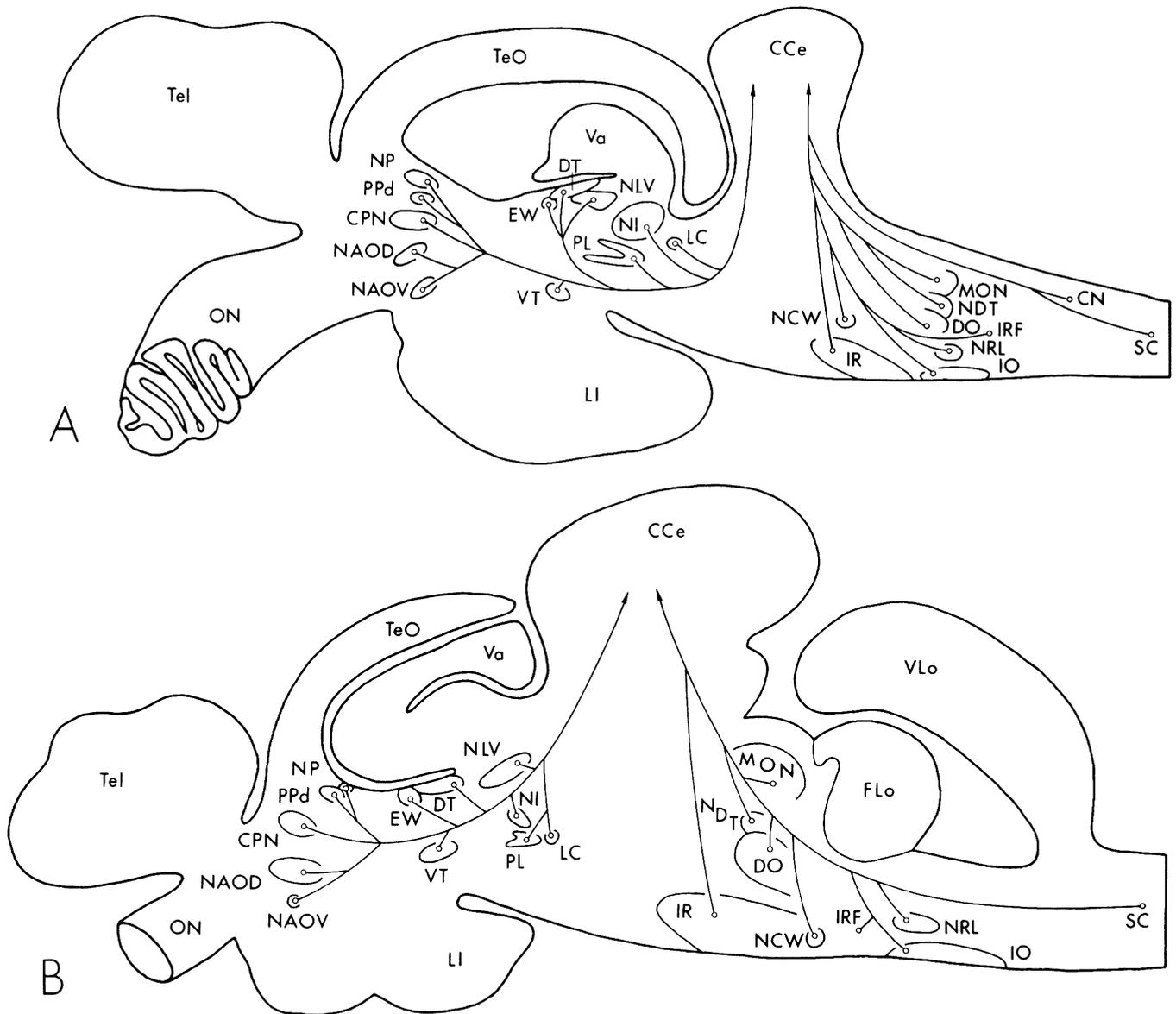


**Fig. 12.** Chartings of efferent connections of the corpus cerebelli in *Lepomis*. Dashes indicate the course of efferent fibers, and small dots are terminal fields (except the ones which indicate HRP spread around the black injection site in F). Bar scale equals 1 mm.

(fig. 11A, 12A, B), the PPd (fig. 12A, B), the NAOV (fig. 11C, 12B), and, sparsely, in the central zone of the optic tectum (fig. 12A). A descending component of the brachium conjunctivum terminates in the contralateral mesencephalic superior and the metencephalic and myelencephalic inferior reticular forma-

tion (fig. 12E, F). All cerebellofugal targets had a corresponding sparser terminal field ipsilaterally, except for the ventral thalamic and periventricular pretectal nuclei and the optic tectum.

In *Lepomis*, the efferent axons that terminate in the torus longitudinalis take a very different course: they



**Fig. 13.** Schematic diagram summarizing afferent connections of the corpus cerebelli in *Lepomis* (A) and *Carassius* (B). Note that the anterior and posterior group of corporepetal nuclei in both species project to the corpus cerebelli through the anterior and posterior cerebellar tract, respectively.

travel first within the ipsilateral anterior cerebellar tract (fig. 12E), and more rostrally within the anterior mesencephalocerebellar tract (fig. 23C, D); they take a steep dorsal turn at the border between the dien-cephalon and the torus longitudinalis to terminate mainly in the ipsilateral torus longitudinalis (fig. 11B, 12B), although some fibers cross in the posterior and

intertectal commissure to enter the contralateral torus (fig. 11B).

A third bundle of efferent fibers travels within the ipsilateral and weaker in the contralateral posterior mesencephalocerebellar tract to arborize and terminate in the granular layer of the valvula cerebelli, just dorsal to NLV (fig. 11D, 12C, D).

The efferent connections of the corpus cerebelli in *Carassius* are so similar to those in *Lepomis* that they are not illustrated separately. A notable exception to this similarity is the absence of a terminal field in the ventral accessory optic nucleus in *Carassius*.

## Discussion

First, we will analyze the available information on the afferent and efferent connections of the corpus cerebelli in teleosts in view of the cypriniform and perciform pattern based on our results and attempt to recognize different patterns of cerebellopetal (i.e. corpopetal) and cerebellofugal organization within teleosts (model analysis). In a second step, we will examine the evolutionary polarity of these patterns among teleosts and other vertebrates (phyletic analysis).

### Model Analysis

*Afferent Connections of the Corpus Cerebelli.* Apart from cells in the CN, which were observed only in *Lepomis*, the posterior group of corpopetal nuclei (fig. 4B–E, 7B–E) is identical in *Lepomis* and *Carassius*. With respect to the anterior group (fig. 2–4A, 5–7A), however, two different patterns of corpopetal organization can be recognized (fig. 13A, B). The perciform pattern (fig. 13A) includes a well-developed NP, PPd and CPN, NAOD and NAOV, DT and VT, EW, PL, a large NI, NLV, and the LC. The cypriniform pattern (fig. 13B), is also characterized by well-developed PPd, CPN, NAOD, DT, VT, EW, PL, NLV and LC, but in contrast to the perciform pattern NP, NAOV and NI are minute.

The recognition of these two patterns allows us to resolve some of the confusion in the literature concerning the corpopetal nuclei in the diencephalic and pretectal region. Four nuclei in this region (PPd, CPN, NAOD, NAOV; fig. 2A, 5A, B, 13A, B) are primary retinofugal targets in both cypriniforms and perciforms, one (NP) is not retinorecipient [see review by Northcutt and Wullimann, 1988], but it does receive telencephalic input in several percomorphs [Ito et al., 1982]. A corpopetal NP [nucleus mesencephalicus dorsalis of Finger, 1978a; the most dorsomedial part, only, of the same named nucleus of Karten and Finger, 1976] has also been reported in silurids, but not in cypriniform teleosts. We suspect that some corpopetal cells dorsal to the posterior commissure may

be NP in *Carassius* (fig. 8B). But silurids and cypriniforms, both of which are ostariophysines, differ from one another nevertheless in the presence of a well-developed cerebellopetal NP (fig. 2A, 5B, 8A, B).

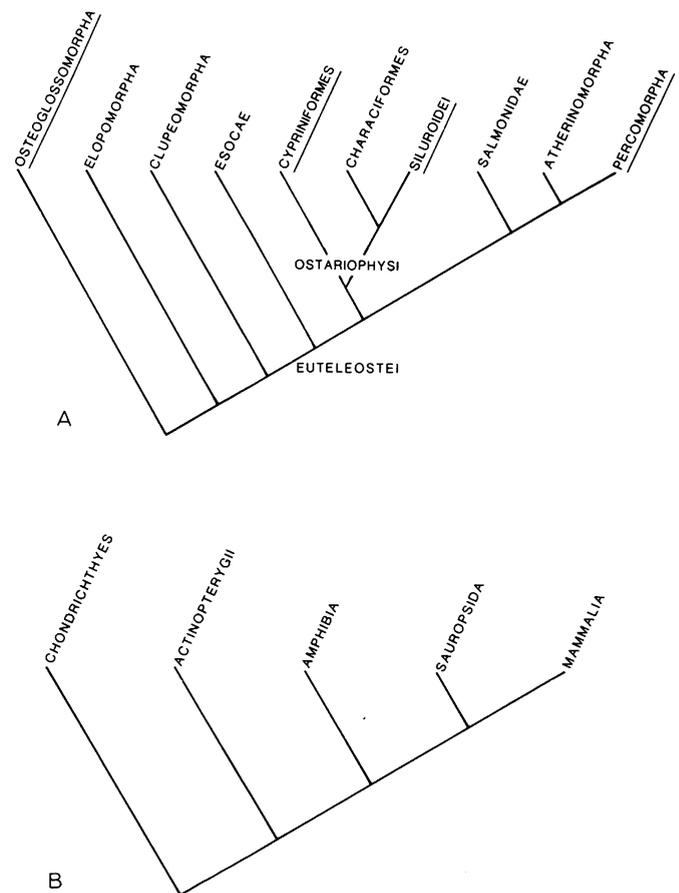
Three of the four retinofugal nuclei have previously been reported to project to the cerebellar corpus in a number of teleosts: PPd [nucleus of the posterior commissure of Grover and Sharma, 1981; and Luiten, 1981], CPN [ventrolateral parts of nucleus mesencephalicus dorsalis of Karten and Finger, 1976; anterior glomerular nucleus of Finger, 1978a, 1983; P1 of Finger and Karten, 1978; area pretectalis of Grover and Sharma, 1981; area pretectalis pars anterior of Ito et al., 1982; nucleus pretectalis dorsalis of Luiten, 1981] and NAOV [P2 of Finger and Karten, 1978; nucleus pretectalis of Grover and Sharma, 1981; nucleus pretectalis ventralis of Luiten, 1981]. Our NAOV, however, has not been reported previously as being cerebellopetal. Except for the paper by Ito et al. [1982], all other studies were on silurid or cypriniform fishes. As NAOV is very small in cypriniforms, this may account for it not being recognized as a cerebellopetal nucleus before. Our results not only demonstrate its existence in both perciforms and cypriniforms, but also its relatively greater development in perciforms (fig. 2A, 5A, 8C, D).

Apart from the diencephalic and pretectal nuclei discussed above, our results were identical in *Lepomis* and *Carassius*, except for the absence of a corpopetal connection from the CN in *Carassius*. This absence, however, is probably due to weak retrograde transport of HRP rather than a reflection of a real structural difference between *Lepomis* and *Carassius*. Whether or not the absence of some cerebellopetal cell groups in reports on ostariophysines [Finger, 1978a] or percomorphs [Ito et al., 1982] compared to our material are also due to procedural reasons or represent real species differences remains unclear. Finger [1978a] reported in addition two cerebellopetal cell groups that we did not find, the mesencephalic trigeminal nucleus and nucleus subeminentialis. We believe that the former corresponds to either our DT or our EW. Nucleus subeminentialis, however, is not labeled in cases where we injected the corpus. We found a corresponding cell group in *Carassius* labeled after valvular injections [Wullimann and Northcutt, in press; unpubl. observations]. The fact that Finger's injections in *Ictalurus* [1978a] included not only the corpus, but also parts of the valvula cerebelli, may

well account for this difference in our respective reports.

In addition to the already discussed diencephalic and mesencephalic nuclei, the following corpopetal cell groups have been found previously in percomorphs [Ito et al., 1982] and ostariophysines [Finger, 1978a]: spinal cord, lateral cuneate nucleus, descending octaval nucleus [acousticolateral line area of Ito et al., 1982; octavovestibular nucleus of Finger, 1978a], inferior olive, lateral reticular nucleus, nucleus of the commissure of Wallenberg, LC and NLV.

While we believe we can explain all discrepancies in the literature regarding known corpopetal connections in percomorphs and ostariophysines, the information on mormyrids [Meek et al., 1986a, b] is more difficult to interpret. In *Gnathonemus*, three nuclei in the diencephalic and pretectal region have been reported to project to the corpus cerebelli: from dorsal to ventral, a small 'nucleus commissurae posterioris', a 'nucleus geniculatus' and a 'nucleus dorsalis anterior pretectalis' [Meek et al., 1986a, b]. These nuclei might appear to correspond to our PPd, CPN and NAOD. However, only nucleus commissurae posterioris, but not the other two corpopetal nuclei, receive retinal input [Lazar et al., 1984; Meek et al., 1986b], as would be expected. Two explanations are possible: due to reduced vision in these electroreceptive teleosts, those two cell groups have lost their retinal input and are, in fact, homologues of our CPN and NAOD; alternatively, the corpopetal nuclear pattern in mormyrids differs from all other teleosts, and the two nuclei under consideration are not homologous to CPN and NAOD. While the first hypothesis seems likely for nucleus geniculatus, the second appears more likely for nucleus dorsalis anterior pretectalis, as this nucleus more resembles the preglomerular nucleus of other teleosts in three ways: (1) its general topological position, ventral to the optic tectum in the diencephalon and extending from its lateral margin medially towards the lateral forebrain bundle; (2) the absence of retinal input, and (3) the presence of input from the torus semicircularis [Finger et al., 1981], which is typical for nucleus preglomerulosus in other teleosts [Murakami et al., 1986; Finger, 1979; 1980; Finger and Bullock, 1982; Ehteler, 1984]. If this interpretation is correct, nucleus dorsalis anterior pretectalis in mormyrids represents an elaboration of nucleus preglomerulosus related to electrosensory information, and its projection to the corpus cerebelli is absent in other teleosts that have been studied so far.



**Fig. 14.** Simplified cladograms expressing the phylogenetic relationships of actinopterygian fishes (A), according to Lauder and Liem [1983] and major vertebrate groups (B). A Underlined taxa indicate groups whose cerebellar connections have been described (including those in this study).

The 'anterior thalamic nucleus' of mormyrids [Bell, 1981], which receives a projection from the octavolateralis center of the torus semicircularis and, in turn, projects to the telencephalon [Bell, 1981], would then be interpreted as that part of nucleus preglomerulosus that is present in other teleosts as well [Northcutt and Wullimann, 1988].

Compared to both ostariophysines [Finger, 1978a] and percomorphs [Ito et al., 1982], mormyrids [Meek et al., 1986a, b] have a limited number of corpopetal nuclei: nucleus reticularis lateralis, inferior olive and NLV. Similar to *Carassius* and *Lepomis*, mormyrids may also have a DT [nucleus dorsalis tegmenti mesencephali of Meek et al., 1986a, b], PL [nucleus lateralis valvulae pars perilemniscalis of Meek et al.,

1986a], NI, LC (nucleus Q of Meek et al., 1986a) and nucleus of the descending trigeminal tract (nucleus funiculi lateralis primus of Meek et al., 1986a). However, mormyrids do not appear to possess a projection to the corpus from spinal levels, and from the CN, the descending octaval and medial octavolateralis nuclei (MON), the nucleus of the commissure of Wallenberg, EW and the VT. However, not all lobes of the corpus cerebelli have been investigated yet in mormyrids.

In short, our results on cypriniform and perciform corpopetal organization help to shed light on the apparent discrepancies in the literature on teleostean cerebellar afferent connections, especially in the diencephalic and pretectal region. Previous studies on cypriniforms [Finger and Karten, 1978; Luiten, 1981] and percomorphs [Ito et al., 1982] support our cypriniform and perciform pattern, respectively. In addition, we report new projections from NAOV, VT, EW and MON to the corpus in both patterns. The relatively sparse projection from NAOV and NI in cypriniform teleosts, as compared to that in perciforms, may be related to the fact that gustation is a dominant sensory modality in the former animals, whereas vision is predominant in most perciforms. It is surprising that silurids – although they are ostariophysines, as are cypriniforms – share with the perciforms the presence of a well-developed corpopetal NP [Finger, 1978a]. Even if one assumes reductions in the visual system of cypriniforms [Northcutt and Wullimann, 1988], this phenomenon would not explain the absence of this telencephalocerebellar pathway [Ito et al., 1982]. Mormyrids clearly exhibit a third, very different pattern of corpopetal organization: some corpopetal diencephalic nuclei have most likely lost their retinal input [nucleus geniculatus of Meek et al., 1986a]; others may have established new cerebellar connections in conjunction with electroreception [nucleus dorsalis anterior pretectalis of Meek et al., 1986a]. On the other hand, these animals may lack some of the well-established corpopetal connections in teleosts.

*Efferent Connections of the Corpus Cerebelli.* Collaterals of retrogradely labeled neurons could potentially be the source of terminal fields visualized by the HRP method and lead to misinterpretations of efferent connections of the corpus cerebelli. We nevertheless believe that our results are valid for two reasons. First, most efferent fibers of the corpus cerebelli exit through a separate tract (brachium conjunctivum, see

Results) and decussate, unlike most of the afferent fibers, to the other side of the brain. Second, our results on the efferent connections of the corpus cerebelli in *Lepomis* and *Carassius* are in general agreement with the few previous experimental studies on teleosts [Braford, 1971; Finger, 1978b, 1983; Meek et al., 1986a, b], some of which were done with different techniques [Braford, 1971].

Our data indicate a previously unreported contralateral terminal field in PPD in both species and confirm the report of Murakami and Morita [1987] on a contralateral projection to the inferior lobe in *Sebastes*; our data from *Lepomis* also confirm a bilateral terminal field in NAOV [area ventralis lateralis of Murakami and Morita, 1987]. On the other hand, a projection to the trigeminal motor nucleus, as reported by Braford in *Carassius* [1971] and Meek et al. in *Gnathonemus* (1986a, b), was not observed in this study. Apart from the absence of an efferent projection to NAOV in *Carassius*, we saw no obvious differences in the corpopetal organization in cypriniforms and perciforms. Again, as in the case of corpopetal connections, this difference may be related to the predominance of gustation versus vision in *Carassius* and *Lepomis*, respectively.

#### *Phyletic Analysis*

We will now try to establish the evolutionary polarity of the two patterns of cerebellar organization observed in teleosts. Our analysis will focus on the afferent (cerebellopetal) connections of the corpus cerebelli as the efferent (cerebellofugal) connections showed only minor differences between the two patterns. We will use the outgroup comparison for this analysis, and we will assume that the phylogenetic relationships of actinopterygians formulated by Lauder and Liem [1983] are valid (fig. 14A). The main difference between the cypriniform and perciform pattern is the very small size of NP, NAOV and NI in the former. No teleostan outgroups to ostariophysines and percomorphs (except the osteoglossomorph mormyrids, see fig. 14A and text below) have been experimentally studied with regard to cerebellar connections of these nuclei. We therefore surveyed the occurrence of NP and NI within teleosts based on normal histological material (table I). As mentioned earlier, a well-developed corpopetal NP has been demonstrated experimentally in silurids [Finger, 1978a], and it can also be clearly recognized histologically in silurids and characiforms (table I). As these two groups

form a sister group to cypriniforms (fig. 14A), both patterns apparently exist within ostariophysines. The NP cannot be identified unambiguously in any outgroup of both ostariophysines and percomorphs (fig. 14A, table I), hence we cannot determine at this point if it is plesiomorphic for euteleosts, except esocids, and has been lost in salmonids and atheriniforms, or alternatively if it is a parallel development in ostariophysines and percomorphs. In the first case, the presence of a minute NP in cypriniforms would have to be interpreted as a derived condition; in the second case, it would be the primitive condition for ostariophysines.

The distribution of NI, on the other hand, presents a clearer picture: a large and histologically characteristic NI, as opposed to a minute one in cypriniforms, is present not only within ostariophysines but in all major teleostean groups (fig. 14A, table I). It is not clear whether the same-named nucleus described in *Lepisosteus osseus* [Northcutt, 1983] is a homologous structure, as its topology and histology differ considerably from the one seen in teleosts. Furthermore, a nucleus isthmi has not been reported in cladistians [Nieuwenhuis, 1983; Senn, 1976a, b]. A NI as defined by Northcutt and Wullimann [1988] and observed in this paper (table I) is most likely a synapomorphy for teleosts, and its reduction in cypriniforms is thus a derived feature. On the other hand, the presence of a small retinofugal NAOV seems to be a plesiomorphic character for actinopterygians [Northcutt and Wullimann, 1988], and its hypertrophy in the perciform pattern is likely an apomorphy.

With respect to the presence of the remaining corpopetal cell groups, the cypriniform and perciform patterns are identical (except for the already discussed discrepancy related to the CN) and we therefore assume that this identical condition is plesiomorphic for euteleosts, if not teleosts. The only other available experimental information on cerebellar connections within teleosts is for mormyrids (*Osteoglossomorpha*, see fig. 14A) [Meek et al., 1986a, b]. These animals reveal a corpopetal pattern different from that in both cypriniforms and perciforms: it comprises an additional projection from a part of nucleus preglomerulosus, but there are no projections from NAOD, NAOV, VT, EW, inferior raphe, nucleus of the commissure of Wallenberg, nucleus octavus descendens, MON, inferior reticular formation, CN and spinal cord.

An outgroup analysis including information on

cartilaginous fishes – the next available outgroup in terms of experimental data (fig. 14B) [Northcutt and Brunken, 1984; Fiebig, 1988] – tells us that the following corpopetal nuclei are most likely plesiomorphic characters for gnathostomes: NAOD, NAOV, CPN, VT, MON, nucleus octavus descendens, inferior reticular formation and spinal cord. The same is true, of course, for nucleus reticularis lateralis, inferior olive and nucleus of the descending trigeminal tract, as these nuclei are recognized as corpopetal sources in all teleosts and cartilaginous fishes examined. Consequently, the mormyrid pattern has to be interpreted as derived to the extent that it differs from these plesiomorphic features. On the other hand, a corpopetal PPD, DT, EW, NLV, PL, LC, nucleus of the commissure of Wallenberg, inferior raphe and CN have not been unequivocally observed in cartilaginous fishes. These nuclear areas may therefore be candidates for synapomorphies at one level or another in the evolution of osteichthyans.

Finally, to put teleost corpopetal patterns into a broader evolutionary context, we will consider tetrapods as the sister group to actinopterygians, and cartilaginous fishes, again, as the outgroup to these two sister groups (fig. 14B), and we will examine the experimentally determined cerebellar inputs in these groups. Certain cerebellopetal projections are present in all gnathostome vertebrates: the spinocerebellar, olivocerebellar, lateral reticulocerebellar, descending octavocerebellar, and descending trigeminocerebellar systems [actinopterygians – Finger, 1978a; this paper; chondrichthyans – Northcutt and Brunken, 1984; Fiebig, 1988; amphibians – Grover and Grüsser-Cornehls, 1984; reptiles – Bangma and ten Donkelaar, 1982; Künzle, 1983; birds and mammals – Clarke, 1977; Gould, 1980; Gilman et al., 1981; Ito, 1984]. These connections can therefore be considered the primitive condition for vertebrate cerebellopetal systems. As the experimental information allowing us to compare the total cerebellar afferent connections is still scanty, especially for cartilaginous fishes [Northcutt and Brunken, 1984; Fiebig, 1988], amphibians [Grover and Grüsser-Cornehls, 1984; Gonzales et al., 1984], reptiles [Schwarz and Schwarz, 1980; Bangma and ten Donkelaar, 1982; Künzle, 1983] and birds [Clarke, 1977; Brecha et al., 1980], it is possible that one or the other of the cerebellopetal nuclei may still be discovered in these vertebrate groups. This seems particularly likely in cases where a cerebellopetal system exists in both actinopterygians and at least some

tetrapods, as does the CN, the inferior raphe and the LC, so that the same system would be expected in cartilaginous fishes as well. While we cannot at this point determine the evolutionary polarity of these characters, there is a clear trend with respect to the total cerebellar afferent connections. Many of the posteriorly located rhombencephalic afferent systems are universally present in all vertebrates, whereas the anterior ones vary tremendously. A telencephalopontocerebellar system, as present in birds and mammals, is absent in both actinopterygian and cartilaginous fishes. In some teleosts, a different anatomical pathway leads from the telencephalon over NP to the cerebellum [Ito et al., 1982]. It is not possible – based on the totally different topological position – that this telencephalocerebellar pathway is homologous to a pontine system, nor can a homologous pathway be discerned in any tetrapod. The medial spiriform nucleus of birds, although telencephalorecipient [Karten, 1971; Zeier and Karten, 1971] and cerebellopetal [Karten and Finger, 1976], is most likely a structure that is convergent to NP in teleosts, as a comparable cerebellopetal nucleus has not been shown in reptiles [Bangma and ten Donkelaar, 1982; Künzle, 1983], amphibians [Grover and Grüsser-Cornehls, 1984] or mammals [Gould, 1980].

It is also difficult to homologize other cerebellopetal connections arising from the anterior group of nuclei in teleosts. Whereas direct cerebellar projections from the accessory optic nuclei and pretectal areas are present in tetrapods [reptiles – Reiner and Karten, 1978; Bangma and ten Donkelaar, 1982; birds – Karten and Finger, 1976; Brauth and Karten, 1977; Clarke, 1977; mammals – Winfield et al., 1978; Haines and Sowa, 1985] and cartilaginous fishes [Northcutt and Brunken, 1984; Fiebig, 1988], as they are in actinopterygians, the homologies are presently difficult to establish, as different numbers of nuclei are involved, and their higher order connectivity is not equally well-known in all three groups. As a hypothesis, we propose that NAOD [Northcutt and Wullimann, 1988; this paper] may be the homologue of the nucleus of the basal optic root in amphibians [Grover and Grüsser-Cornehls, 1984; Fite, 1985] and sauropsids [Bangma and ten Donkelaar, 1982; Künzle, 1983; McKenna and Wallmann, 1985] and the medial terminal nucleus in mammals [McKenna and Wallmann, 1985; Weber, 1985], based on the similarities of general position, retinal input, cerebellar output (except amphibians) and, at least in teleosts

[Finger and Karten, 1978], amphibians [Montgomery et al., 1981] and birds [Brecha et al., 1980], a projection to the oculomotor nucleus. Similarly, CPN may be homologous to the retinorecipient and cerebellopetal nucleus lentiformis mesencephali pars magnocellularis in birds [McKenna and Wallmann, 1985] and the nucleus of the optic tract in mammals [McKenna and Wallmann, 1985; Weber, 1985], although a projection of the latter to the cerebellum has not been shown. Consequently, a corporepetal NAOV would be interpreted as a plesiomorphic character for cartilaginous and bony fishes that was lost in tetrapods.

*In summary*, while a plesiomorphic group of cerebellopetal systems is present in the rhombencephalon of all vertebrates, the anterior cerebellopetal systems seem to be highly variable among vertebrates. A possible reason for this may be that the rhombencephalic systems subserve more basic, evolutionarily older functions, and the anterior systems more specialized ones. In birds and mammals, a telencephalopontocerebellar system is superimposed on a diencephalo/mesencephalocerebellar system present in all other vertebrates. However, the plesiomorphic state for these anterior systems is difficult to establish without more information on the variation of cerebellopetal systems and their higher order connectivity and physiology within cartilaginous and bony fishes.

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