Ontogeny and homology of the neural complex and the claustrum of otophysan Ostariophysi (Actinopterygii: Teleostei)

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1) ABSTRACT

I studied the development and homology of the neural complex and the claustrum in the ostariophysan subgroup Otophysi including for the first time representatives of all four major otophysan lineages.

I found that supradorsal cartilages, paired autogenous elements at the medial side of the neural arches, play a previously unrecognized major role during the ontogeny and evolution of the neural complex. In most otophysan taxa, supradorsals 3 and 4 fuse with supraneurals 2 and 3 (cypriniforms) or with supraneural 3 (characiforms, some siluriforms, gymnotiforms) during ontogeny to form the neural complex. In the majority of siluriforms the neural complex is exclusively formed by supradorsals 3 and 4. In loricarioid siluriforms, a neural complex is missing, the fourth neural arch fuses to the occiput in development, and the first free vertebra is the fifth. Of the four otophysan subgroups, siluriforms are the most and cypriniforms the least diverse in the structure and development of their neural complex. Among characiforms I discovered striking heterochronic shifts in the development of the components that form the neural complex. I review previous hypotheses about the homology of the different elements of the neural complex and discuss these in light of my new findings.

My investigation of the development of the claustrum revealed the following results. The claustrum of cypriniforms has a cartilaginous precursor, which subsequently develops an extensive lamina of membrane bone. The membrane bone component of the claustrum and its close association with the atrium sinus imparis, a perilymphatic space of the We-

berian apparatus, are both synapomorphies of cypriniforms. The characiform claustrum is not preformed in cartilage and originates as a membrane bone ossification, a putative synapomorphy of that taxon. Among siluriforms, the claustrum is present only in more basal groups and originates as an elongate cartilage that ossifies in a characteristic ventrodorsal direction, possibly a synapomorphy of catfishes. Gymnotiforms lack a claustrum. Based on a review of all previous hypothesis of claustrum homology and my new findings, I conclude that the most plausible hypothesis is the one originally proposed by Bloch (1900) that claustra are homologues of the supradorsals of the first vertebra.

2) INTRODUCTION

a) Diversity of Ostariophysi

Ostariophysi are one of the most speciose vertebrate clades and comprise up to 30 % or 6500 of the teleost species (Nelson, 1994). They comprise two monophyletic subgroups, named Anotophysi and Otophysi (Rosen & Greenwood, 1970; Fink & Fink, 1981, 1996). Representing almost 65 % of the freshwater fish fauna Ostariophysi are the dominant group in this habitat worldwide. Few ostariophysans live in marine waters; only around 120 species of the gonorynchiform families Chanidae, Gonorynchidae, and the siluriforms Ariidae, Plotosidae. Ostariophysi are present on all continents except Antarctica and are absent from New Zealand and Greenland.

With just over 35 species, Anotophysi are a small group compared to the Otophysi, which comprise 99.5 % of Ostariophysan diversity. Part of the success of Otophysi can certainly be attributed to the evolutionary development of a unique sound transmitting apparatus discovered by the German anatomist Ernst Heinrich Weber in 1820. Subsequently termed Weberian apparatus, this character complex comprises modifications of the swimbladder, anterior vertebrae and inner ear (see detailed review further below).

4000 species of Otophysi belong to just four family level taxa (Cyprinidae, Loricariidae, Characidae, Balitoridae), of which the Cyprinidae are the largest vertebrate family comprising 2500 species. Otophysi also show an amazing range in size from the smallest known vertebrate, the cyprinid *Paedocypris progenetica* (Kottelat et al., 2006) measuring about 7.9 mm, to giants like the European wels (*Silurus glanis*), which may formerly reach up to 5 m. Otophysi exhibit a huge range of feeding strategies ranging from algae scraping forms like the cypriniforms *Garra*, *Epalzeorhynchus* and *Gyrinocheilus,* the South American prochilodontid characiforms and the loricariid siluriforms, to large predators like the ptychocheiline cypriniforms, the characiforms *Hydrocynus*, *Hoplias* and *Hepsetus*, the siluriforms *Silurus* and *Wallago*, and the gymnotiform *Electrophorus*. The trichomycterid catfishes of the genus *Vandellia* are ectoparasites of larger fishes, in which they enter the branchial cavity and feed on blood from the gill arteries that they pierce with their small but very sharp teeth. They are also infamous for entering the urethra of bathing humans, where they get stuck and may cause serious injuries and infections.

b) The phylogenetic relationships of Ostariophysi

The close relationship of the taxa Cypriniformes, Characiformes, Siluriformes, and Gymnotiformes has been recognized as early as 1885 by Sagemehl based on the shared presence of the Weberian apparatus.

Their phylogenetic relationships to other teleosts, however, have remained a matter of debate. Greenwood et al. (1966) noted a number of skeletal similarities between gonorynchiforms and Sagemehl's Ostariophysi. Pfeiffer (1967) found an unusual cell type, the Schreckstoffzelle (fright reaction cell) and an associated fright reaction in many representatives of Sagemehl’s Ostariophysi and in some species of the teleost order Gonorynchiformes and postulated a close relationship between the two taxa. Rosen & Greenwood (1970) found additional shared derived characters between these two teleostean orders, which they interpreted as evidence for a close relationship of the two taxa.

As a result, they included gonorynchiforms in Ostariophysi and created a new term Otophysi for Sagemehl’s well established taxon name Ostariophysi; the gonorynchiforms were named Anotophysi. Although many authors, like Patterson (1984) disliked this change in taxon names, Rosen & Greenwood’s classification and terminology has been followed by almost all subsequent workers (e.g. Fink & Fink, 1981, 1996). Monophyly of Ostariophysi (sensu Rosen & Greenwood) has since been corroborated by several character sets and has been summarized and reviewed by Fink & Fink (1981, 1996). The most significant characters for a monophyletic Ostariophysi are:

1. **Fright substance cells and fright reaction**. First discovered by v. Frisch (1938, 1941) in *Phoxinus*. The so called fright substance of ostariophysans is released from the fright substance cells when the skin is damaged and leads to a stereotypic flight reaction mediated by Mauthner axons.

(2) The fright substance is not species specific and fright substances from the skin of Otophysi leads also to the fright reaction in Anotophysi and vice versa (Pfeiffer, 1967).

(3) Unculi and breeding tubercles. The epidermis of Ostariophysi shows unicellular ceratinized projections, termed unculi by Roberts (1982) or multicellular ceratinized caps, the breeding tubercles (Collette, 1977).

(4) Position of sacculus and lagena. Both sacculus and lagena and their otoliths are shifted posteriorly and medially when compared to the non-otophysan state (Rosen & Greenwood, 1970).

(5) Structure of swimbladder. The swimbladder of Ostariophysi consists of two chambers separated by a constriction into an anterior smaller and a posterior larger compartment. The anterior part is intimately connected with the ribs of vertebrae 3 and 4 or their derivatives (Rosen & Greenwood, 1970).

The currently accepted phylogenetic hypothesis of ostariophysan intrarelationships is that of Fink & Fink (1981, 1996) (fig. 1). Ostariophysi are divided into two monophyletic groups, the Anotophysi and the Otophysi, adopted from Rosen & Greenwood (1970). Among the 127 characters used by Fink & Fink (1996) for their analysis, those from the Weberian apparatus (36 characters) play an important role for Otophysan relationships. Within Otophysi Cypriniformes form the sister group of the Characiphysi comprising the Characiformes + Siluriformes + Gymnotiformes. Within Characiphysi Siluriformes and Gymnotiformes form a monophyletic group, Siluriphysi, which is the sister group of the Characiformes.

Currently the Clupeomorpha are being discussed as the most likely sister group of Ostariophysi sensu Rosen & Greenwood (Lecointre & Nelson, 1996; Arratia 1997; Saitoh et al. 2003). This larger clade has been termed Otocephala by Johnson & Patterson (1996).

c) Historical review of literature on the Weberian Apparatus

a. Anatomical structure of the Weberian apparatus

In 1820 the German anatomist Ernst Heinrich Weber described a complex apparatus involving a series of three little ossicles that connect the swimbladder with the inner ear in the carp (*Cyprinus carpio*) (fig. 2), wels (*Silurus glanis*) and loach (*Misgurnus fossilis*). He postulated that the whole apparatus has a hearing function and that the three ossicles help to transfer sound to the inner ear and are comparable to the middle-ear ossicles of mammals. The former were named accordingly as *stapes*, *incus*, *malleus*. This idea of a similarity between the three ossicles and the mammalian middle ear ossicles was challenged and rejected only a few years later by Huschke (1822) and Geoffroy St. Hilaire (1824). They argued that the three ossicles in *Cyprinus*, *Silurus*, and *Misgurnus* are modified parts of anterior vertebrae and thus not the same (analogous in their terminology).

The modified anterior vertebrae of cyprinids and silurids were noted before Weber's (1820) contribution and the cyprinid tripus was illustrated by Fischer (1795) (fig. 3) and Rosenthal (1812) (fig. 4) and that of *Silurus* by Rosenthal (1816). However, it was Weber (1820) who recognized and described in detail the different components that form entire complex, comprising not only the three ossicles, but also the lymphatic spaces of the inner ear and the modified swimbladder.

Subsequent to Weber (1820), Heusinger (1826) noted a similar apparatus in a representative of the characiforms (*Gasteropelecus*), Müller (1842, 1845) confirmed its presence in cypriniforms, siluriforms and characiforms, and Baer (1835) and Reinhardt (1852) described it in representatives of the gymnotiforms. It was then Sagemehl (1885), who concluded that "die bekannten vier, mit einem Weber'schen Apparat versehenen Teleostierfamilien, nämlich die Welse, Gymnotiden, Characiniden und Cyprinoiden eine höchst natürliche, gut begrenzte Gruppe des grossen Teleostierstammes bilden."

He coined the term Ostariophysi for this assemblage and was the first to use the term Weberian apparatus for the character complex described by Weber (1820). Much ahead of his time he (1885:11) argued that the Weberian apparatus represents a "vollständige Homologie, die einzig und allein durch Ererbung dieses Apparates von einer den vier Physostomenfamilien gemeinsamen Stammform erklärt werden kann."

Bridge & Haddon (1890) introduced the name Weberian ossicles for the chain of ossicles between the swimbladder and the inner ear (compare fig. 5) and argued for a new terminology of its components to reflect the nonhomology with the mammalian middle ear ossicles. They suggested the new names *scaphium*, *intercalarium* and *tripus* still used today and also included Weber's (1820) *claustrum* in the Weberian ossicles. The term 'os suspensorium' was introduced by Sørensen (1890) for the modified ribs/transverse processes on the fourth vertebra , and Nelson (1948) coined the term *neural complex* for the roof formed above the neural canal of the anterior four vertebrae in Ostariophysi, which differs strikingly from the typical teleost condition (compare fig. 5).

Chranilov (1927) (fig.6) provided a detailed terminology for the different components of the Weberian apparatus, in which he distinguished 4 areas in anteroposterior direction:

1. *regio endolymphatica*: consisting of the canalis communicans transversus, which connects the sacculi of the left and right inner ear and the sinus endolymphaticus weberianus, a blind ending median posterior extension at the middle of the connecting canal.

2. *regio perilymphatica*: a posteriorly directed perilymphatic space, the sinus impar, which bifurcates into bilaterally paired atria sinus imparis at the level of the first vertebra.

3. *ossicula Weberi*: the four Weberian ossicles claustrum, scaphium, intercalarium, and tripus with the last three connected by interossicular ligaments and located in the saccus lymphaticus paravertebralis on both sides of the anterior three vertebrae.

4. *camera aerea weberiana*: the anterior compartment of the bipartite swimbladder, which is connected to the tripus.

Chranilov (1927) did not include the os suspensorium (sensu Sørensen, 1890) or the neural complex (sensu Nelson, 1948) in the Weberian apparatus, although these two characters still form an important integral component of the modifications of that were acquired during the evolution of the apparatus. Interestingly, the meaning of Sørensen's (1890) 'os suspensorium' was greatly restricted by Chranilov (1927) without convincing arguments to describe only the median part of the modified appendages of the fourth vertebra. Unfortunately many subsequent authors adopted “os suspensorium” in this restricted sense, as e.g. Fink & Fink (1981) in their influential paper on the phylogenetic relationships of the Ostariophysi.

b. Function of the Weberian apparatus

Weber (1820) not only described the apparatus named after him in great detail, he also offered the first explanation for its possible function. He concluded that the chain of three ossicles serves to transmit sound from the swimbladder to the inner ear. Hasse (1873) argued that the Weberian apparatus does not have a hearing function but rather serves to measure water pressure surrounding the fish and thus enables it to determine water depth. Sagemehl (1885) thought the apparatus capable of detecting atmospheric pressure changes so that changing weather conditions could be perceived.

Eventually the detailed anatomical investigations by de Burlet (1929, 1934) and the anatomical, behavioural, and physiological studies and experiments of von Frisch and his school (v. Frisch, 1923, 1936, 1938; Stetter, 1929; v. Frisch & Stetter, 1932; Wohlfahrt, 1932, 1938, 1950; v. Frisch & Dijkgraaf, 1935; v. Boutteville, 1935; Disselhorst, 1938; Dijkgraaf & Verheijen, 1950; Dijkgraaf 1952; Poggendorf, 1952) demonstrated without doubt that Weber was right and the apparatus named after him has a hearing function. It is used to receive sound pressure waves with the swimbladder, which are transmitted through the chain of tripus, intercalarium and scaphium to the perilymphatic and endolymphatic spaces of the inner ear, where they are perceived and transduced into nerve impulses at the Macula sacculi. Von Frisch and his school further showed that the Weberian apparatus enhances the capacities to discriminate different sound pressures as well as different frequencies. It also lowers the hearing threshold and expands the frequency range, at which sound pressure waves can be perceived. Whereas most teleosts without a Weberian apparatus are only capable of detecting frequencies in the range of 10-1000 Hz, Ostariophysi can hear between 20-13000 Hz. Among teleosts similar frequency ranges as in Ostariophysi can only be detected by taxa that also have a connection between the inner ear and the swimbladder or a comparable gas filled space, like some Notopteridae, Mormyridae (100-2500 Hz, Coombs & Popper, 1982; McCormick & Popper 1984), Clupeomorpha (up to 180 kHz, Mann et al. 1997), Holocentridae (up to 3000 Hz, Coombs & Popper, 1979) and Anabantoidei (up to 3500 Hz, Saidel & Popper, 1987) and Sciaenidae (600-4000 Hz, Ramcharitar et al. 2004) among the Percomorpha. The biological role of the enhanced hearing capabilities of Ostariophysi is only poorly understood. Some catfishes and characiforms can produce sounds with drumming muscles associated with the swimbladder or stridulatory mechanisms of pectoral or dorsal-fin spines (reviewed by Heyd & Pfeiffer, 2000), which might be used for intraspecific communication.

d) Towards a better understanding of the evolution and development of the Weberian apparatus

Since Weber's (1820) detailed description, one of the central issues in studies on the Weberian apparatus has been the homology of the different components involved. Numerous authors have focused on the homology of the skeletal components of the Weberian apparatus and have approached this question from different angles. Some authors have attempted to resolve the problem through comparative studies of adult specimens (Huschke, 1822; Baudelot, 1868 a, b; Sørensen 1890, 1895; Sagemehl, 1885; Bridge and Haddon, 1890, 1893; Bloch, 1900; Sachs, 1912; Chranilov, 1927, 1929; Ramaswami, 1952 a, b, c, d, 1953, 1955a, b, 1957; Tilak, 1964; Rosen & Greenwood, 1970; Fink and Fink, 1981) others approached it through ontogenetic studies (Müller, 1853; Wright, 1884b; Sørensen, 1890 (fig. 7); Nusbaum, 1908; Matveiev, 1929; Watson, 1939; Bamford, 1948; Butler, 1960; Rosen & Greenwood, 1970; Kulshrestha, 1977; Soni et al., 1978; Radermaker et al., 1989; Vandewalle et al., 1990; Bogutskaya, 1991; Fukushima et al., 1992; Ichiyanagi et al., 1993, 1996, 1997; Coburn and Futey, 1996; Coburn and Grubach, 1998; Bird and Mabee 2003; Grande & Young 2004).

One of the main shortcomings of all previous ontogenetic studies was their exclusive focus on cypriniforms and siluriforms. Agreement on the homology of the different skeletal components of the Weberian apparatus has not been reached and various hypotheses still exist even after more than 185 years of research.

My contribution investigates the early ontogeny of representatives of all four major otophysan subgroups, Cypriniformes, Characiformes, Siluriformes, and Gymnotiformes, using Anotophysi and other basal teleosts as outgroups. My study focuses on the development and homology of the neural complex and the first of the Weberian ossicles, the claustrum. Along with the development of the Weberian apparatus the area above the anterior spinal cord has also been modified comprising a bony roof in adult otophysans, the neural complex (sensu Nelson, 1948). Whereas, many previous authors focused on the homology of the Weberian ossicles, the question of the composition of the neural complex has rarely been raised and never been adequately addressed.

The **first part** of my study will therefore investigate the development of the neural complex among otophysans, review previous ideas about its composition and present a new hypothesis about the homology and evolution of this character complex.

The **second part** of my study will deal with the development and homology of the claustrum, originally not included in the series of *ossicula auditoria* by Weber (1820). The claustrum has often been referred to as the first Weberian ossicle in later papers. The issue of the identity of this small ossicle has received considerable attention in recent years, and yet another hypothesis as to its homology has been formulated (de Pinna & Grande 2003; Bird & Mabee, 2003; Coburn & Chai, 2003; Grande & Young, 2004; Grande & de Pinna 2004). I describe the development of the claustrum in representatives of the different subgroups of Otophysi, review all previous hypothesis of its homology, and then discuss them in light of my new findings.

3) MATERIALS AND METHODS

My study is based exclusively on cleared and double-stained (c&s) specimens of a large number of otophysan and non-otophysan taxa. Most of the series come from own rearing of numerous species at the research aquarium section of the Lehrstuhl für Spezielle Zoologie, Tübingen, a few other eggs and/or fry were purchased from fish farms. I chose the c&s technique, following Taylor & van Dyke's (1985) protocol, over traditional histological techniques for a number of reasons. Most importantly, c&s has the huge advantage that large series of hundreds of developmental stages can be studied in a relatively short time. Histological techniques always require the reconstruction of the sectioned areas of interest, which often are at least slightly deformed. This may lead to erroneous interpretations, as seems to be the case, I think, with several of the older works on the development of the Weberian apparatus in otophysans. These problems, however, do not occur in c&s specimens, as all skeletal components remain in the same three-dimensional context and are easy to study with light microscopy, either with a stereomicroscope at lower magnifications or a compound microscope, if higher magnifications are needed.

One challenge with c&s specimens, however, is their illustration. I have chosen to photograph my specimens, as I was unhappy with a number of drawings reproduced in recent papers on the subject and wanted to show the reader exactly what I was able to see. All c&s specimens were photographed at various magnifications with a Zeiss MC 30 camera attached to a Zeiss Axioplan or with a Jenoptik ProgRes C12plus digital camera attached to a Zeiss Tessovar.

a) Specimens

The following c&s material was studied. Length is given as standard length (SL).

HALECOMORPHI

Amiiformes

Family Amiidae

Amia calva: USNM, uncatalogued, 1 specimen, 41.0 mm SL.

TELEOSTEI

Osteoglossiformes

Familiy Pantodontidae

Pantodon buchholzi: BMNH 2004.8.6.1-24, 24 specimens, 4.2 mm to 69.0 mm SL.

Elopiformes

Family Elopidae

Elops machnata: BMNH 1962.8.28.1-7, 1 specimen, 39.2 mm SL.

Salmoniformes

Family Salmonidae

Oncorhynchus mykiss: 11 specimens, 22.5 to 28.0 mm SL.

Clupeiformes

Family Engraulidae

Anchoa mitchilli: 1 specimen. 23 mm SL.

Ostariophysi

Anotophysi

Family Chanidae

Chanos chanos: 1 specimen, 18.7 mm SL.

Family Kneriidae

Kneria sp.: 125 specimens, 5.2 to 23.0 mm SL.

Otophysi

Cypriniformes

Family Cyprinidae

Subfamily Cyprininae

Cyprinus carpio: 14 specimens, 6.2 to 17.2 mm SL.

Puntius sp. Odessa: 100 specimens, 3.6 to 12.2 mm SL.

Puntius fasciatus: 39 specimens, 4.8 to 13.5 mm SL.

Puntius filamentosus: 61 specimens, 4.8 to 20.0 mm SL.

"Barbus" holotaenia: 70 specimens, 4.2 to 22.1 mm SL.

Subfamily Rasborinae

Devario cf. *aequipinnatus*: 80 specimens, 5.7 to 32.5 mm SL.

Rasbora daniconius: 38 specimens, 5.0 to 12.0 mm SL.

Family Catostomidae

Myxocyprinus asiaticus: 16 specimens, 11.0 mm notochord length (NL) to 30.8 mm SL.

Characiformes

Family Alestidae

Rhabdalestes septentrionalis: 65 specimens, 4.3 mm NL to 11.9 mm SL.

Alestopetersius smykalai: 56 specimens, 5.8 mm NL to 16.0 mm SL.

Family Lebiasinidae

Lebiasina bimaculata: 75 specimens, 4.7 mm NL to 15.0 mm SL.

Pyrrhulina spilota: 26 specimens, 5.0 mm NL to 10.6 mm SL.

Family Erythrinidae

Hoplias malabaricus: 86 specimens, 6.8 to 61 mm SL.

Family Ctenoluciidae

Ctenolucius hujeta: 80 specimens, 4.5 mm NL to 35.7 mm SL.

Siluriformes

Family Diplomystidae

Diplomystes chilensis: AMNH 55321, 60 mm SL.

Family Siluridae

Silurus glanis: 91 specimens, 9.0 mm NL to 35.7 mm SL.

Family Callichthyidae

Megalechis thoracata: 67 specimens, 5.2 to 22.5 mm SL.

Family Loricariidae

Ancistrus sp.: 26 specimens, 5.5 to 11.2 mm SL.
Hemiloricaria beni: 19 specimens, 5.1 to 14.3 mm SL.
Sturisoma aureum: 14 specimens, 7.2 to 10.1 mm SL.

Gymnotiformes

Family Apteronotidae

Apteronotus albifrons: 43 specimens, 7.5 mm NL to 21.3 mm SL.
Apteronotus leptorhynchus: 33 specimens, 8.3 mm NL to 34.0 mm SL.

b) Terminology

(compare fig. 8)

I use ***basidorsals*** for the paired cartilaginous structures on the dorsolateral side of the centrum. Each ***neural arch*** consists of left and right halves that result from ossification (perichondral bone, membrane bone) of the left and right basidorsals. ***Neural spine*** refers to that part of the vertebra that is situated dorsal to the spinal cord and the supradorsals. It projects from the meeting point of the right and left halves of a neural arch and is unpaired and forms in membrane bone on the anterior five vertebrae in the ostariophysan taxa I studied. Neural spines can also be preformed in cartilage and develop from the tip of each arch and thus can be paired in basal teleosts (figs. 11, 12). Following Gadow & Abbott (1895), ***supradorsal*** is used for bilaterally paired autogenous cartilages, chondrifying medial to the tips of both halves of the neural arch and below the dorsal longitudinal ligament. They ossify during subsequent development and fuse to the medial sides of the neural arches (Grassi, 1883). Among basal teleosts, supradorsals are present on neural arches of abdominal vertebrae and usually on those of anterior caudal vertebrae depending on the taxon. In otophysan Ostariophysi supradorsals are only developed on vertebrae 1, 3 and 4. Those on vertebrae 3 and 4 contribute to the neural complex, as I will show below. ***Supraneural***

(Goodrich 1930) is a cartilaginously preformed, unpaired bony element in the dorsal midline between two neural spines of abdominal vertebrae and not homologous to the radials of a pterygiophore (Mabee 1988). I use the term ***supraneural cartilage*** for its cartilaginous precursor. ***Neural complex*** was originally introduced by Nelson (1948, 1949) as a term for the single bone that roofs the neural canal above vertebrae 3 and 4 in some Otophysi. I have extended its meaning slightly and use neural complex for the cartilaginous roof above the anterior four vertebrae and the ossified structures that develop from it.

The neural complex forms from different ontogenetic sources, as we will see below. The term ***membrane bone*** is used for parts of the endoskeleton that are not preformed in cartilage, as suggested by Patterson (1977).

To homologise structures on the first to fourth vertebrae in the different taxa of Otophysi, I made comparisons with the first to fourth vertebrae of outgroup taxa, and not with more posterior vertebrae of the same taxon. I am convinced that serial homology is not the correct way to justify homology, because this can only be achieved by comparison of the structure in question with the same structure in another taxon.

c) Abbreviations used in figures:

ANA	accessory neural arch	**NS**	neural spine
ASI	atrium sinus impar	**OS**	os suspensorium
BD	basidorsal	**Pap**	parapophysis
C	centrum	**R**	rib
CAW	camera aera weberiana	**S**	sacculus

CC	canalis comunicans
Cl	claustrum
ClC	claustral cartilage
CMs	cranial myoseptum
DLLi	dorsal longitudinal ligament
EN	epineural bone
Ic	intercalarium
IL	interossicular ligament
NA	neural arch
NC	neural complex
Sc	scpahium
Sd	supradorsal
SEW	sinus endolymphaticus weberianus
SI	sinus impar
Sn	supraneural
SnC	supraneural cartilage
Tr	tripus
TS	tectum synoticum
V	vertebra
VMs	vertebral myoseptum

4) RESULTS ON THE DEVELOPMENT OF THE NEURAL COPMPLEX

a) Anterior Neural Arches and Associated Structures in Non - Ostariophysi

Pantodon buchholzi

I describe two stages.

10.0 mm (fig. 9). All vertebrae are ossified in this stage, and each bears an elongate neural arch with a broad base. Neural arches are perichondrally ossified and their right and left halves end in membrane bone tips. The anterior most supraneural cartilage is developed in the dorsal midline between neural arches 3 and 4.

11.3 mm (fig. 10). This stage is almost identical to the previous one with one important difference. The left and right halves of the neural arches support large, elongate or triangular supradorsal cartilages subdistal to their tips.

Elops machnata

39.2 mm (fig. 11). All vertebrae are fully developed. The neural arches extend from the centrum dorsally and slightly posteriorly. Each half of the arches ends in a separate neural spine. Arches and spines still have a cartilaginous core surrounded by a thin layer of perichondral bone, except at the distal most tips, which remains exclusively cartilaginous. The base of each arch supports an epineural bone. Conspicuous bilaterally paired spherical supradorsal cartilages are attached to the medial sides of all neural arches/spines at about halfway along the combined length except for the accessory neural arch. A median series of perichondrally ossified supraneurals is situated in between the distal tips of subsequent neural arches with supraneural 1 between the accessory neural arch and the first neural arch.

Oncorhynchus mykiss

24.0 mm (fig. 12). All centra and neural arches are ossified. The neural arches resemble those of *Elops* in shape but differ in that the distal tips of their right and left halves, the neural spines, are in membrane bone. An accessory neural arch sits in front of neural arch 1. The distal tips of its halves are entirely in cartilage. Each subsequent neural arch bears large bilaterally paired supradorsal cartilages at the medial faces of its halves situated slightly below the proximal section of the neural spines. An elongate supraneural 3 cartilage is situated in the dorsal midline between the neural spines of the second and third vertebrae. Another, much larger supraneural cartilage in front of neural arch 1 is situated horizontally; its posterior tip is expanded and slightly turned up.

b) Development of the Anterior Neural Arches and Associated Structures in Anotophysi

Chanos chanos

(Figs. 13, 14). I describe the first five vertebrae of an **18.7 mm** specimen of *Chanos*; an ontogenetic series was not available. All centra of this specimen are already well ossified. Each centrum, except the first, bears a small postzygapophysis posteriorly at its dorsolateral face. Prezygapophyses are developed on the anterolateral face of vertebra 3 and subsequent posterior vertebrae. Dorsally, on the lateral aspect of each centrum, sits a neural arch, still cartilaginous at its base. The more dorsal parts of the neural arch have a cartilaginous core that is perichondrally ossified and bears narrow anterior and smaller posterior flanges of membrane bone. Distally the left and right halves of the neural arches continue as neural spines, which are entirely formed of membrane bone and separated in the dorsal midline. On the medial side of the dorsal tip of each neural arch half sits a cartilage, the supradorsal, which is closely applied to the perichondrally ossified arch. Like the arches, these supradorsals are paired structures and their size decreases posteriorly with the first and largest arch possessing the largest cartilages. The median supraneural cartilages are well developed, the first occurring between the neural spines of the first and second vertebra.

***Kneria* sp.**

My description is based on 4 selected stages that cover the development of the main features of the first five vertebrae.

7.5 mm (fig. 15). All five centra are well ossified and have about the same size. Cartilaginous basidorsals are present on all anterior vertebrae. They all possess a broader base with tapering tips that are widely separated from their partners in the dorsal midline.

8.8 mm (fig. 16). All neural arches are ossified perichondrally and are fused basally to their respective centra. The left and right halves of all neural arches are still separated from their partners in the dorsal midline and those of vertebrae 2-5 have short tips of membrane bone. A single, unpaired supraneural cartilage is present slightly in front of neural arch 2.

9.2 mm (fig. 17). The cartilage of the five neural arches has been mostly replaced by bone, except at the bases where cartilaginous cores remain. The distal membrane bone processes of the arches are much longer and still separated in the dorsal midline, although the distance between the tips of the left and right halves decreases in anteroposterior direction. The supraneural cartilage has increased in size and is located above the distal tips of neural arch 2. A tiny supradorsal cartilage has formed at the tips of the distal membrane process of the second arch.

12.4 mm (fig. 18). Left and right halves of neural arches of vertebrae 1 - 3 have grown toward each other but remain separate from their partners. Left and right halves of neural arches 4 and 5 are fused to each other in the dorsal midline and bear short posteriorly directed median neural spines. The bases of all neural arches have expanded laterally, and there are still small cartilaginous cores visible through the bone. Paired relatively large supradorsal cartilages are developed at the distal tip of each half of neural arch 1. An elongate supradorsal cartilage, probably representing fused supradorsals 2, connects the distal tips of the left and right halves of neural arch 2. An unpaired supradorsal 3 is situated between and slightly below the distal tips of the halves of neural arch 3. The supraneural cartilage extends from the distal ends of the halves of neural arch 2 halfway to those of neural arch 3. There is slight variation in the pattern of supradorsal cartilages among the specimens of our sample. The most common one is the one described for our 12.4 mm specimen, but in other specimens supradorsals 2 can be paired, or individual cartilages may be missing or may fuse. There seems to be ontogenetic variation of the position of the single supraneural. In early stages when it starts to chondrify, it is located at the level or slightly in front of the second neural arch (fig. 16), whereas it is found between the second and third neural arches in all larger specimens (fig. 18).

c) Development of the Neural Complex in Cypriniform Otophysans

In the following paragraphs I will focus on the ontogeny of the neural arches and associated structures of vertebrae 3 and 4, as these form the neural complex. The vertebral elements that form the Weberian ossicles will be described in a separate publication. I start with representatives of the Cypriniformes including cyprinine and rasborine Cyprinidae and Catostomidae.

Devario cf. aequipinnatus

I describe five stages.

6.5 mm (fig. 19). All anterior centra have formed. Neural arch 3 is perichondrally ossified and its tip is in membrane bone. Neural arch 4 is ossified, with the base bearing a perichondral ossification and the tip of the neural arch extended into a long process of membrane bone. The fifth vertebra has a neural arch with a cartilaginous base and its distal processes entirely in membrane bone.

7.1mm (figs. 20, 21). Neural arch 3 has elongated, and the distal membrane bone tips of its left and right halves bear cartilaginous nodules at their medial faces, the supradorsals 3. Neural arch 4 has also grown and its membrane bone processes are much longer. Like neural arch 3, they support cartilaginous supradorsals subdistally at their medial faces. Extending between distal tips of neural arches 3 and 4 is a narrow strip-like elongate supraneural 3 cartilage. A spherical supraneural 2 cartilage is developed in the connective tissue strand in which supraneural 3 is located, but more anteriorly at the level of the second centrum. The dorsolateral view on supradorsals 3 and 4 and supraneurals 2 and 3 shows clearly that they are separate cartilages.

7.6 mm (fig. 22). The third neural arch has increased its width from the base to the tip. Supradorsals 3 have enlarged and started to fuse with both supraneural cartilages in their dorsal areas at the level of the anterior tip of the supraneural 3 cartilage. Supradorsals 4 are also starting to fuse with the posterior tip of the supraneural 3 cartilage.

7.5 mm (fig. 23). Although slightly smaller, this specimen shows a more advanced developmental stage. The most significant change is the complete fusion of cartilaginous supradorsals 3 and 4 with supraneural 2 and 3 cartilages into the large roof of the neural complex.

14.5 mm (fig. 24). Neural arches 3 and 4 have grown and become stouter and their distal tips much wider to support the neural complex. The fourth neural arch bears a long neural spine at its distal tip. The cartilage mass of the neural complex shows six centres (four can be seen in lateral view) from which ossification has spread over the cartilage, two for supradorsals 3, two for supradorsals 4, one for supraneural 2, and one for supraneural 3. Supraneural 5 is present as a perichondrally ossified cartilage with an anterior lamina of membrane bone between neural spines 4 and 5.

Cyprinus carpio

I describe four developmental stages.

8.6 mm (fig. 25). All anterior centra are ossified. Neural arch 3 has a broad base and pointed tip. It is a perichondral ossification ending distally in a short needle-like tip of membrane bone. Neural arch 4 is slightly larger than neural arch 3, but is also a perichondral ossification with a needle-like tip of membrane bone.

9.1 mm (fig. 26). Neural arches 3 and 4 have grown further and their tips of membrane bone are longer. Supradorsal 3 and 4 cartilages are developed at the subdistal tip of the right and left halves of neural arches

3 and 4, respectively. The supraneural 2 and 3 cartilages have started to chondrify.

9.8 mm (fig. 27). The supraneural 2, but especially the supraneural 3 cartilages are much larger and have started to fuse. The latter has a roughly triangular shape. Supradorsals 3 and 4 have grown and started to contact the median supraneural 3 cartilage.

11.1 mm (fig. 28). The supraneural and supradorsal cartilages are fused to each other to form the neural complex. Supraneural 3 is represented by a thin perichondral ossification around the dorsal and posterior area of the neural complex. The supraneural 5 cartilage has chondrified in front of the neural spine of the fifth vertebra.

Puntius sp

I describe six stages.

4.7 mm (fig. 29). The basidorsal 3 is cartilaginous with a broad base and a tapering tip. The basidorsal 4 has a distal perichondral ossification, neural arch 4, which extends into a pointed tip of membrane bone.

5.1 mm (fig. 30). Basidorsal 3 still has a cartilaginous base, but its tip is now perichondrally ossified as neural arch 3 and bears a short process of membrane bone. Neural arch 4 is stouter with a longer distal membrane bone extension. Its subdistal tip supports a supradorsal cartilage.

5.3 mm (fig. 31). This is a slightly larger specimen of a comparable developmental stage. A dorsal view clearly shows the supradorsal cartilage at the medial tip of the left half of neural arch 4.

5.1 mm (fig. 32). Although this specimen is about the same size as the previous two, it is nevertheless further developed. Neural arches 3 and 4 are enlarged and have much wider bases. The tip of neural arch 4 extends as a short neural spine. Supradorsals 3 at the distal tips of the expanded halves of neural arch 3 are already fused to the elongate median supraneural 3 cartilage above neural arches 3 and 4. Posteriorly, the cartilage mass of supraneural 3 is in contact with supradorsal 4. The small median supraneural 2 cartilage has developed in front of the cartilage mass consisting of the fused supraneural 3 and the bilaterally paired supradorsals 3 and 4.

5.4 mm (fig. 33). Neural arch 3 has broadened even more. The supraneural 3 cartilage and supradorsals 3 and 4 show larger areas of fusion. The supraneural 2 cartilage has also started to fuse into this complex at its posterior tip, but it is still mostly separate.

7.3 mm (fig. 34). At this stage the neural arches 3 and 4 are stouter and broader and their distal tips are expanded to support the large neural complex. Neural arch 4 bears a long neural spine that extends dorsally parallel to the posterior edge of the neural complex. The supraneural 2 cartilage has completely fused into the neural complex resulting in a saddle-shaped cartilage. The supraneural 5 cartilage is present in front of the neural spine of the fifth vertebra.

Myxocyprinus asiaticus

I describe three stages that have the neural complex fully developed and lack earlier stages that show a separate origin of supradorsals for this species.

16.3 mm (fig. 35). Neural arches 3 and 4 are largely cartilaginous and have broadly expanded bases and tips. Their slender middle parts are perichondrally ossified. Neural arch 4 bears a long neural spine of membrane bone. The different components of the neural complex have already fused, but their former limits are still discernible. Supraneural 3 has developed as a perichondral ossification covering the dorsal face of the posterior neural complex from which a thin lamella of membrane bone projects anterodorsally.

16.8 mm (fig. 36). Neural arches 3 and 4 have an even broader base and tip, which support the supradorsal part of the neural complex. The perichondral ossification of the middle region is more extensive but still leaves the base entirely cartilaginous. The bony supraneural 2 has ossified perichondrally around the anterior dorsal face of the neural complex. The membrane bone crest of supraneural 3 is more extensive. The elongate supraneural 5 cartilage has chondrified between the neural spines of vertebrae 4 and 5.

20.1 mm (fig. 37). Ossification of the neural complex has advanced further, so that the large areas of cartilage are surrounded by perichondral bone. Only small strips of cartilage are left between supraneurals 2 and 3 and the ossifications of supradorsals 3 and 4. The median keel of membrane bone of supraneural 3 has become even higher.

Rasbora daniconius

(Fig. 38). I describe an **11.9 mm** specimen to demonstrate that this species shows the same principal arrangement of the components of the neural complex as in other cypriniforms. The neural arches 3 and 4 are already well ossified, the latter bearing a long neural spine at its posterior distal tip. Both neural arches support large supradorsal cartilages, which have already fused with supraneural cartilages 2 and 3 into the neural complex. There are six endochondral ossifications in the large cartilage mass, representing the paired ossified supradorsals 3 and 4 and the median supraneurals 2 and 3. The latter shows a short dorsal process of membrane bone. This stage thus closely resembles our 14.5 mm *Devario* and the 16.8 mm *Myxocyprinus*.

d) Development of the Neural Complex in Characiform Otophysans

I report the development of two African species of the family Alestidae, two South American Lebiasinidae, and one representative each of the South American Ctenolucidae and Erythrinidae.

Rhabdalestes septentrionalis

I describe five stages

7.1 mm (fig. 39). All centra are developed as membrane bone cylinders around the chorda. Neural arch 3 is a perichondral bone around the distal area of a small conical cartilage, basidorsal 3. Its tip extends into a short pointed process of membrane bone. Neural arch 4 is also perichondrally ossified around a cartilaginous base and bears a well-developed distal extension of membrane bone.

7.3 mm (fig.40). The left and right halves of neural arch 3 have a long distal process of membrane bone that curve anteriorly. Neural arch 4 has even longer distal processes of membrane bone, but is still separated from its partner. The triangular supraneural 3 cartilage has chondrified above vertebra two.

7.5 mm (figs. 41, 42). The anterior curvature of the distal membranous part of the left and right halves of neural arch 3 is more pronounced. Their distal tips each bear a cartilaginous nodule, supradorsal 3, at their medial sides. Neural arch 4 is completely ossified with a long posteriorly curving process of membrane bone. Subdistally, the tips of the left and right halves of the neural arch bear the large spherical cartilaginous supradorsals 4. Supraneural 3 is now a large elongate element above neural arches 1-3, but still separate from supradorsals 3 and 4. This is especially obvious in dorsal view. The anterior part of supraneural 3 projects into paired basal processes and an unpaired anterodorsal process (marked with arrows in fig. 41).

8.0 mm (fig. 43). The base of neural arch 3 has developed a posteroventrally directed short lateral process of membrane bone. The tips of the right and left halves of neural arch 3 continue into bowl-shaped ossifications that support the paired supradorsals 3. The latter are fused to the neural complex, but their original boundaries are still discernible. Neural arch 4 has a broader base through development of a ventral membrane bone process at its posterior face. Supradorsals 4 are also fused to the neural complex and supported by bowl-shaped ossifications continuing from the subdistal area of the left and right halves of neural arch 4. As with supradorsals 3, their original boundaries are still visible. The median supraneural 3 is fused with the paired supradorsals 3 and 4 into the neural complex, of which it forms the largest component. Its anteroventral corners project from the body of the cartilage mass. Its anterodorsal process is more conspicuous, and the perichondral ossification of supraneural 3 surrounds its base and covers the dorsal face of the cartilage. A small projection of membrane bone has formed pointing anterodorsally. The distal tip of the anterodorsal process of the supraneural 3 cartilage, its anteroventral corners, and its base remain with no signs of ossification. The supraneural cartilages 4 and 5 are developed, 4 in front of the distal tips of neural arch 4, and 5 in front of the distal tip of the neural spine of the fifth centrum.

8.4 mm (fig. 44). The membrane process at the base of neural arch 3 is stouter. The tips of the left and right halves of the neural arch are expanded capping the supradorsals 3 area of the neural complex. Neural arch 4 has a greatly broadened base and body, spanning the entire width of the centrum. The dorsal part of its body supports the supradorsal 4 area of the neural complex, and its neural spine is longer. Supraneural cartilages 4 and 5 are a little larger. The neural complex is higher and stouter. The ossification of supraneural 3 covers larger areas of the cartilage. The membrane bone process originating from the perichondral ossification of its anterodorsal process is larger and points anterodorsally.

Alestopetersius smykalai

I describe four stages.

8.3 mm (fig. 45). The anterior centra are ossified. Neural arch 3 has a cartilaginous core at its base but is otherwise fully ossified with a process of membrane bone curving anteriorly. The distal tips of its left and right halves support the paired cartilage nodules of supradorsals 3. Neural arch 4 is also ossified, but has a more extensive and elongate cartilage core. Its distal tip projects posteriorly as a membrane bone neural spine. The distal ends of the halves of neural arch 4 each bear a supradorsal 4 on their anteromedial faces. The elongate, median supraneural 3 cartilage has chondrified and extends from the level of the posterior end of centrum 3 to the level of centrum 1. It is still completely separate from supradorsals 3 and 4.

8.7 mm (fig. 46). The base of neural arch 3 bears a posteroventrally directed lateral process, similar to the one in *R. septentrionalis*. The distal tips of its left and right halves are expanded to support the larger supradorsals 3, and the same is true for neural arch 4. Supradorsals 4 have also enlarged, so that both paired supradorsals approach the even larger supraneural 3 cartilage closely.

8.6 mm (fig. 47). Although slightly smaller, this specimen shows a more advanced stage of differentiation of the neural complex. Both supradorsals are fused to the supraneural 3 cartilage, but the boundaries of supradorsal 4 are still visible. The anterodorsal process of the neural complex has ossified perichondrally forming supraneural 3, the anterior face of which extends into a short flange of membrane bone.

9.1 mm (fig. 48). Neural arches 3 and 4 have enlarged and are much stouter. The base of neural arch 4 has a posteroventral process of membrane bone that extends down to the centrum and is fused with it. The ossifications that support the cartilage of supradorsals 3 and 4 and are continuous with neural arches 3 and 4, respectively, have expanded and extend further dorsally. The ossification of supraneural 3 is more extensive covering the dorsal face of the cartilage. Its membrane bone process is larger.

Lebiasina bimaculata

I describe five stages.

7.7 mm (fig. 49). Basidorsal 3 is a small conical cartilage on the third centrum. Its distal tip has started to ossify perichondrally thus forming neural arch 3. The fourth neural arch is much further developed, almost completely ossified along its length and with long membrane bone process at the tips of its left and right halves.

8.0 mm (fig. 50). Both halves of neural arch 3 bear short processes of membrane bone at their tips, but the base still has a large cartilaginous core. Neural arch 4 is similar to the previous stage, but now supports the supradorsal 4 cartilages subdistal to the tips of its halves. The elongate supraneural 3 cartilage has chondrified above neural arch 2.

9.0 mm (fig. 51). Both halves of neural arch 3 are conspicuously curved anteriorly and support small supradorsal 3 cartilages at their distal membrane tips. Neural arch 4 has enlarged, and its associated supradorsals 4 are much larger. The latter contact the posterior end of the greatly enlarged supraneural 3 cartilage, but are not fused with it. An elongate anterodorsal process is developed on the supraneural 3 cartilage. The supraneural 5 cartilage has chondrified in front of the neural spine of the fifth vertebra.

9.9 mm (fig. 52). The supraneural 3 cartilage and supradorsals 4 have enlarged further, but supradorsals 3 still lag behind. The anteroventral tip of the supraneural 3 cartilage and the anterior corner of supradorsals 4 are almost in contact with supradorsal 3. The boundaries between supraneural 3 cartilage and supradorsals 4 are still clearly visible.

11.2 mm (fig. 53). The base of neural arch 3 has formed a posteroventrally directed process, as in the other two characiforms described above. All components of the neural complex are in contact now, with their limits still discernible. Supraneural 3 is developed as a perichondral ossification around the anterodorsal process and dorsal face of the supraneural 3 cartilage.

Pyrrhulina spilota

I describe five stages.

6.0 mm (fig. 54). All anterior centra are ossified. Basidorsal 3 consists only of a few chondrocytes on the dorsolateral face of the third centrum. The fourth neural arch well developed with a long process of membrane bone that extends dorsally slightly beyond the neural tube. The supraneural 3 cartilage is chondrified as an elongate narrow rod of cartilage extending from the anterior end of the fourth centrum anterodorsally to the level of the anterior end of the second centrum.

6.2 mm (fig. 55). Neural arch 3 is much smaller than neural arch 4, and has developed as a thin perichondral lamella with a short dorsally projecting process of membrane bone. Neural arch 4 supports paired spherical supradorsal 4 cartilages at the subdistal tip of its left and right halves. The supraneural 3 cartilage has enlarged considerably, and its posterior end approaches supradorsals 4.

6.4 mm (fig. 56). Neural arch 3 has grown further and extends dorsally as a membrane bone process that curves slightly anteriorly. Neural arch 4 has enlarged and its base still retains a cartilaginous core. The subdistal tips of its left and right halves are expanded to support the larger supradorsals 4. The posterior end of the long and rod-like supraneural 3 cartilage contacts the anterior faces of the supradorsals 4.

7.4 mm (fig. 57). This stage is much further developed. Neural arch 3 is larger and stouter. It bears a posteroventrally and laterally directed process of membrane bone at its base, very similar to that found in the other characiforms. The dorsal tips of its left and right halves are expanded and support large supradorsals 3. Neural arch 4 has widened considerably, and the tips of its halves are more expanded to accommodate the large supradorsals 4. The supraneural 3 cartilage and supradorsals 3 and 4 are in close contact, but the limits of the individual structures are still visible. The anterodorsal process of the supraneural 3 cartilage has ossified perichondrally as supraneural 3.

8.2 mm (fig. 58). This stage mostly resembles the previous one. The neural arches have grown further and the association of the different components of the neural complex has become more intimate. Supradorsals 3 appear to have fused with the supraneural 3 cartilage, however, the boundaries of the cartilage of supradorsal 4 can still be discerned.

Ctenolucius hujeta

I describe four stages.

10.2 mm (fig. 59). Neural arch 3 is developed as a short conical perichondrally ossified cartilage with a needle-like anteriorly curving process of membrane bone. Neural arch 4 is much larger, and its distal membrane bone process is much longer than that of the third. The supraneural 3 cartilage has chondrified above neural arches 1 and 2.

13.5 mm (fig. 60). Neural arch 3 is well ossified now and extends further dorsally where its left and right halves end in anteriorly curved membrane bone processes that support the supradorsals 3. Neural arch 4 is much stouter and has a much broader base. The dorsal ends of its halves are expanded into cup-shaped faces that support large supradorsal 4 cartilages. From there a neural spine projects posterodorsally. The supraneural 3 cartilage has become larger, extending now between the level of the first and the third vertebra. It is still completely separate from either supradorsals 3 or 4. The supraneural 4 cartilage has started to chondrify in front of the distal tip of the neural spine of the fourth vertebra.

16.2 mm (figs. 61, 62). Neural arch 3 has broadened and its halves show expanded tips that support the larger cartilages of supradorsals 3. Neural arch 4 has also broadened, and the expanded distal cup of its halves support the much larger, round supradorsals 4. The supraneural 3 cartilage touches supradorsals 3 and 4, but the zone of separation is still clearly visible. This separation is especially obvious in dorsal view. Supraneural 4 has elongated.

23.3 mm (fig. 63). Neural arch 3 has expanded considerably and spans almost the width of its centrum. The same is true for neural arch 4. The distal ends of the halves of both neural arches have expanded to cup the cartilages of supradorsals 3 and 4. The dorsal face of the cartilage of the neural complex and its anterodorsal process bear the perichondral and membrane bone ossification of supraneural 3, which covers the upper third of the cartilage like a saddle.

Hoplias malabaricus

I describe five stages.

7.4 mm (fig. 64). All centra are developed as thin ossifications around the chorda. Basidorsal 3 is a pointed conical cartilage. Basidorsal 4, which is about double the length of basidorsal 3, is perichondrally ossified with a short membrane bone tip thus forming neural arch 4.

7.7 mm (fig. 65). Neural arch 3 is perichondrally ossified and its distal tip in membrane bone is curved anteriorly. Neural arch 4 is completely ossified perichondrally, and its distal tip extends in membrane bone. Below and medial to the backwardly curved neural spine supradorsal 4 begins to develop as a knob of cartilage. The roughly triangular supraneural 3 cartilage has chondrified above the tips of neural arches 2 to 4.

8.1 mm (fig. 66). The distal needle-like tip of neural arch 3 is conspicuously curved anteriorly. Neural arch 4 resembles that of the previous stage, but the supradorsals 4 that it supports are much larger. The supraneural 3 cartilage approaches supradorsals 4 closely, but is still separated from them. Its anteroventral area projects into bilaterally paired arms and an anterodorsal process is developed.

8.5 mm (fig. 67). The close-up of the left side of this stage shows the supradorsal 3 on the distal tip of the left half of neural arch 3. But like supradorsal 4, it is still separate from the supraneural 3 cartilage.

9.7 mm (fig. 68). Neural arch 3 is much stouter and the tips of its halves are expanded into a cup to support supradorsals 3. Neural arch 4 has expanded too, especially its subdistal parts that are associated with supradorsals 4. The supraneural 3 cartilage has now fused to supradorsals 3 and 4 and bears a long anterodorsal process that approaches the occipital region. This process and the dorsal face of the body of the neural complex have perichondrally ossified as supraneural 3.

e) Development of the Neural Complex in Gymnotiform Otophysans

Apteronotus leptorhynchus

I describe four stages.

9.0 mm (fig. 69). Basidorsals 3 and 4 are represented by two elongate conical cartilages.

10.6 mm (fig. 70). Neural arches 3 and 4 have developed a distal membrane process and their bodies, except their cartilaginous bases (basidorsals 3 and 4), are present as perichondral bone. A small supradorsal 3 is developed at the base of the membrane process of the halves of neural arch 3, and the neural arch 4 halves bear small supradorsals 4 subdistal to their tips. These cartilages are clearly visible in the close-up of our **10.8 mm** specimen (fig. 71).

11.2 mm (fig. 72). Neural arches 3 and 4 have not changed much compared to the previous stage, but a thin thread of cartilage interconnects the supradorsals 3 and supradorsals 4 of each side. There is no cartilaginous connection across the midline. A well-developed, vertically oriented supraneural 3 cartilage is present above the second centrum and between the distal area of neural arch 3 and the tectum synoticum of the occiput. The supraneural 3 cartilage approaches supradorsals 3 closely.

11.9 mm (fig. 73). Neural arches 3 and 4 have grown, and their ossifications reach down to the bases, with their cores still in cartilage. The cross-connection of supradorsals 3 and 4 is wider. The supraneural 3 cartilage is fused with supradorsal 3 and with the dorsal area of the cartilage connecting the supradorsals. It bears a long anterodorsal process that runs parallel to the synotic tectum.

Apteronotus albifrons

I describe four stages.

11.0 mm (fig. 74). Neural arches 3 and 4 are already well-ossified perichondrally at their bases and have membrane bone processes at their tips. The tips of the left and right halves of neural arch 3 support small supradorsal 3 cartilages.

12.0 mm (fig. 75). Neural arches 3 and 4 have not changed significantly. However, a cartilaginous bridge now interconnects supradorsals 3 and 4 of each side. The dorsal area of this connecting cartilage and supradorsals 3 are fused with the supraneural 3 cartilage, resembling closely the 11.9 mm specimen of *A. leptorhynchus*.

16.0 mm (fig. 76, 77). Neural arches 3 and 4 have grown. Supraneural 3 has developed as a perichondral ossification around most of the length of the anterodorsal process of the cartilage. A close-up of the neural complex in dorsal view illustrates its posterior incisure that results from incomplete closure of the gap between the connecting cartilage of supradorsals 3 and 4.

19.8 mm (fig. 78). Neural arches 3 and 4 have grown further and their tips are more expanded to support the larger neural complex. The anterodorsal tip of the neural complex is curved anteriorly and has elongated along the synotic tectum. It is covered by a thin perichondral ossification, supraneural 3, except at its distal end.

f) Development of the Neural Complex in Siluriform Otophysans

The neural complex of siluriforms has been highly modified in the different subgroups and the most primitive condition is exhibited by representatives of the family Diplomystidae. As an ontogenetic series of a diplomystid was unavailable, I start this section with a juvenile specimen of *Diplomystes chilensis* that shows all essential features. I also provide the description of the ontogeny of *Silurus glanis*, a siluriform with a relatively unmodified neural complex. This is contrasted with *Ancistrus* sp., a representative with one of the most highly derived structures of the neural complex among catfishes.

Diplomystes chilensis

60.0 mm (fig. 79). Vertebrae 3 and 4 and their neural arches are fused completely to each other. The neural spine of neural arch 4 is strongly developed and points posterodorsally. Anteroventrally it continues into a ridge on the neural arch that projects as a lateral process from the centrum. Anterodorsal to that ridge is a flange of bone that projects anteriorly toward the braincase and covers the lateral part of the still cartilaginous part of the neural complex. The dorsal tip of this cartilage is capped by supraneural 3. The posterior part of the tectum synoticum remains cartilaginous.

Silurus glanis

I describe five stages.

11.6 mm (fig. 80). The halves of neural arch 3 are short conical cartilages, perichondrally ossified at their tip, which bear long needle-like membrane bone processes that curves slightly anteriorly. Neural arch 4 is more elongate, but also perichondrally ossified with a short membrane bone process at the tips of its halves. Subdistally, a few chondrocytes represent the developing supradorsal 4 cartilages.

12.4 mm (fig. 81). The anterior curvature of the distal membrane bone process of the neural arch 3 halves is stronger. Their tips support the cartilages of supradorsals 3 medially. The mediodistal tips of the membrane bone processes of the left and right halves of neural arch 4 bear the supradorsal 4 cartilages. A narrow strip of cartilage interconnects supradorsals 3 and 4 of each side. A supraneural is not developed.

13.4 mm (fig. 82). The distal membrane processes of neural arch 3 have elongated and support larger supradorsals 3. Neural arch 4 is much stouter and it bears a long posterodorsally directed neural spine. Supradorsals 4 have also enlarged, and the strips of cartilage connecting them to supradorsals 3 are higher.

15.4 mm (figs. 83, 84). The connecting cartilages of supradorsals 3 and 4 have expanded dorsomedially so that both sides are now confluent forming a cartilaginous roof above neural arches 3 and 4. Its dorsal face has an elongate posteriorly directed process. Its posterior end shows a dorsomedian incisure that results from incomplete fusion of supradorsals 4 to each other, as described above for the two gymnotiforms. A supraneural has not chondrified, so the neural complex is formed solely by supradorsals 3 and 4. The halves of neural arches 3 and 4 of each side are almost connected to each other by a bony bridge at the ventrolateral edge of the neural complex, originating from the halves of each arch and meeting at about midway.

16.6 mm (fig. 85). Neural arch 4 has expanded and has grown considerably, its base now spanning the width of its centrum. The ossification between the arches 3 and 4 has become more extensive and has entered larger areas of the cartilage of the neural complex.

***Ancistrus* sp.**

I describe three stages.

6.3 mm (fig. 86). The anterior centra are not ossified. Basidorsal 3 is missing and the first basidorsal behind the occiput is basidorsal 4. Its axis is inclined toward the occiput and its tip points anteriorly to the synotic tectum. The base of basidorsal 4 is confluent with basiventral 4, a conical cartilage on the side of the centrum.

6.5 mm (fig. 87). Basidorsal 4 has grown further toward the occiput and a narrow space separates its tip from the synotic tectum.

7.5 mm (fig. 88). The tip of basidorsal 4 now contacts the synotic tectum of the occiput, but its distal boundaries are still visible. Its middle part is ossified perichondrally as neural arch 4. Subsequently, neural arch 4 and its associated basiventral 4 show a complicated ontogenetic pattern involving incorporation of the arch into the back of the skull, and the development of the os suspensorium. I found an almost identical development as that just described for *Ancistrus* in other loricarioids, the callichthyid *Megalechis* and the loricariids *Sturisoma* and *Hemiloricaria*. A detailed description of these developmental processes is beyond the scope of this study, but it is important to note that the neural complex does not form in *Ancistrus* or the other loricarioids I studied.

5) DISCUSSION

My data above show that supradorsal cartilages developing at the medial faces of neural arches 3 and 4 during ontogeny contribute an important component to the formation of the neural complex in otophysan fishes.

The significance of supradorsals 3 and 4, however, varies among otophysans and is summarized in fig. 115. In all cypriniforms I studied, the spherical supraneural 2 cartilage chondrifies at the level of the posterior end of the first vertebra or at the level of the second vertebra. The more elongate supraneural 3 cartilage appears at the level of the third vertebra and soon elongates further posteriorly. Supradorsals fuse with supraneural cartilages in a distinctive pattern to form a cartilaginous roof above the neural canal, the neural complex, extending from the back of the skull to the fourth vertebra. Supradorsals 4 fuse with the posterior end of the supraneural 3 cartilage, and supradorsals 3 fuse with the anterior end of supraneural 3 and the posterior end of supraneural 2 cartilages. Subsequently, six centres of ossifications develop in the neural complex, four for the paired supradorsals 3 and 4 and two for the median supraneurals 2 and 3.

In all my characiforms, the single supraneural cartilage chondrifies above the second vertebra, thus slightly more anteriorly compared to the supraneural 3 cartilage in cypriniforms. In the two alestids, the erythrinid, and the ctenolucid, the supraneural 3 cartilage then fuses with the two pairs of supradorsals 3 and 4, which appear at about the same time, with supradorsals 3 lagging slightly behind. In my two lebiasinids, the whole third arch conspicuously lags behind the fourth in its development. Neural arch 4 is fully ossified and bears large supradorsals, when the third arch is not more than a short cartilage cone with an apical membrane process. Thus, supraneural 3 reaches supradorsals 4 first and only later contacts supradorsals 3. I do not know how widespread this delayed development of neural arch 3 is among characiforms.

In the two gymnotiforms I investigated, supradorsals 3 and 4 develop an interconnecting strip of cartilage, and only later the single supraneural cartilage fuses with supradorsals 3 and the dorsal area of the interconnecting cartilage.

The structure of the neural complex of the siluriform *Diplomystes*, a member of the most basal catfish clade, is similar to that of gymnotiforms. A small supraneural 3 is developed on the anterodorsal corner of the neural complex. In *Silurus*, however, supraneural 3 is absent. Only the interconnecting cartilage between supradorsals 3 and 4 develops and fuses with its opposite member to form the neural complex. Finally, in the highly derived loricariid *Ancistrus* and the other loricarioids I studied, a neural complex is completely lacking and the fourth neural arch fuses with the occiput. In addition to supradorsals 3 and 4 only those of the first vertebra are developed and represent the claustra, a hypothesis that I will develop further below. Supradorsals 2 and those of vertebrae posterior to the fourth are lacking in otophysans.

Supradorsal cartilages have been known since they were described as "Schlusstücke" more than 150 years (Stannius, 1849) in salmonids and esocids. They have since been reported by a number of authors (Müller, 1853; Goette, 1879; Grassi, 1883; Scheel, 1893; Gadow & Abbott, 1895; Bloch 1900; Schauinsland, 1906; Remane, 1936; François, 1966; Rosen & Greenwood, 1970; Bartsch, 1988; Arratia, 1997) in different teleosts (see figs. 9, 10, 11, 12, 13, 14, 17, 18 for *Pantodon*, *Elops*, *Oncorhynchus*, *Chanos*, *Kneria*; they are further present in *Hiodon*, *Osteoglossum*, *Scleropages*, *Megalops*, pers. obs.), and occur also in *Amia* (pers. obs.; Hay, 1895; Schauinsland, 1906; Remane, 1936; Grande & Bemis, 1998) and *Lepisosteus* (Gegenbaur, 1867; Balfour & Parker, 1882; Schauinsland, 1906; Remane, 1936) among nonteleostean actinopterygians. Similar cartilages are also known from Dipnoi (see Arratia & Schultze, 2001), but their homology is not resolved.

It is surprising to me that no previous author realized that supradorsals present a major part to the formation of the neural complex of Otophysi during development. Fink & Fink (1981) doubted the presence of supradorsals altogether, stating that (p. 325-326): "Rosen & Greenwood (1970) and others have used the term “supradorsal” for the dorsal part of the neural arch. However, supradorsal properly refers to a separate median cartilage dorsal to the neural arch (basidorsal) element in elasmobranchiomorphs and has been only tentatively applied to the paired cartilages in many actinopterygians (Goodrich, 1958: 34). Since these paired cartilages appear not to be separate elements, but simply cartilage of the arches along their midline synchondral joint, the term supradorsal seems inappropriate."

A number of authors have followed Fink and Fink's (1981) conclusion, as e.g. Coburn and Futey (1996), and Coburn and Chai (2003). De Pinna and Grande (2003: 843) added to the confusion with the following incorrect statement: “Rosen and Greenwood (1970) homologized the claustrum with a dissociated dorsomedial portion of the first neural arch (which they called supradorsal, following François, 1966), an idea endorsed by Fink and Fink (1981) and apparently first proposed by Hora (1922).” This statement contains two errors. Rosen and Greenwood (1970) considered supradorsals to be elements separate from the neural arches, and Fink and Fink (1981) specifically argued against this hypothesis, as noted above.

Fink and Fink's (1981) statement refuting the presence of supradorsals in Ostariophysi consists of two parts: 1) the first deals with the homology of supradorsal cartilages of teleosts and those of elasmobranchiomorphs; 2) the second with the absence of supradorsals as autogenous anatomical entities. I will address both in sequence.

1) The term "supradorsal" was created by Gadow & Abbott (1895: 171). These authors specifically mentioned Stannius (1849), Müller (1853), and Grassi (1883), who previously described the structures they named supradorsals in *Esox*, *Salmo*, and *Coregonus*. Thus, the term supradorsals was not specifically restricted to cartilaginous structures in elasmobranchiomorphs but was equally applied to the paired cartilages at the dorsal tip of neural arches in a variety of osteichthyans. Fink & Fink (1981) are thus mistaken that supradorsals occur only in elasmobranchiomorphs.

Fink & Fink (1981) were apparently unaware of a number of previous papers clearly demonstrating that supradorsal cartilages are autogenous structures (Stannius, 1849; Müller, 1853; Goette, 1879; Scheel, 1893;

Grassi, 1883; Gadow & Abbott, 1895; Bloch 1900; François, 1966). My observations in my ostariophysan and outgroup developmental material confirm that supradorsals arise as separate cartilages **after** the neural arches have ossified, demonstrating unambiguously that they are autogenous cartilages and not part of the cartilage of the neural arch itself. A useful landmark to delimit supradorsals is their relation to the dorsal longitudinal ligament that extends between the braincase and the caudal area. They are situated invariably on the medial side of the arches and below this ligament, as pointed out previously by a number of authors (Stannius, 1849; Goette, 1879; Grassi, 1883; Scheel, 1893; Gadow & Abbott, 1895).

Having established the significance of supradorsals 3 and 4 for the formation of the neural complex in otophysans, I now turn to the different hypotheses about the homology of this structure and discuss them in light of my findings. I consider it essential to review all previous hypotheses, even if those are considered out of date now. This is especially important, because a large number of key papers were published in languages other than English and therefore often do not receive the attention they deserve in many of the recent papers on the Weberian apparatus.

a) Homology of the Neural Complex

Apart from Grassi (1883) and Sagemehl (1885), who were uncertain about the homology of the neural complex, 6 hypotheses can be distinguished according to the structures that were claimed to form the neural complex.

(1.) Neural complex formed by neural spines (Weber, 1820; Wright, 1884a, 1884b; Nusbaum, 1908; Sachs, 1912; Chranilov, 1926, 1927, 1929; Watson 1939; Nelson 1948, 1949)

(2.) Neural complex formed by neural arch 2 and neural spines 2 and 3 (Ramaswami, 1952a, 1952b, 1953, 1955a, 1955b, 1957)

(3.) Neural complex formed exclusively by neural arches (Kulshrestha, 1977)

(4.) Neural complex formed exclusively by supraneurals (Baudelot, 1868; Bogutskaya, 1991; Fukushima et al., 1992, Ichiyanagi et al., 1993, 1996, 1997)

(5.) *Neural complex formed by neural arches and supraneurals* (Watson, 1939; Bamford, 1948; Fink and Fink, 1981; Coburn and Futey 1996; Bird and Mabee, 2003; Grande and Young, 2004)

(6.) Neural complex formed by contribution of supradorsals (Müller, 1853; Bloch, 1900; Bamford, 1948; Butler, 1960; Vandewalle et al., 1989).

Clearly the systematic position of the taxa that the authors studied had a great influence on their ideas about the homology of the neural complex, and I therefore have organised the following discussion section into four parts according to the four otophysan subgroups, Cypriniformes, Characiformes, Siluriformes, and Gymnotiformes.

b) The Neural Complex in Cypriniformes

(1.) Neural complex formed by neural spines

The two bones in the neural complex of *Cyprinus carpio* and *Barbatula barbatula* were described and labelled by Weber (1820) as neural spines of the first and second vertebrae. The idea that neural spines form the neural complex in cypriniforms was supported by Nusbaum (1908) and Sachs (1912), although the former erroneously considered parts of the anterior three vertebrae to have been incorporated into the occipital skull roof and therefore concluded that vertebrae 3 and 4 are actually vertebrae 4 and 5. Chranilov (1926, 1927, 1929) considered the two ossifications in adult cyprinids to represent neural spines 2 and 3. Watson (1939) thought that neural spines contributed to the neural complex, but his ideas are dealt with below.

Although Matveiev (1929) agreed that neural spines contribute to the formation of the neural complex, he assumed an additional contribution of supraneurals (his "Dorsospinalia"), a view also shared by Nelson (1948: 229), who held that the "lamina and neural spines of the third vertebra plus possible interspinous elements" formed the neural complex.

In none of my developmental series of cypriniforms or other otophysans, I could find that neural spines 1 or 2 were involved in the formation of the neural complex. The two separate ossifications in the dorsal part of the neural complex of cypriniforms are clearly supraneural elements, as they are preformed in cartilage, unlike neural spines of anterior vertebrae, which form in membrane bone in Otophysi. The supraneural elements correspond to supraneurals 2 and 3, as suggested by Patterson (1984) and adopted by Fink & Fink (1996). A neural spine, as that part of the vertebra dorsal to the spinal canal and the supradorsals, is not developed on neural arch 3 in any of our otophysan representatives. Neural arch 4, however, bears a relatively normally developed neural spine in our material. We thus can reject the hypothesis that neural spines contribute to the formation of the neural complex.

(2.) Neural complex formed by neural arch 2 and neural spines 2 and 3

A hypothesis similar to that of the authors mentioned in the previous paragraph appears in the series of publications by Ramaswami (1952a, 1952b, 1953, 1954, 1957). He assumed that the anterior (= supraneural 2) of the two bones in the neural complex of adult cypriniforms represents neural arch 2, and the posterior bone (= supraneural 3) comprises fused neural spines 2 and 3. As already discussed above, the second neural arch or spine does not contribute to the formation of the neural complex, and a neural spine is lacking on the third vertebra. Therefore none of the mentioned elements contribute to the neural complex, and this invalidates Ramaswami's hypothesis.

(3.) Neural complex formed exclusively by neural arches

Kulshrestha (1977) considered that neural arches of vertebrae 2 to 4 exclusively form the neural complex in the cyprinid *Labeo rohita* with no contribution from the supraneurals. As I have noted in the previous paragraphs, neither the second vertebra nor neural arches 3 and 4 participate in neural complex formation. Although closely associated with neural arches 3 and 4, supradorsals 3 and 4, which form a large part of the neural complex, are nevertheless autogenous elements, and as such are not part of neural arches 3 and 4. Supradorsal elements were unknown to Kulshrestha (1977).

(4.) Neural complex formed exclusively by supraneurals

The idea that supraneurals contribute to the neural complex dates back to Baudelot (1868), who considered the roof above the anterior vertebrae to consist of "intercruraux" (= supraneurals in our current terminology). Subsequently, only a few authors considered the neural complex to be formed exclusively by supraneurals. One of them (Bogutskaya, 1991: 117-118) held that the neural complex in cypriniforms would be possibly "formed only by fused interneurals" (= supraneurals), and she referred to the resulting ossifications as "complex neuralis" (= supraneural 2) and "planum neurale" (= supraneural 3).

I agree in part with Bogutskaya (1991) that supraneural cartilages contribute to the neural complex in cypriniforms, but not exclusively, as she claimed. Equally important are the supradorsals, which were unknown to her, as she neither mentioned nor illustrated them. The cartilage mass that Fukushima et al. (1992) and Ichiyanagi et al. (1996) reported during development of three cypriniforms was referred to as 'cartilaginous supraneural', because it seemed to develop only from one anlage. In contrast, I found two separate chondrification centres in our developmental material of seven cypriniform species. Fusion of these two centres with each other and with the supradorsal cartilages occurs relatively fast after chondrification. Interestingly, Fukushima et al. (1992) and Ichiyanagi et al. (1996) reported six ossification centres in the cartilage mass without being aware of their potential significance: two in the dorsal midline, corresponding to supraneural 2 and 3, and four at the position of the dorsal end of the neural arches 3 and 4, corresponding to supradorsals 3 and 4. Apparently, the developmental stages that Fukushima et al. (1992) and Ichiyanagi et al. (1996) illustrated were not as closely spaced as needed to resolve separate chondrification centres for the two supraneural cartilages and supradorsals 3 and 4.

(5.) Neural complex formed by neural arches and supraneurals

Most other authors, who agreed that supraneurals are involved in the formation of the neural complex, usually assumed also a participation of the distal ends of neural arches of vertebrae 3-4 (Watson, 1939; Fink and Fink, 1981; Coburn & Futey 1996). Investigating the skeletal ontogeny of the goldfish, Watson (1939, p. 455) noted that the "large mass of cartilage" above the anterior vertebrae would become "ossified to form the neural spine and arches of the 'compound' vertebra", and that the "basidorsal of the fourth arch is fused with this mass, as is also part of the basidorsal of the second vertebra." In his summary he concluded that the "basidorsals of the second (part only), third and fourth vertebrae fuse with the first three interspinous bones" (or rather their cartilaginous precursors) and would be contributing to the cartilage mass. In a footnote (Watson, 1939: 456) he admitted that the "participation of the basidorsal of the second vertebra was not detected in the young stages, but was inferred..." In his fig. 7 (Watson, 1939: 460), he labelled the ossification in the cartilage mass as third neural spine. I cannot explain these contradictory statements, but it seems that Watson (1939) was uncertain and confused as to what parts of the skeleton of a regular vertebral segment contribute to the formation of the neural complex. It appears to me that some of this confusion arose because Watson (1939) was lacking important ontogenetic stages of the neural complex, as the 12 mm stage he illustrated (Watson, 1939: Fig. 3) already has a fully developed cartilaginous roof above the neural canal. He thus could only have speculated what may have contributed to the formation of a complex structure without having demonstrated the actual development. Unfortunately, Fink & Fink (1981) concluded, based on Watson (1939), that the “dorsomedial portion of the second neural arch … forms part of the cartilage block roofing the neural canal anteriorly.” As I have detailed above, in my closely spaced developmental series of seven different cypriniforms I found the neural complex to develop from supraneurals 2 and 3 and supradorsals 3 and 4. The second neural arch never contributes to its formation.

Coburn & Futey (1996), and more recently Bird & Mabee (2003) and Grande and Young (2004), showed that the supraneural part of the neural complex of cypriniforms arises from two chondrification centres, referred to as supraneural 2 and 3. These coalesce during development, but eventually ossify as two different bones, a fact that, as such, has been known for a long time. Previously, only a large cartilaginous mass had been recognized by authors who studied the ontogeny of the neural complex in cypriniforms (Nusbaum, 1908; Matveiev, 1929; Watson, 1939; Vandewalle et al. 1989, 1990; Bogutskaya, 1991; Fukushima et al., 1992; Ichiyanagi et al, 1993). My study fully supports this aspect of Coburn and Futey's (1996), Bird and Mabee’s (2003), and Grande and Young’s (2004) observations.

In contrast to Coburn and Futey (1995), I did not find a paired origin of supraneural 2 in any of the cypriniforms I studied nor did Bird & Mabee (2003) or Grande and Young (2004). I checked some of Coburn & Futey’s (1996) material and can confirm the paired origin of supraneural 2 in *Luxilus* and *Carpiodes*. It remains unclear if the paired origin represents individual variation within a taxon or is the normal way of development and defines certain subtaxa.

The most recent studies providing information on the development of the neural complex in a cypriniform, the zebrafish *Danio rerio*, are Bird & Mabee (2003) and Grande & Young (2004).

Bird & Mabee (2003: 345) described the separate chondrifications of supraneurals 2 and 3, which then would become “surrounded by and continuous with the roofing cartilage”, characterized as “a larval structure located dorsal to the neural tube”, which “differentiates to surround supraneural 2, supraneural 3, and the neural arch and spine of vertebra 3.” Bird & Mabee (2003: 345) further noted “the formation of the roofing cartilage independent from neural arches 3 and 4 and supraneurals 2 and 3", and claimed that this observation was "consistent with those of Bogutskaya (1991) and Coburn & Futey (1996) from a wide variety of cypriniforms." However, when I checked these publications I found that they described the roofing cartilage (our neural complex) as formed by supraneurals and neural arches, not independently, as claimed by Bird & Mabee (2003). In all the cypriniforms I studied I found that the neural complex is formed by supraneural cartilages 2 and 3 and supradorsals 3 and 4; the latter structures were overlooked by Coburn & Futey (1996), Bird & Mabee (2003), and Grande & Young (2004).

Grande and Young (2004: 252) cautioned "the use of the term supraneural" for supraneural 3 and 4 and recommended they be referred to as "neural plate two and three" following Howes (1980). Grande and Young's (2003: 252) justification for this was that the "supraneurals associated with the Weberian apparatus in *Danio rerio* differ from Mabee's (1988) description in being laterally expanded elements that ossify from the complex cartilage." Mabee (1988: 828) defined supraneurals as "slender, median T-shaped or rod-like, bony or cartilaginous elements that lie in the median skeletogenous septum between the cranium and the dorsal fin." I see no reason why this definition would not apply to the supraneural cartilages 2 and 3 of Otophysi. Furthermore, the shape of supraneurals varies dramatically within the highly diverse teleosts and thus deviates markedly from Mabee's (1989) definition, e.g. in *Esox* (Grande, 1999; own observations), *Glossanodon* and *Mallotus* (see Johnson and Patterson, 1996: fig. 12C, E). I thus see no justification for Grande and Young's (2004) recommendation to use different terms for the same structures.

(6.) Neural complex is formed with the contribution of supradorsals

Müller (1853), and subsequently Bloch (1900), concluded that the unpaired elements in the dorsal midline of the neural complex in cypriniforms are homologous to the paired cartilages that previous authors had reported in esocids and salmonids (Stannius, 1849; Goette, 1879; Scheel, 1893; Grassi, 1883). In my current terminology, the two authors thus homologized the two supraneurals of cypriniforms with supradorsals of esocids and salmonids and would therefore have concluded that supradorsals contributed to the neural complex. This homology, however, is incorrect, because I found that supraneurals 2 and 3 arise as unpaired cartilages situated in or above the dorsal longitudinal ligament from the very beginning, and that neural arches 3 and 4 possess paired supradorsals situated below this ligament.

Butler (1960: 533) stated that in the catostomid *Pantosteus*, the "supradorsal or neural spine elements of these vertebrae [nos. 2, 3, 4] form a large, continuous neural spine that is the most dorsal portion of the pars sustentaculum." Judging from this remark, he seems to have equated supradorsal with neural spine with no justification or explanation, thought that the neural spines of vertebrae 2 to 4 had fused, and labelled that part of the neural complex as 'neural spine' (Butler 1960: fig. 2-4).

Vandewalle, et al. (1989) published a figure and a brief description of an 18.5 mm specimen of the cypriniform *Barbus barbus*. In the figure, they labelled four cartilaginous structures as supradorsals 1-4, with supradorsal 1 equated with the claustrum. In the text they noted (Vandewalle et al., 1989: 364) that "There lie typical supradorsals above the 3rd and 4th basidorsals...Thus there is one supradorsal at the level of each of the first four vertebrae, it is the first record of such a situation." I found several problems with their figure: the structure labelled supraneural (SN) is the posterior part of the cartilaginous roof of the skull that projects from the tectum synoticum caudally; the elements labelled supradorsals 3-4 seem to lie lateral to the neural arches; I have never observed an element in the position of their supradorsal 2 in any of the taxa I studied; basidorsals 3 and 4 are shown as confluent proximally, as are basiventrals 3 and 4. In a subsequent paper on the development of the Weberian apparatus in the same species, *Barbus barbus*, Vandewalle et al. (1990) did not discuss their earlier observations. When describing the 18.5 mm stage they mainly referred to their earlier paper (Vandewalle et al., 1989) and provided only more extensive descriptions of earlier stages up to 18-day-old larvae without citing the length of their specimens.

I conclude that previous authors who seemed to report the contribution of supradorsal cartilages to the formation of the neural complex used this name for various structures not homologous with my supradorsals.

c) The Neural Complex in Characiformes

Of the above 6 hypotheses of homology of the neural complex, only those numbered 1 and 4 were formulated for characiforms.

(1.) Neural complex formed by neural spines

For several decades, authors studying the osteology of characiforms (Weitzman, 1954, 1962, 1964; Roberts 1966, 1969) used the term "neural complex", most likely in a descriptive sense, for the single ossification in characiforms, as first suggested by Nelson (1949). Nelson (1949: 500) claimed that the neural complex of the characid *Rhaphiodon vulpinus* consists of "the third neural spine and possibly the second neural spine and/or interspinous elements." As described above, the second arch does not contribute to the neural complex in any of the characiforms I studied. We also did not find a neural spine on the third vertebra. I thus can reject at least this part of his hypothesis and have to add that he was unaware of supradorsal cartilages and their role in the formation of the neural complex. However I found that, as he suggested, a supraneural (= his interspinous bone) forms a large part of the dorsal roof of the neural complex.

(4.) Neural complex formed exclusively by supraneurals

While studying the development of the neural complex in cypriniforms, Bogutskaya (1991) also remarked on the putative homology of the neural complex in characiforms. She considered the single ossification in characiforms to be composed of "complex neuralis + planum neurale of representatives of the Cypriniformes." She is incorrect in claiming that the single supraneural ossification of characiforms is the result of fusion of supraneurals 2 and 3, as she postulated such a fusion without having studied any developmental material of characiforms. In all my ontogenetic series of characiforms, I found only one centre of chondrification that subsequently ossifies from one centre and forms the single supraneural in characiforms. My observations thus invalidate her hypothesis.

The only authors who apparently studied early developmental stages of a characiform were Rosen & Greenwood (1970). Their material of *Brycon* sp., however, was stained only for bone, as cartilage staining (Dingerkus & Uhler, 1977) was not available at the time. Although Rosen & Greenwood (1970) were aware of the greatly enlarged supradorsals of the anterior vertebrae in *Chanos*, they did not mention supradorsals in *Brycon*. Because they could not identify supradorsal cartilages, they hypothesized that the neural complex of *Brycon* is formed by a supraneural and noted that neural arch 4 is greatly enlarged. My material of different characiforms demonstrates the importance of supradorsals 3 and 4 during development of the neural complex.

d) The Neural Complex in Gymnotiformes

Little has been published on the anatomy of the neural complex in gymnotiforms. Surprisingly and unfortunately, Albert (2001), the latest monograph on gymnotiform phylogeny, contains no information on the Weberian apparatus and the neural complex. Previous authors like Mago-Leccia (1978) or de la Hoz and Chardon (1984) usually used the term ‘neural complex’ in a purely descriptive sense without indicating its homology. The main hypothesis of homology of the neural complex in gymnotiforms is thus the implicit statement in Fink and Fink (1981) contained in their figure 18, in which they considered what I term neural complex to comprise supraneural 3 and the tips of neural arches 3 and 4. As I discussed above, Fink and Fink (1981) erroneously disputed the presence of supradorsal cartilages, and therefore were unaware of their significance for the formation of the neural complex.

e) The Neural Complex in Siluriformes

Only two of the six hypotheses of neural complex homology have been discussed for siluriforms.

(4.) Neural complex formed by supraneurals

In the siluriform *Silurus asotus*, Ichiyanagi et al. (1993: 206-207) noted that the compound neural arch 3+4 is connected to its partner "through a cartilaginous mass, supraneural" and that the "cartilaginous supraneural was fused to the neural arch 3+4 on both sides through ossification", without specifying the source for this ossification. In the development of another siluriform, *Pseudobagrus ichikawai*, Ichiyanagi et al. (1997: 95) described that a "cartilaginous mass, which later developed dorsally into the supraneural, had appeared mid-dorsally to the anterior part of vertebrae by 9.1 mm SL, its ventral part having been fused with the rod shaped bones 3 and 4 and ossifying." Although Ichiyanagi et al. (1993, 1997) described the presence of a supraneural that ossifies in development, they did not report the autogenous chondrification or the separate ossification of this 'supraneural'. It is apparent that, as in the case of cypriniforms (Fukushima et al., 1992; Ichiyanagi et al., 1996), Ichiyanagi et al. (1993, 1997) lacked some of the essential developmental stages to resolve the ontogeny of the neural complex and its composition. This becomes clear, when one compares fig. 1D with fig. 1E of Ichiyanagi et al. (1993). Fig. 1D shows the neural arches 3 and 4 ossified and no sign of the neural complex, but fig. 1E, their next stage, has the neural arches 3 and 4 already fused and a large cartilage roofing the neural canal. The same is true for fig. 1D and 1E of Ichiyanagi et al. (1997).

(5.) Neural complex formed by neural arches and supraneurals

Bamford (1948: 387) described "the dorsal fusion into one mass of cartilage of the third and fourth supradorsals on either side and the third supraneural" in the siluriform *Galeichthys felis* and stated that he labelled the cartilages he found and figured "in accordance with the nomenclature of Goodrich (1930)." Bamford’s (1948) drawings (figs. 13, 14, 15) of a 14 mm specimen show a large homogenous mass of cartilage above the neural canal of vertebrae 2 to 4 that at its posterior end is confluent with the upper end of neural arch 4. From his labelling it is apparent that he considered what he calls the 'third supraneural' as an anterior serial homolog of pterygiophores. Pterygiophores and supraneurals were not distinguished clearly at that time (Mabee, 1988). From the list of specimens available to Bamford (1948) it is also evident that the only specimen smaller than the 14 mm specimen he figured was 8 mm. Because he did not comment on that stage in his description of the development of the Weberian ossicles, it is reasonable to assume that it did not possess any significant information in regard to the complex in question. If that is the case, however, the 14 mm stage was the earliest available, and the dorsal roofing cartilage was already fully developed. Thus its components were inferred from their position rather than actually observed as developmentally autogenous entities. This may explain why Bamford (1948) called the upper part of the neural arch 3 and 4 supradorsal, although it is still continuous with the cartilage of the neural arch.

I found that supradorsal cartilages develop autogenously at the ossified tips of the neural arches and thus are never in cartilaginous continuity with the neural arches. I therefore conclude that Bamford’s (1948) report of supradorsals in *Galeichthys* was based on different structures, most likely the distal parts of the neural arches.

In my developmental series of *Silurus glanis*, there are large supradorsal cartilages on neural arches 3 and 4 that first form a connecting cartilage between each other, which then fuses with the connecting cartilage of the opposite side. I did not encounter any sign of a supraneural, either as cartilage or as ossification. The bone that covers the neural canal in adult *Silurus* is solely derived from ossification of the cartilage that results from connection and fusion of supradorsal cartilages. I think that this pattern of development is true for most siluriforms except those that have retained a small supraneural 3, like *Diplomystes*, or those in which a neural complex is completely lacking, like the loricarioids I studied.

This hypothesis gains additional support from Ichiyanagi et al. (1993, 1997), who studied a silurid and a bagrid species but illustrated no separate supraneural bones. Their description of the neural complex is not very detailed and it remains unclear if they considered the resulting bony roof to comprise in part also a supraneural ossification.

In a developmental osteological study of the channel catfish, *Ictalurus punctatus*, Grande & Shardo (2002) illustrated a separate cartilage above neural arches 2 to 4 in a 12.3 mm specimen, which they labelled supraneural. During subsequent development, this cartilage is said to contact the tips of neural arches 3 and 4 and eventually the "neural arches of the compound centrum enlarge and fuse with the anterior supraneural" (Grande and Shardo, 2002). Their illustrations are drawings of the respective stages and show a cartilaginous element that gets incorporated into the fused neural arches 3 and 4. It is left unclear if this incorporation that they call 'fusion' occurs after the supraneural has ossified, because a fusion seems impossible between a cartilage and a bone, as the cartilage remains surrounded by a perichondrium, and actual fusion would be expected at the level of bones. I thus have some problems understanding Grande & Shardo's (2002) description. Their 13.6 mm and 16.3 mm stages closely resemble my stages 15.4 mm and 16.6 mm of *Silurus*, but the cartilage connecting the tips of neural arches 3 and 4 of *Silurus* arises clearly from supradorsal cartilages without any supraneural contribution. Grande & Shardo (2002) do not mention supradorsal cartilages, so we are left undecided as to what these authors reported. A reinvestigation of their material is necessary to resolve this issue.

Ontogenetic information for other siluriforms is limited, but judging from the adult condition in a number of siluriform skeletons and c&s

specimens I checked, a separate supraneural bone is absent from most siluriforms, except diplomystids, some pimelodids (*Pinirampus* AMNH 55901, *Platynematichthys* AMNH 39903, *Pseudoplatystoma* AMNH 56299), some ictalurids (*Pylodictis* AMNH 94809, 88842), and schilbids (*Schilbe* AMNH 6617, *Eutropius* AMNH 6636, *Siluranodon* AMNH 55368). This contradicts Arratia's (1992) previous claim that all siluriforms except diplomystids lack supraneurals.

In my 60 mm specimen of *Diplomystes chilensis* (AMNH 55327), a small supraneural sits on top of the anterodorsal corner of the neural complex. This condition was also figured by Fink & Fink (1981), Arratia (1987), and Azpelicueta (1994). Chardon (1968) illustrated the single supraneural in *Diplomystes* but called it neural spine of the third vertebra.

Arratia (1987) illustrated and described a single specimen of *Diplomystes chilensis* with two separate supraneurals. She concluded that the single element in all other specimens, and even all other diplomystids, actually represented a fusion of two supraneurals (Arratia, 1987: 29, 74). Fink & Fink (1996) commented on this hypothesis and I concur with their conclusion that there is no evidence of such a fusion between supraneural ossifications in otophysans. In contrast to Arratia (1987), Arratia (1992: 125) interpreted the "presence of a compound element or of two separate elements in *Diplomystes chilensis* and *Olivaichthys viedmensis*" as "a synapomorphy shared by these two species", thus revising her former hypothesis (Arratia, 1987: 74) that ossified supraneurals 3-4 in diplomystids are a primitive character and rather considering this character to be derived within diplomystids. At present, I feel that the fact that two ossifications have been reported in only a single specimen of one species of *Diplomystes* is not enough evidence to postulate a fusion of these elements in all other specimens of this species and all other diplomystids that have only one bone. Until fusion has been demonstrated by ontogenetic studies, I would rather consider the two bones in the single specimen to be an individual aberration.

Arratia (1992) also interpreted the "presence of a single, small, ossified supraneural" as an autapomorphy of Diplomystidae. I see no reason for this assumption, because the presence of a supraneural is a plesiomorphy shared with characiforms and gymnotiforms and its small size is most likely a character of siluriforms.

Fink & Fink (1996: fig. 4) illustrated drawings of two ontogenetic stages of *Silurus* and one of *Ictalurus* and labelled the cartilaginous neural complex as 'cartilage of supraneural + neural arches 3 and 4', but provided no justification for this homology. They did not describe or illustrate earlier stages and so I assume that their homology statement was based on the spatial similarity of the anterior part of the cartilaginous neural complex with that of other Otophysi that have a supraneural ossification. Fink & Fink (1996: 234) also mentioned a perichondrally ossified supraneural in a 23 day old *Silurus* (length not given), a juvenile ictalurid (*Pylodictis*) and a plotosid (*Plotosus*). I cannot comment on the latter two taxa, but in my developmental series of *Silurus glanis* consisting of 91 specimens ranging from 9.0 mm to 35.7 mm, there is no supraneural cartilage present at any stage, the cartilaginous roof of the neural complex is solely formed by fusion of supradorsals 3 and 4, there is no supraneural ossification, and the bony roof of later developmental stages is solely formed by ossifications spreading from the tip of the neural arches close to the previous supradorsal anlagen into the cartilage. I am uncertain if this ossification originates from autogenously ossifying supradorsals or from the neural arches. If the neural complex in other siluriforms that lack a supraneural as adults develops in a similar way as that described for

Silurus, a fact which may be inferred from the similarity in adult structure between *Silurus* and many catfishes, then one may conclude that all siluriforms, with the exception of diplomystids, some pimelodids, ictalurids, and schilbids, have lost the single supraneural, and the neural complex is solely formed by ossification of the cartilage that results from fusion of supradorsals 3 and 4 to each other.

Coburn and Grubach (1998) described the ontogeny of the Weberian apparatus in the callichthyid *Corydoras* and reported fusion of the anterior most neural arch with the occiput. However, they interpreted that arch to be the fifth, following Alexander's (1964) and Chardon's (1968) view, which seems to be accepted by recent authors (see e.g. Schaefer, 1987; 1990; 1997; Chardon et al., 2003). Coburn and Grubach (1998) consequently concluded that the basidorsals of the fourth vertebra are lacking. Alexander's (1964) idea actually dates back to Regan (1911: 576), who noted for callichthyids: "sixth vertebra free…complex vertebra ankylosed with fifth and with the skull." I am convinced that this hypothesis is erroneous and that the anterior most neural arch that fuses with the synotic tectum in loricarioids and its associated vertebra is actually the fourth, because it later forms the os suspensorium, inarguably a feature of the fourth otophysan vertebra.

The absence of the neural complex and the fusion of the fourth neural arch with the synotic tectum in the loricariids and the callichthyid I studied appears to be an unusual character that might define a larger monophyletic group among catfishes, most likely the Loricarioidei, as they share a similar osteological structure of that region. Because comparative ontogenetic data as detailed as mine are lacking for most other siluriforms, this hypothesis will have to be tested with additional material.

6) SUMMARY AND CONCLUSIONS (NEURAL COMPLEX)

Supradorsals are bilaterally paired autogenous cartilages that occur at the distal tips of left and right halves of neural arches in many basal teleosts. Among Otophysi, supradorsals are only developed on neural arches 1, 3 and 4 and are absent from all remaining arches. Supradorsals 3 and 4 play a previously unrecognized major role during the ontogeny and evolution of the neural complex of otophysan Ostariophysi. Supradorsals 3 and 4 fuse with supraneurals 2 and 3 (cypriniforms) or supraneural 3 (characiforms, some siluriforms, gymnotiforms) during development to form the neural complex. In most siluriforms the neural complex is exclusively formed by supradorsals 3 and 4. In some siluriforms the neural complex is missing and the fourth neural arch is fused to the occiput. Of the four otophysan subgroups, siluriforms are the most and cypriniforms the least diverse in the structure and development of their neural complex.

7) RESULTS ON THE DEVELOPMENT AND HOMOLOGY OF THE CLAUSTRUM

a) Development of the claustrum in Cypriniformes.

I studied the development of the claustrum in eight species of cypriniforms and illustrate six of them (compare figs. 89-98)

In all my cypriniform taxa the claustrum is preformed in cartilage and represents a small spherical nodule, the claustral cartilage, situated anterior and slightly medial to the distal end of the ascending process of the scaphium. It is present around the time when supraneural cartilages 2 and 3 have chondrified and started to fuse with supradorsal cartilages 3 and 4. The exact stage when the claustral cartilage starts to form is hard to determine because even when fully formed it only consists of up to a dozen chondrocytes. Soon after its chondrification, the claustral cartilage ossifies perichondrally around its anterior surface thus forming the claustrum, and subsequently develops an anteriorly directed, extensive, but thin, lamina of membrane bone. In its initial stages this lamina does not stain very well with alizarin and may be easily overlooked . During subsequent development the lamina grows further anteriorly and ventrally, so that it covers the space between the neural complex and the back of the skull and runs along the medial side of the concha scaphii being covered laterally by it. The claustral cartilage persists into the juvenile stage as the posterior cartilaginous core of the claustrum and approaches the cartilage mass of the neural complex very closely.

b) Development of the claustrum in Characiformes.

I describe and illustrate the development of the claustrum in six species of characiforms from four different families (compare figs. 99-106).

The claustrum in characiforms has no cartilaginous precursor and ossifies in membrane bone between the anteroventral corner of the neural complex and the dorsal edge of the concha scaphii in the two alestids, in *Hoplias malabaricus* and *Ctenolucius hujeta* (figs. 99-104). The first signs of the small ossification are visible when the neural complex is fully formed and the supraneural 3 has started to ossify. The claustrum is a thin splint of bone in the two alestids, and has a more roundish appearance in *Hoplias malabaricus* and *Ctenolucius hujeta*. In *Lebiasina bimaculata,* the claustra of both sides are still separate in a 12.1 mm specimen (fig. 105) and originate at a relatively more dorsal position than in the alestids, *Hoplias malabaricus*, and *Ctenolucius hujeta* between the dorsolateral edge of the foramen magnum and the anteroventral edge of the neural complex. The claustra are fused in the dorsal midline in my 15.0 mm specimen, where they are closely associated with the anterior edge of the neural complex. The first signs of the claustra in *Pyrrhulina* are present in a 7.5 mm specimen as a median unpaired ossification at the anterior edge of the base of the neural complex. In the 8.2 mm specimen that I figure (fig. 106), the claustrum is already well developed and forms a roof above the neural canal from the anterior base of the neural complex to the dorsal edge of the foramen magnum.

c) Development of the claustrum in Siluriformes.

I begin with the description of a juvenile *Diplomystes*, a representative of the sister group to all other catfishes, and provide developmental information for *Silurus glanis*.

The **60 mm** specimen of *Diplomystes chilensis* has a fully formed Weberian apparatus situated between the large complex centrum and the back of the skull. The claustrum is a vertical, elongate and cylindrical bone that continues dorsally into the remnant of the claustral cartilage (see figs. 107,108). It is situated in the space limited ventrally by the concha scaphii, posteriorly by the ascending process of the scaphium and the anterior cartilaginous edge of the neural complex, anteriorly by the exoccipital and dorsally by a chondroid mass extending from the posterior edge of the cartilage of the tectum synoticum.

In *Silurus glanis* the claustral cartilage develops about halfway between the ascending process of the scaphium and the back of the neurocranium. It is an oval mass of chondrocytes that stain poorly with alcian in the **13.4 mm** specimen (fig. 109). At that time, neural arches 3 and 4 are well developed and supradorsal cartilages 3 and 4 are large and have started to fuse to each other forming a longitudinal bridge. Subsequently the claustral cartilage elongates and grows in a dorsoventral direction, and its ventral tip starts to ossify perichondrally forming the claustrum (fig. 110). It is now in a positional relationship to surrounding structures similar to that in the juvenile *Diplomystes chilensis*.

I did not find any sign of the claustrum in any of our developmental material of the clariid *Clarias* or the loricarioids *Megalechis*, *Hemiloricaria*, *Ancistrus*, and *Sturisoma*.

d) Remarks on the development of Gymnotiformes.

The claustrum is absent in gymnotiforms and there are no signs of it during the development of the anterior vertebrae in the two species of *Apteronotus* that I studied. Interestingly the ventrolateral part of the supraneural 3 cartilage of our **10.6 mm** specimen (fig. 111) of *Apteronotus leptorhynchus* is in a position relative to the ascending process of the scaphium similar to that of the claustrum in *Silurus glanis* and *Diplomystes chilensis*. This positional relationship changes dramatically during subsequent growth, so that in the juvenile the anteroventral corner of the neural complex cartilage mass is far removed from the ascending process of the scaphium (see fig. 112).

8) DISCUSSION

a) Development of the claustra

The vast majority of papers about the development of the Weberian apparatus concerns representatives of the cypriniforms (Müller, 1853; Scheel 1893; Nusbaum, 1908; Matveiev, 1929; Watson, 1939; Butler, 1960; Kulshrestha, 1977; Soni et al., 1978; Vandewalle et al. 1989, 1990; Bogutskaya 1991; Fukushima et al. 1992; Ichiyanagi et al., 1996; Coburn & Futey, 1996; Bird & Mabee, 2003; Grande & Young, 2004). Fewer studies deal with siluriforms (Ballantyne, 1930; Bamford, 1948; Mookerjee et al. 1954; Hoedeman, 1960; Radermaker et al. 1989; Ichiyanagi et al. 1993, 1997; Fink & Fink, 1996; Coburn & Grubach, 1998; Grande & Shardo, 2002), and virtually no studies exist for either characiforms or gymnotiforms.

The early papers on the development of the Weberian ossicles in cypriniforms (Watson, 1939; Butler, 1960), but also some more recent studies (Kulshrestha, 1977; Bogutskaya, 1991), stressed that the claustrum originates as membrane bone without a cartilaginous precursor. However, Soni et al. (1978) noted that a cartilaginous core was present in the posterior part of the claustrum in their 18 mm specimen of *Rasbora daniconius*. Subsequently, Ichiyanagi et al. (1996) confirmed for *Zacco* and *Tribolodon*, Coburn & Futey (1996) for a number of cyprinids and catostomids, and Bird & Mabee (2003) and Grande & Young (2004) for zebrafish, that the claustra are preformed in cartilage. This is exactly what I found in the eight species of cypriniforms I studied.

I can only speculate about the reasons that led earlier authors to report a membranous origin of the claustrum in cypriniforms. Some may be due to erroneous observations, some to lack of large series of developmental stages, others to the difficulties with the method of serial sectioning applied in the early studies, and still others to the diversity of claustrum formation in cypriniforms, of which we only have limited knowledge yet. Furthermore the cartilaginous precursor may well have been lost from the development of the claustrum in certain subgroups of cypriniforms, as seems to be the rule for characiforms (see below).

The claustrum in cypriniforms in general has a characteristic shape, structure, and anatomical association as pointed out by Chranilov (1929). It consists of a triangular plate, termed corpus claustri by Chranilov (1929), and a ventrally directed scutulum claustri, which forms part of the medial wall of the atrium sinus imparis. The latter is a modified extra cranial perilymphatic space of the inner ear and part of the Weberian apparatus. Chranilov's (1929) corpus claustri is the dorsal part of the membranous lamina of the claustrum along with the ossification resulting from the claustral cartilage, and his scutulum claustri is the ventral part of the membrane bone lamina. The claustra of characiforms and siluriforms lack the membrane bone lamina and its association with the atrium sinus imparis, and therefore the presence of these characters in Cypriniformes represent autapomorphies of this taxon.

With the exception of the 9 mm specimen of *Brycon* illustrated and described by Rosen & Greenwood (1970), no additional information on the development of the characiform Weberian apparatus seems to have been published. For Rosen & Greenwood (1970) alcian blue staining of cartilage was unavailable and their figure and description refer only to the ossified skeleton. In all the six species of characiforms I studied, the claustrum formed without a cartilaginous precursor and ossified directly in membrane bone. Given that the claustrum is preformed in cartilage in cypriniforms and siluriforms (see below), the membranous origin of claustra in characiforms must be interpreted as secondary. This is not surprising, as substitution of cartilaginous precursors by membrane bone is a common theme among teleosts and may affect endoskeletal elements of the head and axial skeleton (Emelianov, 1928, 1935, 1939; Patterson, 1975, 1977; Britz & Johnson, 2002, 2004). I hypothesize that the membranous origin of the claustrum is a potential synapomorphy of Characiformes, a hypothesis that should be tested with additional representatives of this clade. I was quite surprised to find that the claustra fuse during development of *Lebiasina* and, as far as I can tell, are unpaired structures from the beginning in *Pyrrhulina*, both representatives of the family Lebiasinidae. The study of additional species of this family will have to demonstrate if the unpaired claustra might be a synapomorphy of the representatives of this family.

Of the papers on the skeletal development of siluriforms that include at least some information on the ontogeny of the Weberian ossicles (Ballantyne, 1930; Bamford, 1948; Mookerjee et al., 1954; Hoedeman, 1960; Radermaker et al., 1988; Ichiyanagi et al., 1993, 1997; Fink & Fink, 1996; Coburn & Grubach, 1998; Grande & Shardo, 2002), only four (Ichiyanagi et al., 1993, 1997; Fink & Fink, 1996; Grande & Shardo, 2002) deal with representatives of siluriform taxa that possess claustra. Ichiyanagi et al. (1993, 1997) described the claustrum in *Silurus asotus* and *Pseudobagrus ichikawai* as an elongate cartilage situated between the ascending process of the scaphium and the back of the skull. It ossifies first at its ventral tip, which is identical to the situation Fink & Fink (1996) figured for *Ictalurus* sp. and *S. glanis*, Grande & Shardo (2002) reported for *Ictalurus punctatus*, and me observed in *S. glanis* and *Diplomystes chilensis*. If confirmed in representatives of other families of siluriforms, this unusual ventrodorsal sequence of ossification of the claustrum appears to be a synapomorphy of catfishes.

The claustrum is absent in adult gymnotiforms, a shared derived character of that group (Fink & Fink, 1981), and I also found no evidence of the claustrum during development. One might be tempted to consider the anteroventral tip of the neural complex in larval *Apteronotus* to represent the claustrum because of its similar position and shape. However, this tip does not form from an autogenous precursor, and I therefore consider it to be part of the neural complex.

b) Homology of the claustra

The skeletal changes that have occurred along with the development of the Weberian apparatus in Otophysi rank among the most complex structural modifications in vertebrates. Although studied by a large number of researchers with different approaches, homology of the different skeletal components involved is still under debate, and a consensus has not been reached. This is especially true for the claustrum, the homology of which has been the subject of a number of recent papers (Coburn & Futey, 1996; de Pinna & Grande 2003; Bird & Mabee, 2003; Coburn & Chai, 2003; Grande & de Pinna 2004; Grande & Young, 2004).

As I have argued above, supradorsal cartilages in Otophysi play an important and previously unappreciated role in the formation of the neural complex, a roof above the neural canal of the anterior vertebrae of cypriniforms, characiforms, gymnotiforms and some siluriforms. Supradorsal cartilages, which have been described already in the 19th century (Stannius, 1849; Müller, 1853; Goette, 1879; Grassi, 1883 Scheel, 1893), occur in a wide range of basal teleosts, but have been also reported from nonteleostean actinopterygians. Supradorsals have been mentioned only rarely in the recent literature (Francois, 1966; Rosen & Greenwood, 1970) and were ignored by most recent otophysan workers.

As I have shown, supradorsals chondrify as bilaterally paired autogenous little cartilages medially at the distal tips of both halves of neural arches after those have ossified. During subsequent development supradorsals ossify and may eventually fuse to the neural arches. As with the neural complex, I am convinced that the significance of supradorsals in discussions on the homology of the claustra has also been underappreciated.

In the following paragraphs I want to review and discuss previous hypotheses of claustrum homology before I present my own ideas. In the past, six different hypotheses have been formulated:

I. The claustra are part of the occipital skull (Grassi, 1883; Sagemehl, 1885)

II. The claustra represent the modified neural spine of the first arch or part thereof (Huschke, 1822; Nusbaum, 1881, 1908; Wright 1884a; Bridge & Haddon, 1893; Reis, 1906; Chranilov, 1926, 1927, 1929; Matveiev, 1929)

III. The claustra are modified supraneurals 1 (Baudelot 1868a, 1868b, 1873; Sørensen, 1890)

IV. The claustra are dissociated parts of the first neural arch (Hora, 1922; Fink & Fink, 1981, 1996)

V. The claustra are modified supradorsals (Bloch, 1900; Rosen & Greenwood, 1970)

VI. The claustra represent the modified accessory neural arch (de Pinna & Grande, 2003; Grande & de Pinna, 2004)

I. The claustra are part of the occipital skull

The idea that the claustrum belongs to the posterior part of the skull was formulated by Grassi (1883), without any supportive evidence, and by Sagemehl (1885: 55-58), based on the course of nerves. He noted that in characiforms the spinal nerve that belongs to the intervertebral space between the first and second vertebra exits in front of the second neural arch, the intercalarium. He concluded that therefore the stapes and claustrum must belong to either the first neural arch or the occipital arch, i.e. the posterior cranium. The course of nerves in characiforms did not help to distinguish between these two hypotheses, but Sagemehl (1885) claimed that in *Silurus* an additional nerve would exit between the stapes and claustrum, thus showing that the stapes belongs to the first vertebra and the claustrum to the occipital skull region. Bridge & Haddon (1889: 312), however, refuted this idea because they could not verify Sagemehl's claim of an additional nerve in *Silurus*.

Sørensen (1890) and later Bloch (1900) commented on this hypothesis and rejected it. It has played no role in discussions since then and is solely of historical interest.

II. The claustra are the modified neural spine of the first arch

This hypothesis was formulated by Nusbaum (1881: 556), and supported by Wright (1884a: 249), Bridge & Haddon (1893: 69), Reis (1906), Nusbaum (1908), Chranilov (1926), and Matveiev (1929). Bloch (1900) pointed out that this homology is unjustified, because neural spines on the anterior vertebrae in Ostariophysi are not preformed in cartilage but form in membrane bone. At least in cypriniforms and siluriforms, claustra are preformed in cartilage, representing the plesiomorphic condition with the membranous origin of the characiforms being derived. There is thus no similarity between the claustra and the neural spines of the first vertebra that would justify this homology proposition, and I am not going to discuss it further.

III. The claustra are modified supraneurals 1

Baudelot (1868a: 333; 1868b, 1873) believed the claustrum to represent a supraneural that had secondarily become paired ("os intercrural partagé en deux"). A similar view was expressed by Sørensen (1890), who considered the claustra to be the anterior metameres ("1 ste Hvirvels Slutstykke") of those elements that ossify in the cartilaginous roof of the neural canal above neural arches 2 - 4 and which in recent terminology are called supraneurals. He considered the paired state of the claustra in the adult as secondary because he reported these elements to be unpaired in the juvenile cypriniform *Leuciscus rutilus* he studied. He homologized the series of supraneurals with the "ossa imparia" of sturgeons, which are the unpaired separate cartilages that articulate proximally with the neural arches. The identical hypothesis that the claustra represent a paired supraneural 1 was recently proposed by Coburn & Futey (1996) who overlooked Baudelot's (1868) and Sørensen's (1890) ideas. Coburn & Futey (1996) based their interpretation on the fact that in some of the cypriniforms they studied, they found supraneural 2 to develop from two chondrification centers. Previously, supraneurals were reported to develop always from unpaired primordia (Mabee 1988). I did not find a double origin of supraneural 2 in any of my cypriniforms studied, but was able to confirm it in some of Coburn & Futey's specimens. As the majority of cypriniforms investigated to date show an unpaired origin of supraneurals 2, it remains unclear if the paired origin represents individual variation within a taxon or is the normal way of development for certain cypriniform taxa. Notwithstanding a possible paired origin for supraneural 2 in some cypriniforms, Coburn & Futey's (1996) hypothesis requires two assumptions for which there is currently no evidence: (1) the presence of supraneural one in Otophysi and (2) its paired origin. Fink & Fink (1981, 1996: 233) cited the "absence of supraneural anterior to the neural arch of the anteriormost vertebra" (= supraneural 1) as a synapomorphy of Ostariophysi, and I fully agree with their conclusion, which then invalidates Coburn & Futey's (1996) hypothesis.

IV. The claustra are dissociated parts of the first neural arch

This hypothesis dates back to Hora (1922) and was recently revived by Fink and Fink (1981: 327) who noted the "claustrum being formed by the dissociated dorsomedial portion of the first neural arch." They (Fink & Fink, 1981: 325) criticized Rosen and Greenwood for having "used the term 'supradorsal' for the dorsal part of the neural arch" and concluded that since "these paired structures appear not to be separate elements but simply cartilage of the arches along their midline synchondral joint, the term supradorsal seems inappropriate." I discussed Fink and Fink's (1981) erroneous rejection of supradorsals as separate anatomical entities above, where I demonstrated that supradorsals are autogenous elements that chondrify after the neural arch has ossified. They are not part of the cartilage of the neural arch, as implied by Fink & Fink (1981).

V. The claustra are modified supradorsals 1

This hypothesis was developed first by Bloch (1900). He homologized the claustra with those cartilages that were originally reported by Stannius (1849) in *Esox* and *Salmo*, termed "Primordialknorpel" by Goette (1879), and "Schlussstücke" by Bloch (1900). The latter author further thought that supraneurals 2 and 3 are serial metameres of the claustra and thus homologs of the cartilages in *Salmo* and *Esox*. The term supradorsals for these structures was coined by Gadow and Abbott (1895) and is used also herein. Rosen & Greenwood (1970) specifically homologized the claustra in *Brycon* with the supradorsal cartilages of the first vertebra of *Chanos* and had clearly overlooked Bloch's (1900) earlier hypothesis. Subsequently also Vandewalle et al. (1989, 1990) and Ichiyanagi et al. (1993) used the term supradorsal, but only the latter specifically referred to Rosen & Greenwood (1970) thus agreeing with their homology proposition.

I think that Bloch (1900) and Rosen & Greenwood (1970) were right and I will present evidence for this hypothesis below.

VI. The claustra represent the modified accessory neural arch

This most recent hypothesis was formulated by de Pinna & Grande (2003) and Grande & de Pinna (2004). Many basal teleosts have a neural arch with no associated centrum between the first vertebra and the back of the skull, for which Fink & Weitzman (1982: 58, fig. 5) coined the term "accessory neural arch" in their skeletal study of *Diplophos*. The two earliest references I could find to this structure are by Brühl (1856: 1), who reported an "accessorisches Bogenelement der Occipitalregion" (accessory arch element of the occipital region) in a number of teleosts among them several clupeoids and *Esox*, and by Bruch (1861) who noted a neural arch without associated centrum between the occiput and first vertebra in *Salmo*. The few authors who subsequently mentioned the accessory neural arch, like e.g. Taverne (1974) or Bemis & Forey (2001), usually argued that it would represent the remnant of a vertebra, the centrum of which was fused into the back of the skull, although Patterson & Johnson (1995: 17) concluded that "it does not represent the remains of a missing vertebra."

Fink & Fink (1981: 326) reported an "unattached neural arch anterior to the arch of the first vertebral centrum" in "*Polypterus*, *Amia*, and many primitive teleosts (e.g. *Elops*, *Dorosoma*, *Harengula*, *Anchoa*, *Esox*, *Dip-*

lophos)" and considered its absence to be a synapomorphy of Ostariophysi. Patterson & Johnson (1995) noted the presence of an accessory neural arch in a number of basal teleosts up to and including the Aulopiformes, but could not confirm Fink & Fink's (1981) observation in their specimens of *Polypterus* and *Albula*. They (1995: 17) concluded that "given the mosaic pattern of presence and absence of ANA [accessory neural arch] in lower teleostean groups, there are two possible interpretations: either it is synapomorphous at some level and has been lost repeatedly, or it has arisen repeatedly and is nonhomologous from group to group."

Recently, de Pinna & Grande (2003) and Grande & de Pinna (2004) have argued that the claustra of otophysan Ostariophysi are homologues of the accessory neural arch of clupeomorphs. The authors presented a complex string of arguments that is not easy to disentangle and contains several inaccuracies and errors.

Their arguments were summarized by de Pinna & Grande (2003: 842) as follows: "homology between ANA and claustrum is supported by similarities evident both in adult configuration and in development:

(1) archlike structure;

(2) topographical relationships to other vertebral elements and the neural canal;

(3) derivation from paired cartilages which differentiate on the dorsolateral surface of the neural canal, distant from the notochord from the onset of chondrification;

(4) delayed chondrification and ossification relative to other basidorsal derivatives and supraneurals." These arguments reappear in Grande & de Pinna (2004) as structural, topological and ontoge-

netic arguments, though in a slightly different form and with different wording.

I will address all four points of de Pinna & Grande (2003) in sequence and comment on Grande & de Pinna's (2004) three arguments.

(1) Archlike structure ("The archlike shape of the claustrum in all otophysans, especially in young stages, bears marked resemblance to ANA.")

This obviously is a shape character, for which it is difficult to reach an objective agreement about its similarity. The claustra of *Zacco* and the accessory neural arch of *Pellonula* depicted by de Pinna & Grande (2003) in their fig. 3 might look similar in shape to them, but not to others, including me. Because they did not specify what an “arch like shape” comprises, it is impossible to test this similarity. One is thus left with a statement by de Pinna & Grande (2003) with which one can agree or disagree. I disagree and do not discuss this 'similarity' any further. Grande & de Pinna (2004) expanded on this argument that they termed 'structural'. They noted that "The claustrum, contrary to Fink & Fink (1981, 1996), is not homologous with neural arch 1", however Fink & Fink (1981, 1996) never made such a claim, as is evident from this quote (italics are mine): "In otophysans the first neural arch is modified to form the scaphium and claustrum, *the claustrum being formed by the dissociated dorsomedial portion of the first arch*." Grande & de Pinna (2004: 433) went on stating that "Although some variation in claustrum structure is evident among otophysans, both the claustrum in otophysans and the accessory neural arch in clupeocephalans form protective structures over the neural canal." As with the arch like shape, the authors do not specify what the similarity of the two structures is and what the “protective” component actually comprises that would make them similar, a prerequisite for claiming that they are the same thing. I thus summarize this point concluding that their structural argument is unconvincing and I reject the idea of a structural similarity of the accessory neural arch and the claustra.

(2) Topographical relationships to other vertebral elements and the neural canal

De Pinna & Grande (2003: 842-843) stated that "the claustrum is positioned anterior to the neural spine of the first centrum...which agrees with the position of ANA in nonotophysan lower teleosts." Looking at the position of the claustrum and ANA in relation to the first neural arch, however, there are apparent differences: the claustrum is situated more dorsally and posteriorly and develops in a position slightly more anterodorsally at the tip of the first neural arch. This difference was also noted by de Pinna & Grande (2003: 843) and Grande & de Pinna (2004), but explained away by special pleading that the different position of the claustrum "relative to the spine of the scaphium is caused by the anterior expansion of the concha scaphium towards the exoccipitals. In other words, the claustrum, now displaced, would have fit between vertebra 1 and the cranium if it were not for the expanded scaphium."

This, however, assumes without justification that the claustrum was in a different position before the development of the concha scaphii, for which I find no evidence. Furthermore, de Pinna & Grande (2003) and Grande & de Pinna (2004) overlooked that the claustrum also develops medial to the dorsal tip of the scaphium, very unlike the accessory neural arch, which is in line with subsequent neural arches (see figs. 11, 12).

I thus conclude that the topological argument of de Pinna & Grande (2003) and Grande & de Pinna (2004) is superficial and the only remaining similarity between the claustrum and the accessory neural arch is their position between the first vertebra and the occiput.

(3) Derivation from paired cartilages that differentiate on the dorsolateral surface of the neural canal, distant from the notochord from the onset of chondrification

This argument has two individual components, ontogenetic and topologic. Both are similarities shared between the accessory neural arch and the claustrum, at least to some extent, given the topological differences in relation to the tip of the first neural arch discussed above. This argument is not listed separately in Grande & de Pinna (2004), but only referred to in one sentence in their paragraph on ontogeny.

Claustra are not preformed in cartilage in any of the characiforms we studied, which must be considered secondary based on presence of cartilaginously preformed claustra in cypriniforms and siluriforms and the phylogenetic relationships of otophysan subgroups hypothesized by Fink & Fink (1981, 1996).

I agree that the origin from paired cartilages and their position at the dorsoposterior face of the neural canal are two similarities shared by claustra and the accessory neural arch.

(4) Delayed chondrification and ossification relative to other basidorsal derivatives and supraneurals

This argument of de Pinna & Grande (2003: 843) refers to the timing of the developmental origin of accessory neural arches, which begins when "all vertebral centra, neural spines, supraneurals, parapophyses and pleural ribs are already well differentiated." About the developmental timing of the claustra de Pinna & Grande (2003: 843) noted that "The same offset developmental timing happens with the claustrum, which has been repeatedly shown to be the last Weberian ossicle to develop, both in chondrification and ossification."

Grande & de Pinna (2004: 434-435) worded their previous argument slightly differently stating that "The ontogenetic timing of the accessory neural arch and the claustrum is markedly delayed from that of anterior neural arches and supraneurals...In clupeomorphs the accessory neural arch begins to form after all neural arches and supraneural elements have formed and begin to ossify...In all otophysan developmental series examined...all supraneurals and dorsal fin radials have formed before the claustrum takes on its characteristic structure."

The statements in de Pinna & Grande (2003) and Grande & de Pinna (2004) about the similarity in developmental timing between the accessory neural arch and the claustra relative to other structure of the vertebral column contain several sub-statements as follows:

- the accessory neural arch develops after vertebral centra, neural spines, supraneurals, parapophyses and pleural ribs
- the claustrum develops after the other Weberian ossicles, after supraneurals and dorsal fin radials, and after anterior neural arches.

As is evident, only two sub-statements provide information for the developmental timing shared by both, accessory neural arch and claustra, relative to other structures, which thus can be considered similarities: accessory neural arches and claustra form after anterior neural arches and supraneurals.

This, however, is only partly true. In their initial stages of development the claustra in the cypriniforms I studied comprise only few chondrocytes, which can be easily overlooked, when not well stained or studied with inadequate optical equipment. I found that claustra make their first appearance as cartilaginous nodules well after neural arches have chondrified and ossified and centra have ossified, but only slightly after supraneural cartilages have chondrified. Ichiyanagi et al (1996) reported the claustra of *Tribolodon* to chondrify before complete chondrification of the neural complex.

Claustra also start to ossify long before any of the two supraneurals in all cypriniforms I studied. Obviously, there is much more diversity than Grande & de Pinna (2004) expected and their claim about the shared similarity in delay of ontogenetic timing is thus contradicted.

In my developmental series of characiforms, however, the claustra, which are not preformed in cartilage, are developmentally delayed and ossify in membrane bone after supraneural 3 has started to ossify. I cannot provide any such information for siluriforms, as the species I studied do not have a supraneural cartilage or supraneural (see above). However, the claustra in *Silurus* have clearly chondrified by the time supradorsals 3 and 4 have just established their longitudinal cartilaginous connection.

In summary, of the 4 arguments presented by de Pinna & Grande (2003) to support the hypothesis that the claustra are homologous to the accessory neural arch, only the "derivation from paired cartilages which differentiate on the dorsolateral surface of the neural canal, distant from the notochord from the onset of chondrification" and their "delayed chondrification relative to other basidorsal derivatives" withstand closer scrutiny.

In the following paragraphs I will develop my hypothesis about the homology of the claustra. As demonstrated above supradorsal cartilages are present on the medial side of the distal tip of most anterior neural arches in a number of basal teleosts, including representatives of the otophysan sister group, the Anotophysi. Supradorsals are also undoubtedly present on neural arches 3 and 4 in otophysans. I argue below that the claustra are homologous to the supradorsal cartilages of the first vertebra, as previously suggested by Bloch (1900) and Rosen & Greenwood (1970). I cite a number of similarities of both structures that I think provide more convincing evidence and lead to a more parsimonious, better founded hypothesis of homology.

1. Claustra and supradorsal cartilages are paired, autogenously chondrifying elements. This argument was listed by de Pinna & Grande (2003) and Grande & de Pinna (2004) as a similarity of the claustra and the accessory neural arch, but the same is also true for the claustra and supradorsal cartilages.

2. Although I would not consider this an important similarity the **"delayed chondrification relative to other basidorsal derivatives"** of de Pinna & Grande (2003) is also shared by the claustra and the supradorsal cartilages. But in addition to those similarities that apply to the accessory neural, the claustra and supradorsal cartilages, there are two similarities shared only by the latter two.

3. Claustra and supradorsal cartilages chondrify at an identical position relative to their respective arches. The cartilaginously preformed claustra in cypriniforms and siluriforms and the claustra arising as membrane bone in characiforms have the same spatial relationship to the first arch, as the supradorsal cartilages of the first arch in the outgroup taxa (see fig. 10, 11, 12, for *Pantodon, Elops*, *Oncorhynchus*) or the third and fourth supradorsal cartilages in the Otophysi to their respective arches. They are situated on the medial side and subdistally to the tip of their respective arches and usually extend anteriorly beyond the neural arch. This is a clear difference from the accessory neural arch, which is in line with and at the same level as subsequent neural arches (figs. 11, 12).

4. Claustra chondrify in association with the anterior most vertebral myoseptum and not with the last cranial myoseptum. During a reinvestigation of the posterior limit of the teleostean skull Britz & Johnson (in prep.) discovered an additional argument contradicting a homology between the accessory neural arch and the claustra. In general, teleosts have three myosepta attached to the back of their skull (Allis, 1899; Patterson & Johnson, 1995; Britz & Johnson, in prep.). In teleosts that have an accessory neural arch, like the engraulid *Anchoa mitchilli* (fig. 113), it is associated with the last cranial myoseptum. The claustra on the contrary are invariably associated with the anterior most vertebral myoseptum and thus differ greatly from the accessory neural arch (fig. 114). The supradorsal cartilages of the first vertebra in basal teleosts are also associated with the first vertebral myoseptum and thus share another important topological similarity with the claustra.

9) SUMMARY AND CONCLUSIONS (CLAUSTRUM)

Supradorsal cartilages play a previously unrecognized major role during the ontogeny and evolution of the neural complex of otophysan Ostariophysi. Supradorsals 3 and 4 fuse with supraneurals 2 and 3 (cypriniforms) or supraneural 3 (characiforms, some siluriforms, gymnotiforms) during development to form the neural complex. In most siluriforms the neural complex is exclusively formed by supradorsals 3 and 4. In some siluriforms, a neural complex is missing and the fourth neural arch is fused to the occiput. Of the four otophysan subgroups, siluriforms are the most and cypriniforms the least diverse in the structure and development of their neural complex. Characiforms seem to exhibit striking heterochronic shifts in the development of the components that form the neural complex.

My detailed comparative data on the development of the claustrum in otophysan Ostariophysi demonstrates that it originates and develops differently in the three otophysan subgroups. It arises as a claustral cartilage in cypriniforms and siluriforms and as a membrane bone claustrum in characiforms. The claustral cartilage of cypriniforms ossifies perichondrally at its anterior end and develops an extensive, thin, anteroventrally directed lamina of membrane bone, an autapomorphy of that group. The ventrally directed part of this lamina and the concha scaphii enclose the perilymphatic atrium sinus imparis like shells of a bivalve. The claustral cartilage of the siluriforms that retain this structure ossifies perichondrally in a ventrodorsal direction and develops no membranous components. The claustrum originates medial to the ascending process of the scaphium in Cypriniformes and Characiformes, the primitive condition for otophysans. It is situated only slightly medial or almost in line with the ascending process in the siluriforms, a more derived state. Claustrum and scaphium are both associated with the first vertebral myoseptum.

After having reviewed previous hypotheses of claustrum homology, I conclude that Bloch's (1900) original view, also formulated by Rosen & Greenwood (1970), is the most plausible hypothesis: the claustrum is the homologue of the first supradorsals. I favour this hypothesis over all others because of the close similarity between the claustrum and supradorsal 1 in origin and position to surrounding structures.

10) SIGNIFICANCE OF THE ONTOGENETIC RESULTS OF THIS STUDY FOR THE PHYLOGENETIC FRAMEWORK OF OTOPHYSI

The results of the present comparative study of the ontogeny and homology of the neural complex and claustrum in Otophysi enlarge the character set on which our ideas of the phylogenetic relationships of Ostariophysi are based. My results thus complement Fink & Fink's (1981, 1996) data set adding an ontogenetic perspective, but they do not change the relationships of the larger subgroups as shown in fig. 1. It can be concluded that the last common ancestor of all Otophysi had a neural complex that was similar to the situation we find in most cypriniforms today and contained the following autapomorphies compared to the anotophysan condition (compar fig. 115):

- Paired supradorsals 3 and 4 fused with supraneural cartilages 2 and 3 to form the cartilaginous neural complex, in which supraneurals 2 and 3 ossified.
- The claustrum was preformed in cartilage, but unlike the cypriniform condition most likely did not have any membrane bone component. The association of the claustrum with the medial wall of the sinus impar does not belong to the 'Grundplan' (character set of the last common ancestor) of Otophysi, but is a synapomorphy of Cypriniformes. It is still unknown what the function of the claustrum within the Weberian apparatus is and therefore nothing can be said about the functional significance of the presence or absence of its membrane bone component.
- In the last common ancestor of Characiphysi (Characiformes + Siluriformes + Gymnotiformes) supraneural 2 was lost and the neu-

ral complex was formed by ontogenetic fusion of supradorsals 3 and 4 and supraneural cartilage 3 only; both characters represent autapomorphies of that taxon. The claustrum was still preformed in cartilage.

- The structure of the neural complex in the 'Grundplan' of Characiformes was very similar to that of Characiphysi. However, the cartilaginous precursor was lost at this node, a synapomorphy of characiforms.
- The last common ancestor of Siluriformes had a neural complex and claustrum that was not different from that of Characiphysi. However major modifications took place during the diversification of the siluriform subtaxa, which will be discussed further below under evolutionary tendencies.
- The claustrum does not belong to the 'Grundplan' of Gymnotiformes and its absence is a synapomorphy of that group. The reasons for its loss are unclear, but because it does not seem to be involved in the immediate functioning of the whole apparatus, this is not too surprising.

11) EVOLUTIONARY TENDENCIES IN THE FORMATION AND STRUCTURE OF THE WEBERIAN APPARATUS

The Weberian apparatus is a beautiful example how almost identical metameric units become integrated into a larger functional and anatomical complex and how they lose their similarity during the course of the evolution of this complex.

The anterior vertebrae of Anotophysi, although slightly different in size and shape, still show all components of a typical teleost vertebra: neural arches preformed in cartilage with associated supradorsals, supraneurals intercalated with neural spines, cartilaginous basiventrals that later ossify as parapophyses, separate centra, and normal ribs starting at vertebra no 3. These components which previously had no immediate functional connection became integrated into one larger complex, the skeletal part of the Weberian apparatus, during the evolution of the Otophysi.

In the last common ancestor of Otophysi, this integration into a sound transmitting apparatus was already established. However, this apparatus has been further modified within the otophysan subgroups sometimes in similar but also in different ways. One common tendency encountered in cypriniforms and siluriforms is the consolidation of vertebrae. In some cyprinids like *Cyprinus carpio*, the centra of vertebrae 2 and 3 fuse during ontogeny into a larger stiff compound centrum. The same is true for the 'Grundplan' of siluriforms in which centra 2, 3 and 4 form a compound centrum. Both fusion events might be correlated with a stiffening of the anterior vertebral region that would facilitate the accurate transmission of sound pressure waves through the Weberian ossicles. This tendency is further elaborated within siluriforms and the most extreme examples are certainly the callichthyids and loricariids. Here the anterior vertebrae do not seem to develop, the cartilaginous neural arch of the fourth vertebra fuses with the tectum synoticum of the occipital skull, the Weberian ossicles are reduced from four to two and shifted into the skull, and the anterior compartment of the swimbladder is apired and housed in two bony bullae that are attached to the back of the skull. This anatomical integration of the Weberian apparatus into the back of the skull also means a functional integration, which results in an extreme shortening of the distance between the swimbladder, the place of sound reception and the inner ear, the place of sound perception and transduction. In this context the loss of the intercalarium means one piece less in the chain of ossicles that transmits the sound pressures waves. One would expect that these changes in loricarioids result in a much improved apparatus and there is every reason to hypothesize this, however, functional and physiological data of this group of Otophysi are still lacking and are an exciting area for future research.

12) FUTURE RESEARCH ON THE NEURAL COMPLEX AND WEBERIAN APPARATUS

The next logical step leading to a better understanding of the structure and evolution of the Weberian apparatus will certainly be ontogenetic studies to resolve the homology of its other skeletal components the remaining three Weberian ossicles scpahium, intercalarium, tripus and the os suspensorium. If these future investigations would be performed in a similar way as the present study, they will have the great potential of helping to resolve the current debates about homology issues and might actually lead to a consensus.

As detailed above, the siluriforms are the otophysan group, in which the characiphysan neural complex is further modified to extremes that are difficult to interpret, as in the callichthyids and loricariids. The posterior part of the loricarioid skull is still poorly understood, including all the modifications of the shoulder girdle and Weberian apparatus. Future ontogenetic studies incorporating a number of loricarioid taxa will certainly help to correctly analyse the anatomical structure of this area of the loricarioid skull and help to understand the evolutionary changes that lead to these amazing changes. Studies on the development of this part of the catfish skull will not only resolve controversies about the homology of the components involved but also almost certainly help to understand the complex phylogenetic history of catfishes, one of the largest groups of teleosts.

Another area for future research among Otophysi are the interesting heterochronic changes I encountered in the development of the Weberian apparatus among different characiform groups. As with catfishes, such a study will almost certainly provide interesting characters for our attempts to resolve the phylogenetic relationships of characiforms.

13) THE COMPARATIVE ONTOGENETIC APPROACH TO RESOLVE HOMOLOGY ISSUES

The Weberian apparatus represents a textbook example of a highly morphologically derived character complex. Since its discovery in 1820, researchers have tried to resolve the identity of the different components involved. This has been done during the first phase of investigation solely by comparison of the adult state with that of teleosts that lack the apparatus. This approach has yielded a number of convincing hypotheses, but a consensus was not reached.

The second phase of investigation has been characterized by ontogenetic studies, which however, were restricted to the few taxa for which developmental material was available. It was also quite laborious as these were only able to include few developmental stages. With the invention of clearing and double staining (Dingerkus & Uhler, 1977) large numbers of specimens could be processed, but the number of available taxa has still remained as the major limitation.

My approach is therefore quite unique as it incorporates for the first time representatives of all otophysan subgroups with dozens of developmental stages per species. The ontogenetic approach to resolve homologies is based on the fact that frequently highly modified adult character states that are difficult to compare across taxa originate in ontogeny from less modified states, which are therefore easier to compare.

In the case of the neural complex ontogeny reveals, how many and which components contribute to its formation in the different otophysan groups. This approach combined with high quality illustrations of ontogenetic stages has been highly successful, I think, for the resolution of the homologies of the neural complex and claustrum and performed in a similar way can be expected to provide similar results for the other components of the Weberian apparatus.

I hope I have demonstrated the great power of ontogeny as a tool to resolve homology issues. This seems especially true for actinopterygian fishes with their unparalleled anatomical diversity among vertebrates. My study on the ontogeny and homology of the neural complex and claustrum of Otophysi is the first part of a large-scale project to unravel the homologies of the different components of the Weberian apparatus. This can only be done, I think, by applying a rigorous comparative-ontogenetic approach with a new standard of high quality illustrations in the same way as I have done here for the neural complex and the claustra.

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16) PLATES

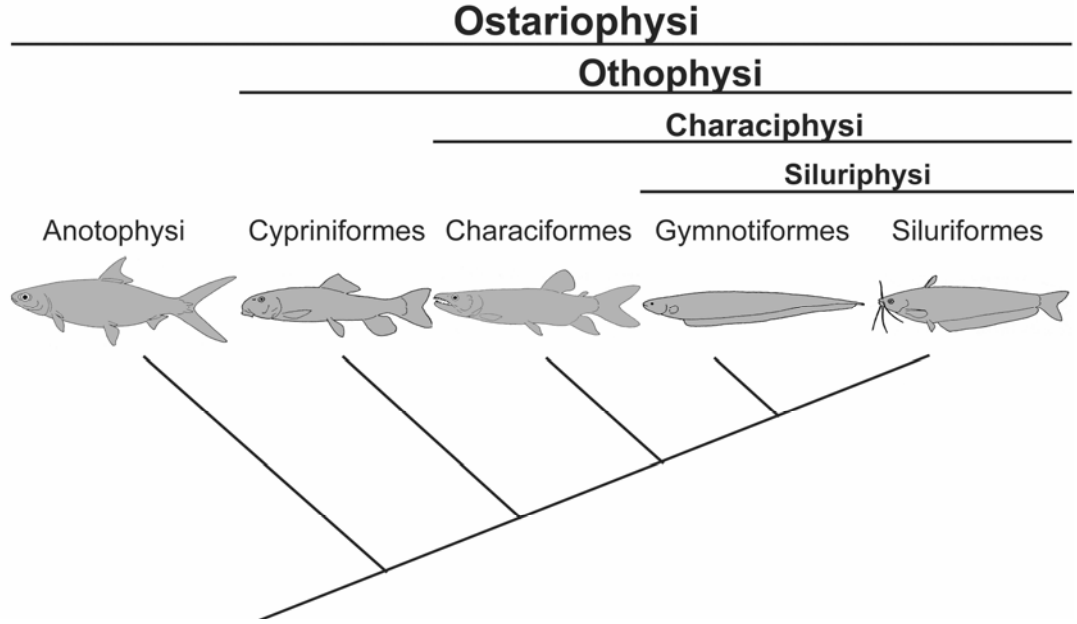

Fig. 1 Phylogenetic intrarelationships of Ostariophysi after Fink & Fink (1981, 1996)

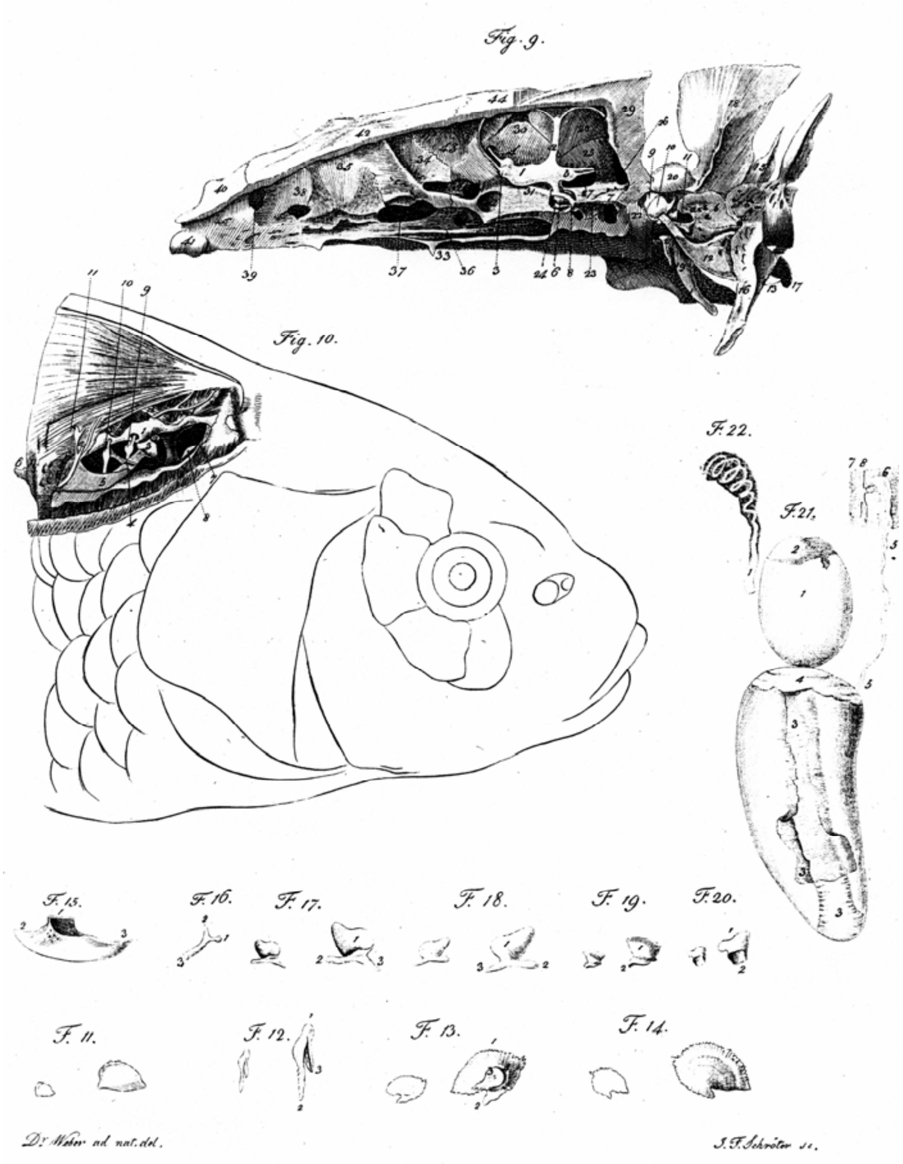

Fig. 2 Weber's (1820) illustration of the sound conducting apparatus of *Cyprinus carpio*, which was later named after him and is now known as the Weberian apparatus

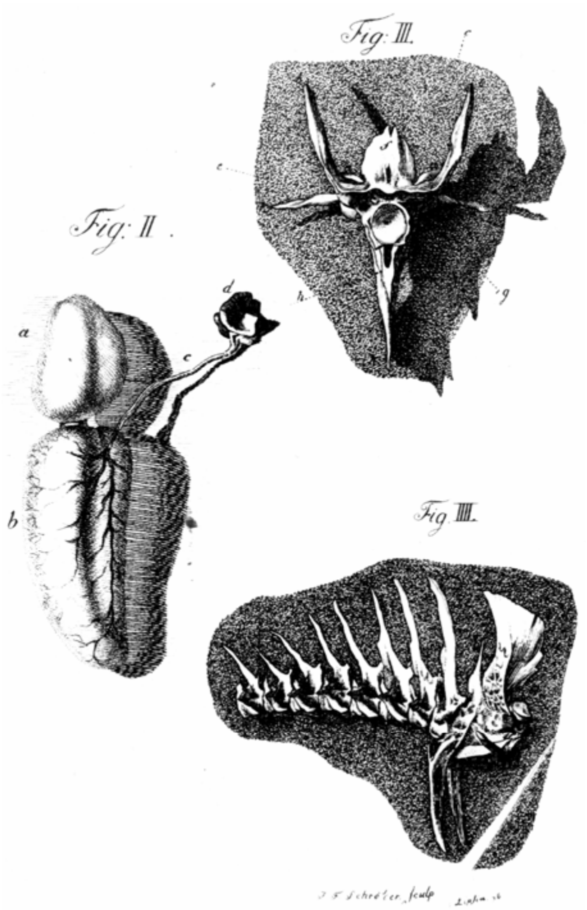

Fig. 3 Fischer's (1795) illustration of the modified anterior vertebrae of a cyprinid.

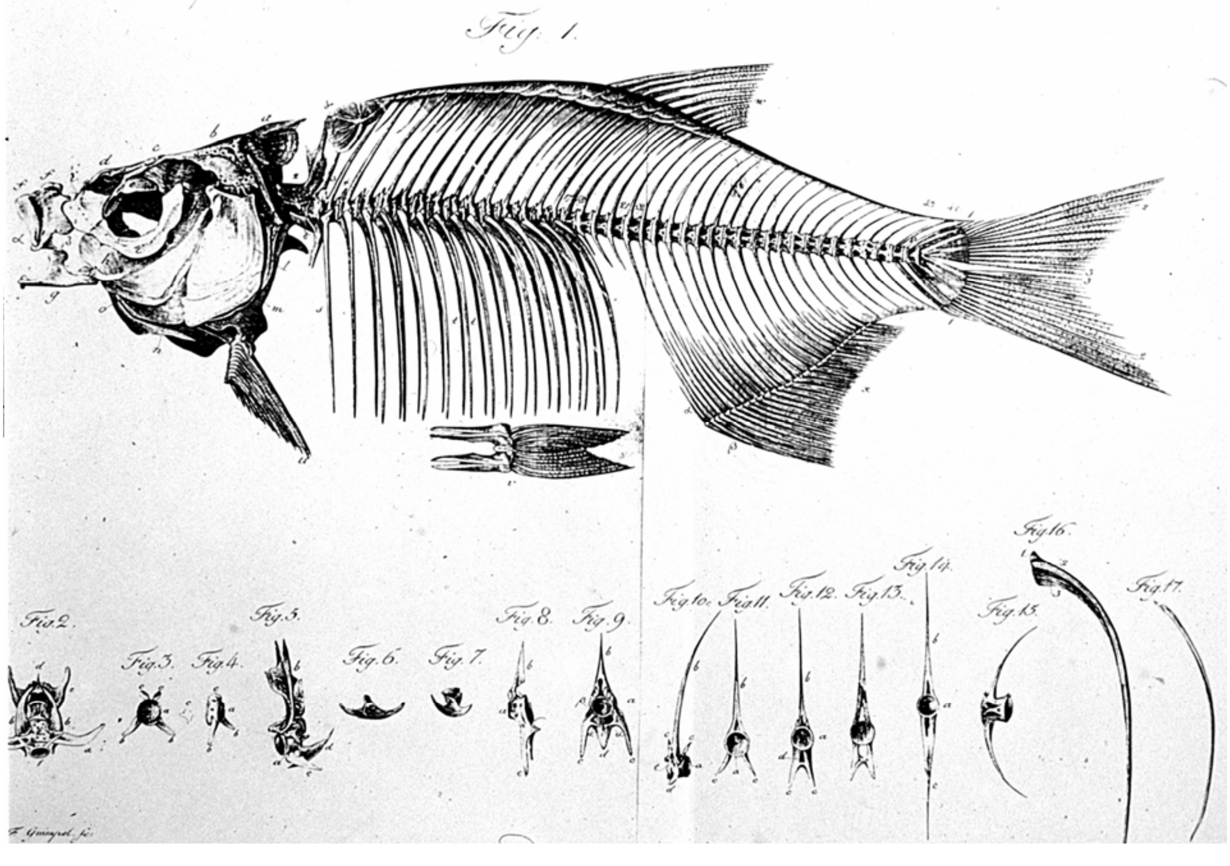

Fig. 4 Rosenthal's (1812) illustration of the modified anterior vertebrae in *Abramis brama*.

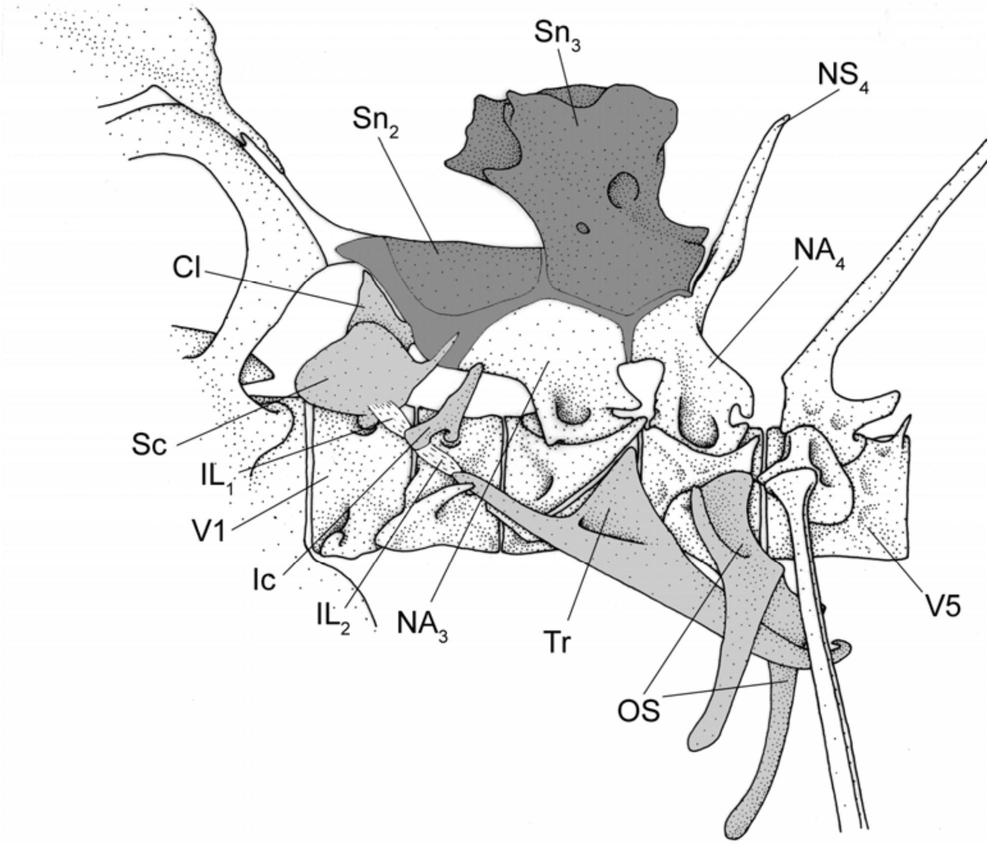

Fig. 5 Weberian ossicles and neural complex of *Opsariichthys uncirostris*, lateral view, modified from Fink & Fink (1981). Note that all components comprising the neural complex are marked in dark grey the four Weberian ossicles and the os suspensorium in light grey.

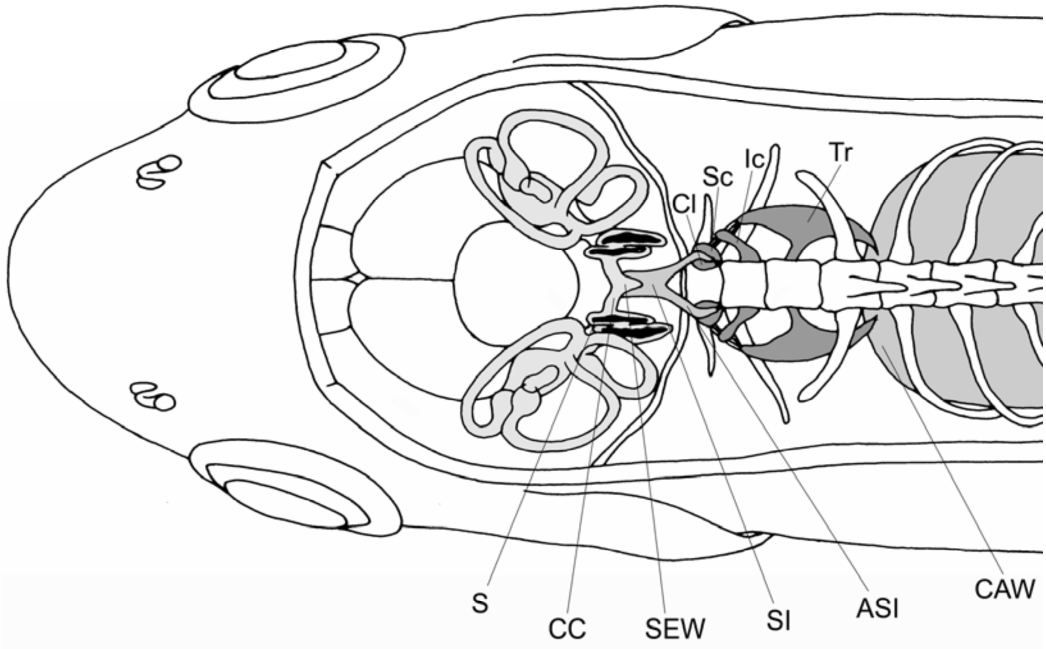

Fig. 6 *Phoxinus phoxinus*, modified from von Frisch (1936). Note that the Weberian apparatus comprises parts of the inner ear, the four anterior vertebrae and their associated structures and part of the swimbladder. The neural complex is not shown.

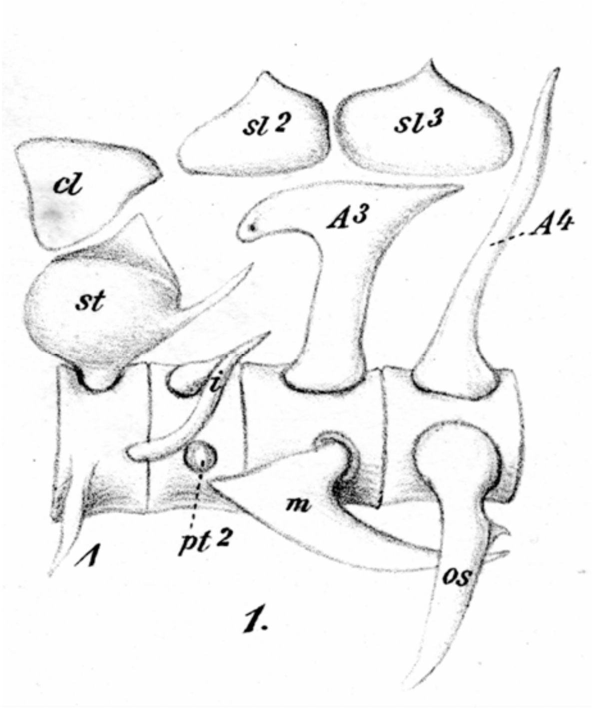

Fig. 7 Developmental stage of the four anterior vertebrae of *Leuciscus rutilus* after Sørensen, 1890

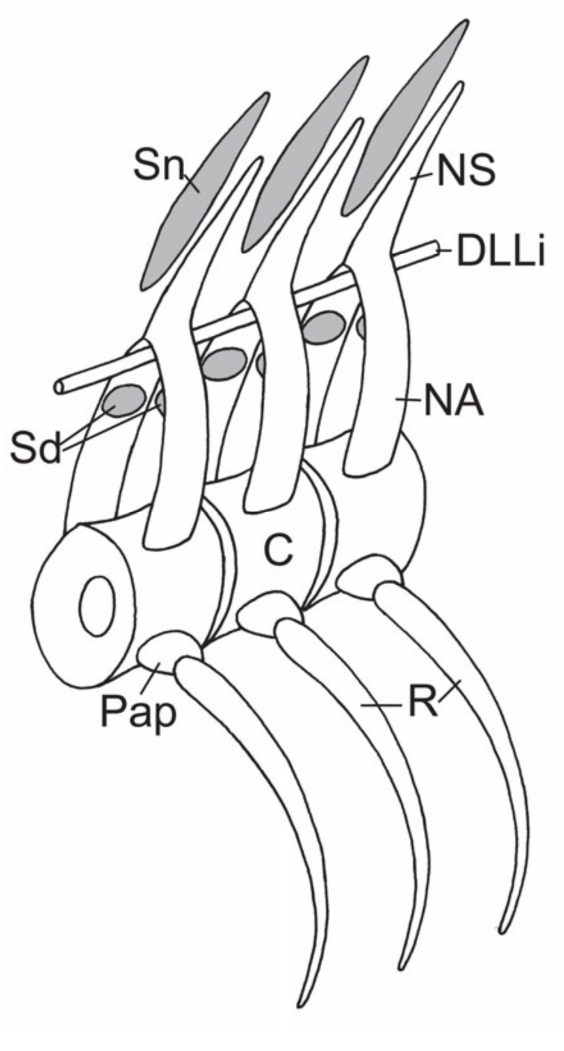

Fig.8 Schematic representation illustrating the typical components of anterior abdominal vertebrae in a basal teleost. Supraneurals and supradorsals marked in grey.

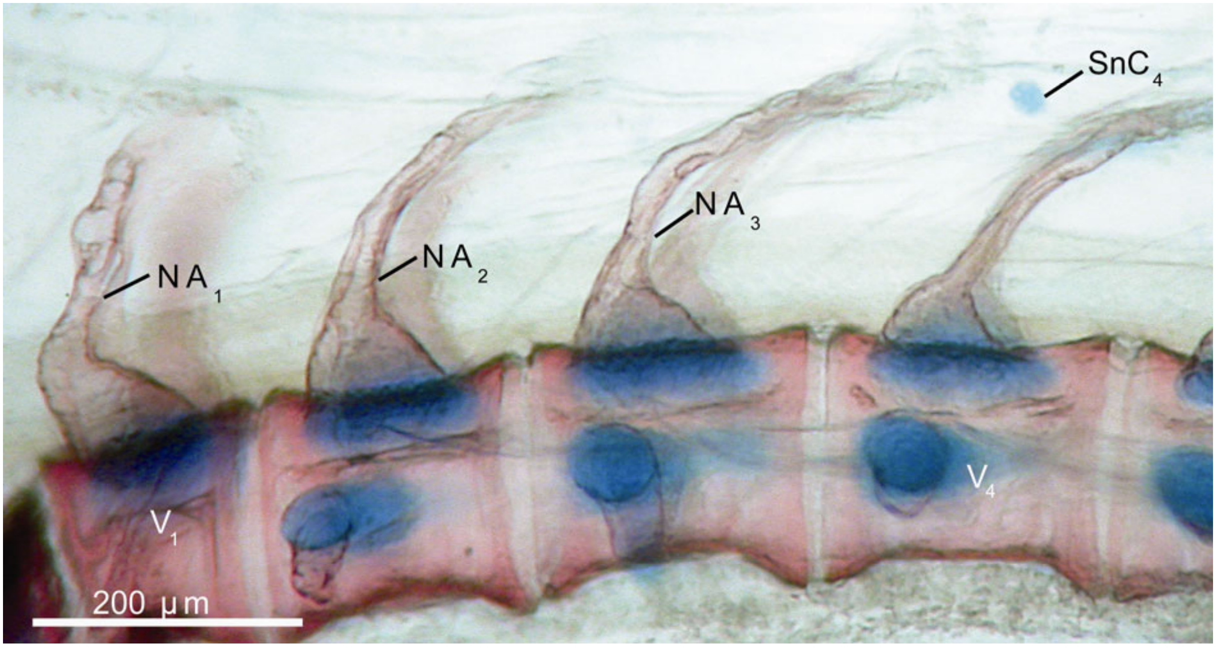

Fig. 9 Anterior neural arches and associated structures in non-Ostariophysi. *Pantodon buchholzi*, 10.0 mm, lateral view.

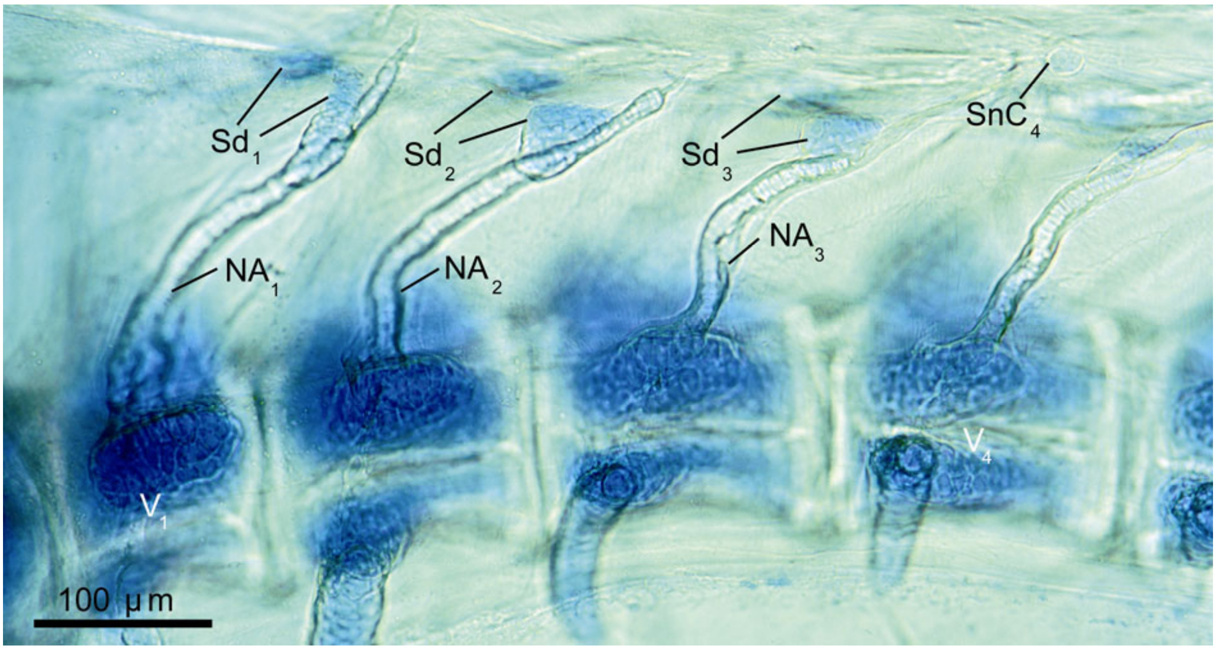

Fig. 10 Anterior neural arches and associated structures in non-Ostariophysi. *Pantodon buchholzi*, 11.3 mm, lateral and slightly anterodorsal view.

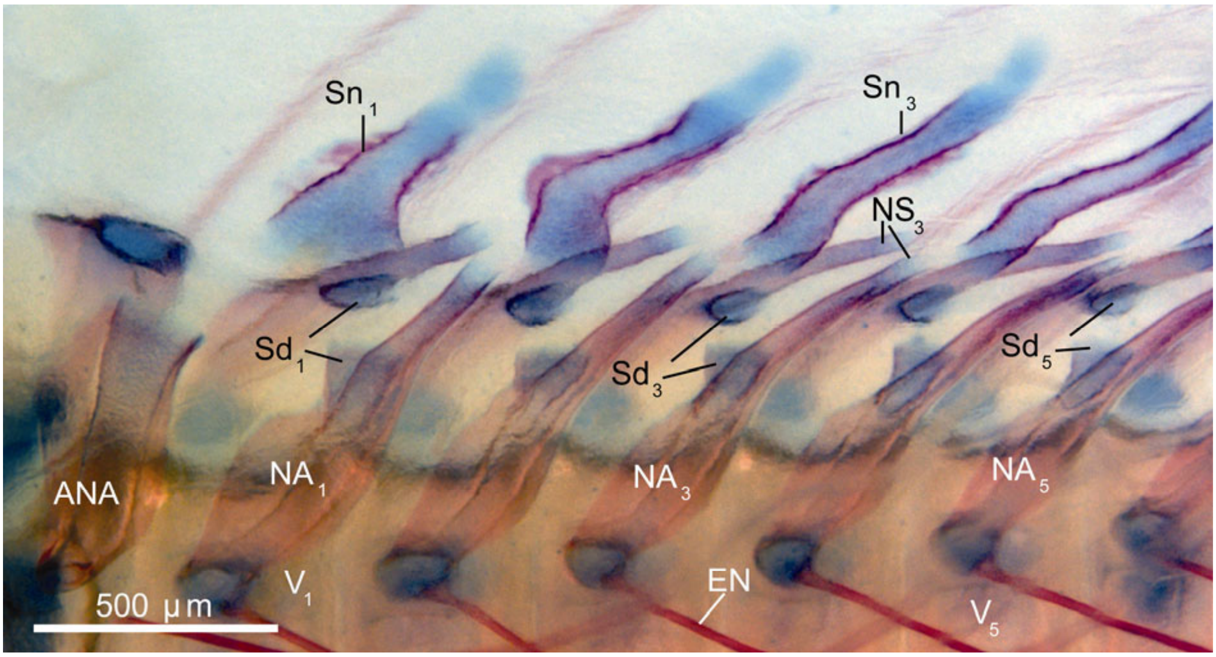

Fig. 11 Anterior neural arches and associated structures in non-Ostariophysi. *Elops machnata*, 39.2 mm, lateral and slightly anterodorsal view.

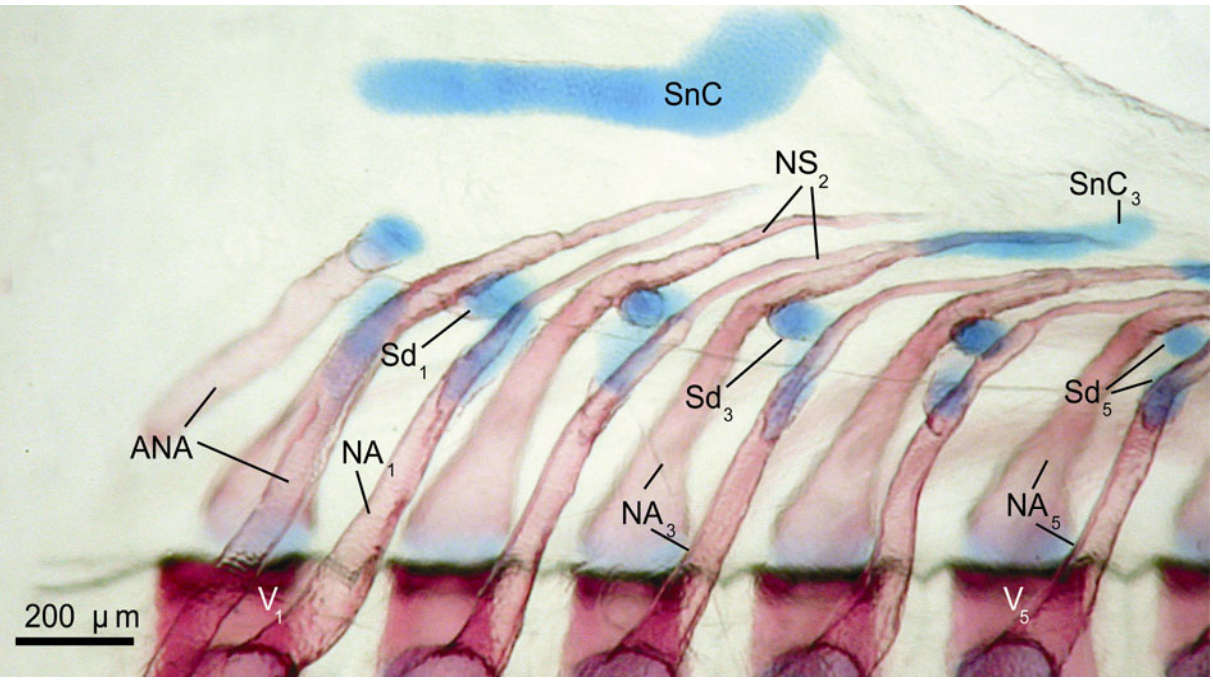

Fig. 12 Anterior neural arches and associated structures in non-Ostariophysi. *Oncorhynchus mykiss*, 24.0 mm, lateral and slightly anterodorsal view.

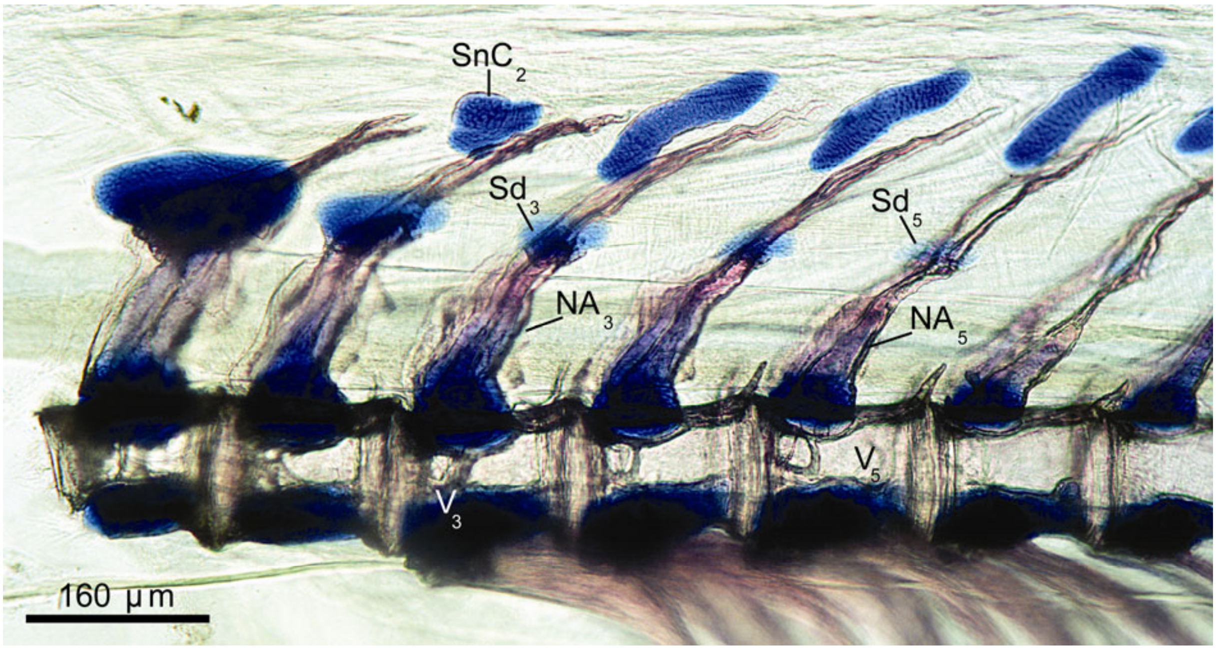

Fig. 13 Anterior neural arches and associated structures in Anotophysi.
Chanos chanos, 18.7 mm, lateral view.

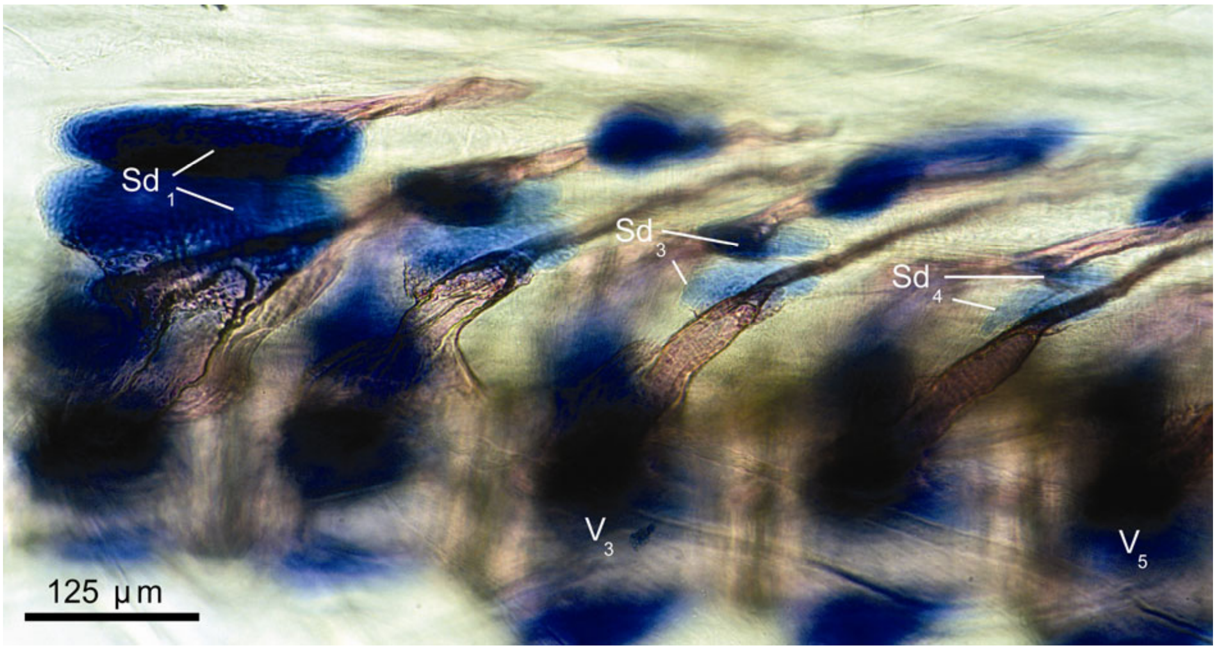

Fig. 14 Anterior neural arches and associated structures in Anotophysi.
Chanos chanos, 18.7 mm, same as Fig. 13 but in close up and dorsolateral view.

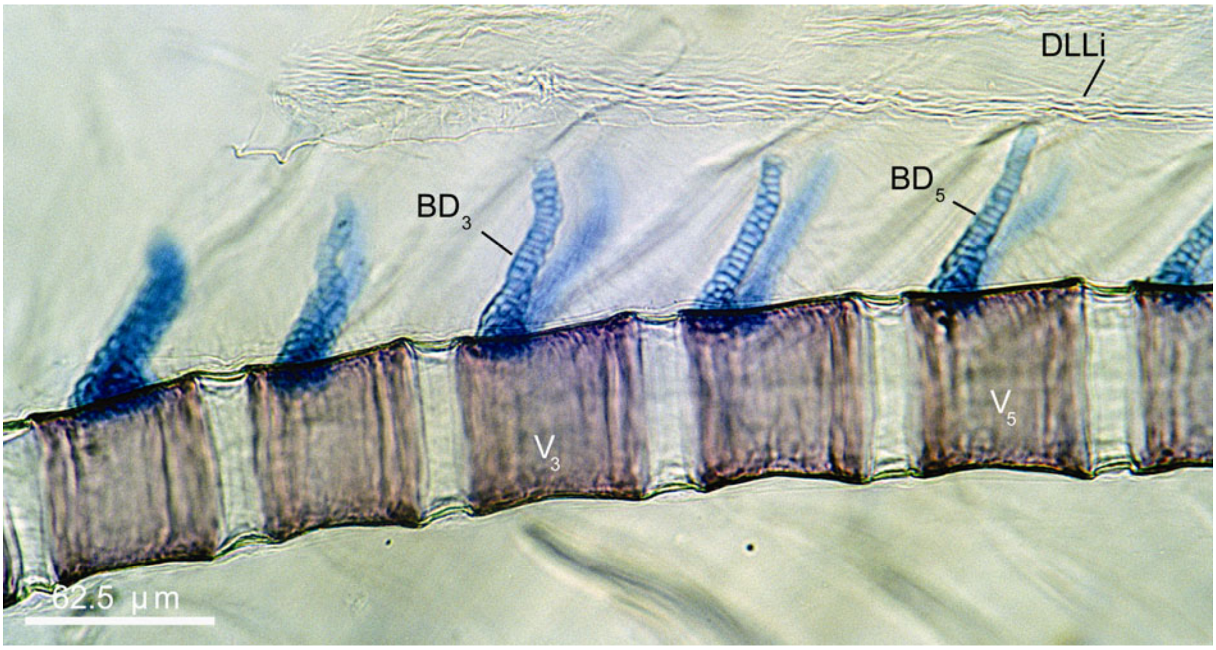

Fig. 15 Anterior neural arches and associated structures in Anotophysi. *Kneria* sp., 7.5 mm, lateral view.

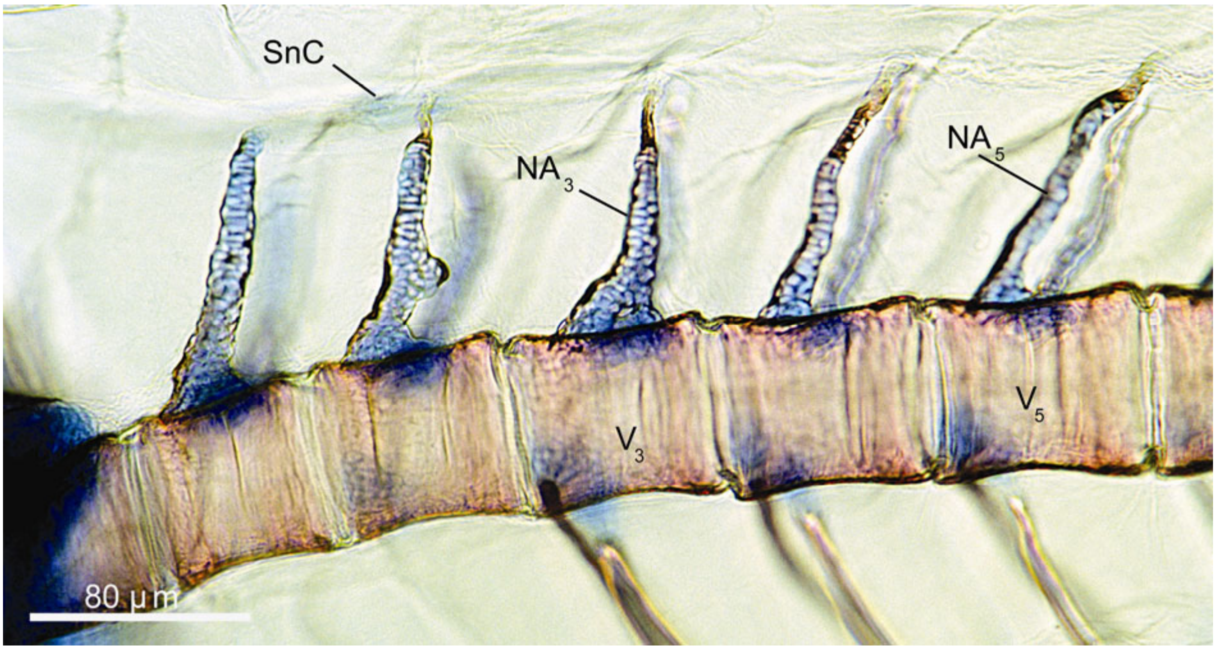

Fig. 16 Anterior neural arches and associated structures in Anotophysi. *Kneria* sp., 8.8 mm, lateral view.

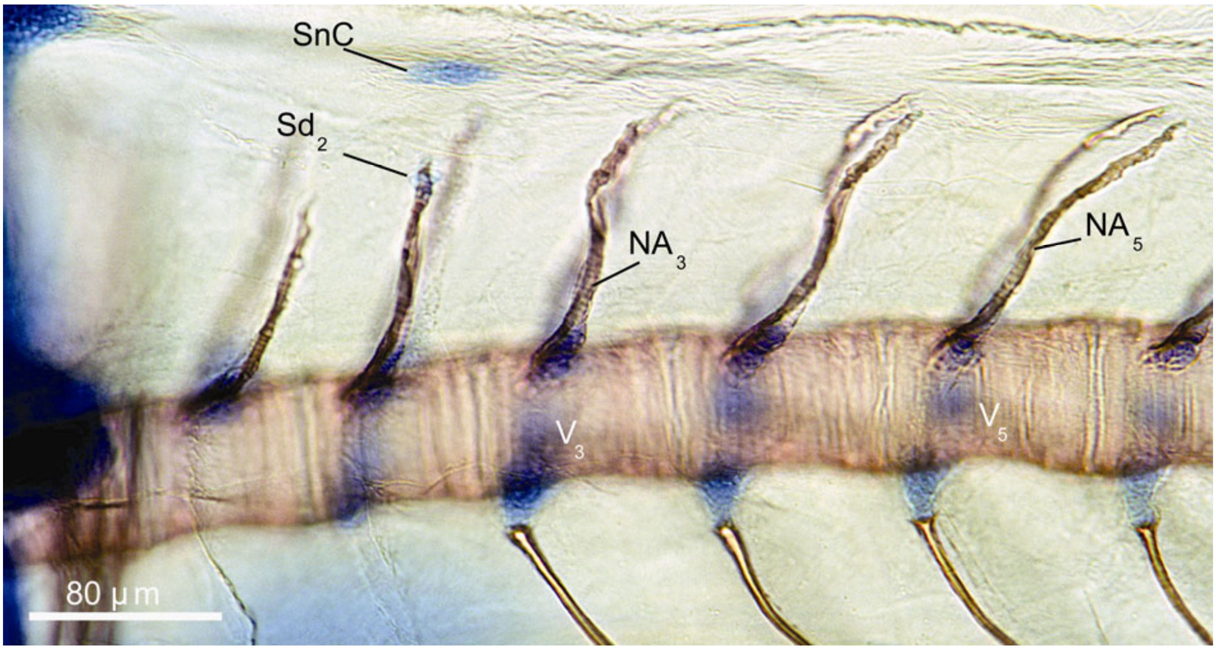

Fig. 17 Anterior neural arches and associated structures in Anotophysi. *Kneria* sp., 9.2 mm., lateral view.

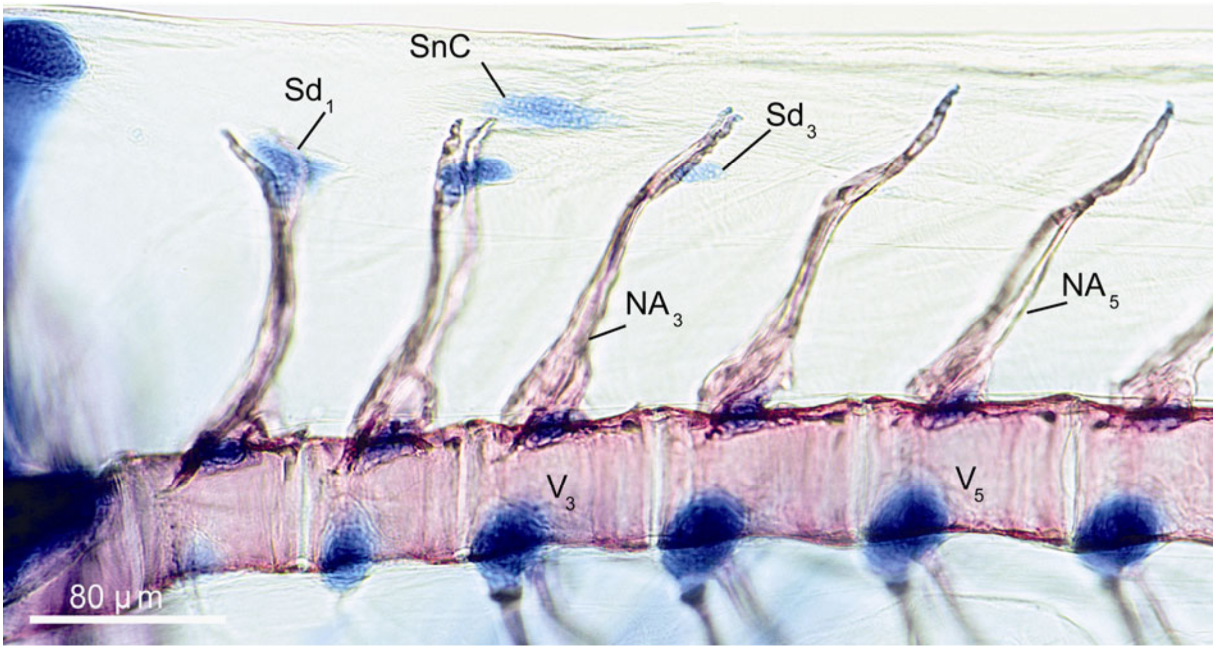

Fig. 18 Anterior neural arches and associated structures in Anotophysi. *Kneria* sp., 12,4 mm, lateral view.

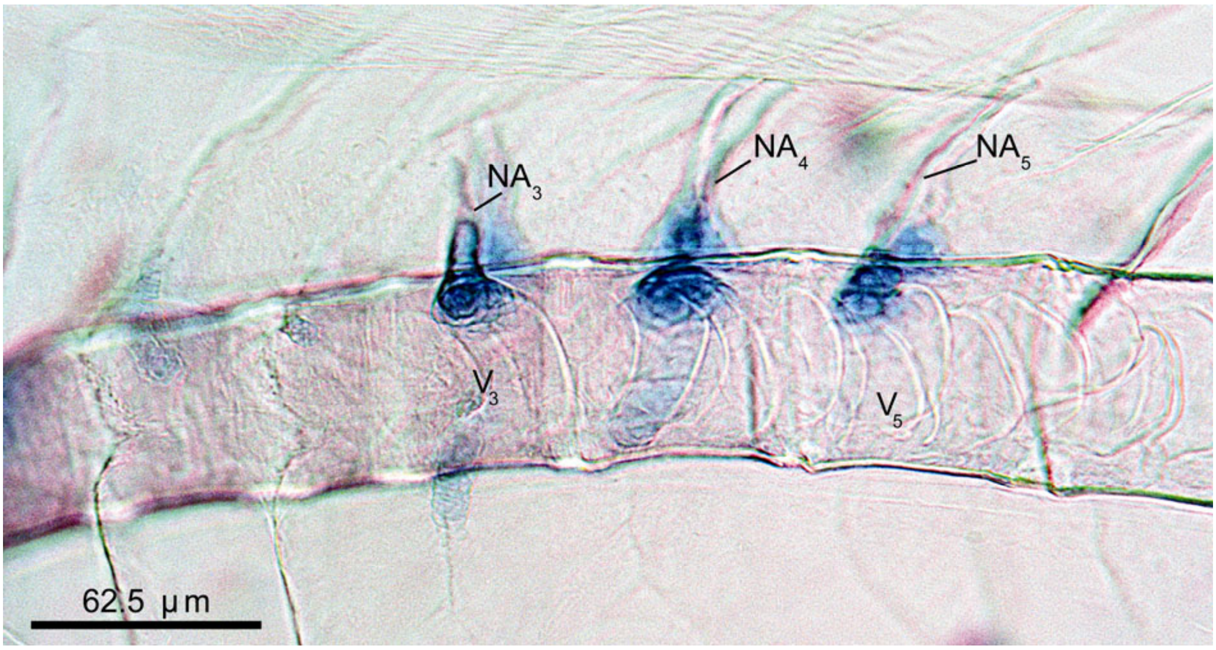

Fig. 19 Developmental stages of the neural complex in Cypriniformes. *Devario aequipinnatus*, 6.5 mm, lateral view.

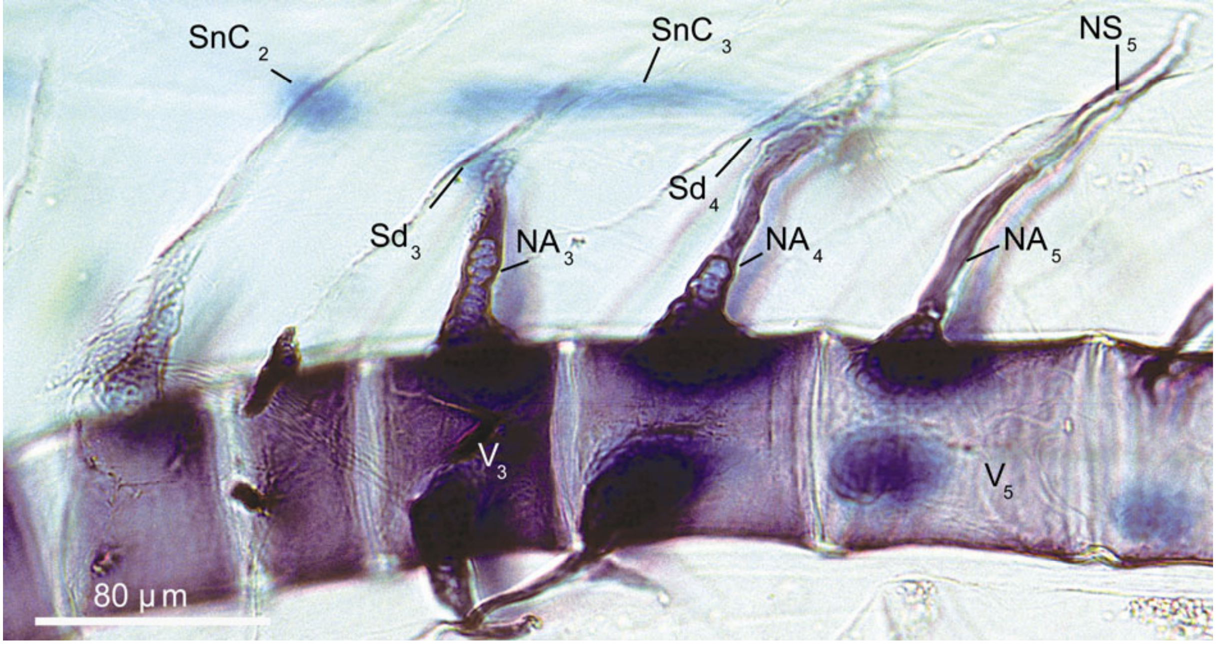

Fig. 20 Developmental stages of the neural complex in Cypriniformes. *Devario aequipinnatus*, 7.1 mm, lateral view.

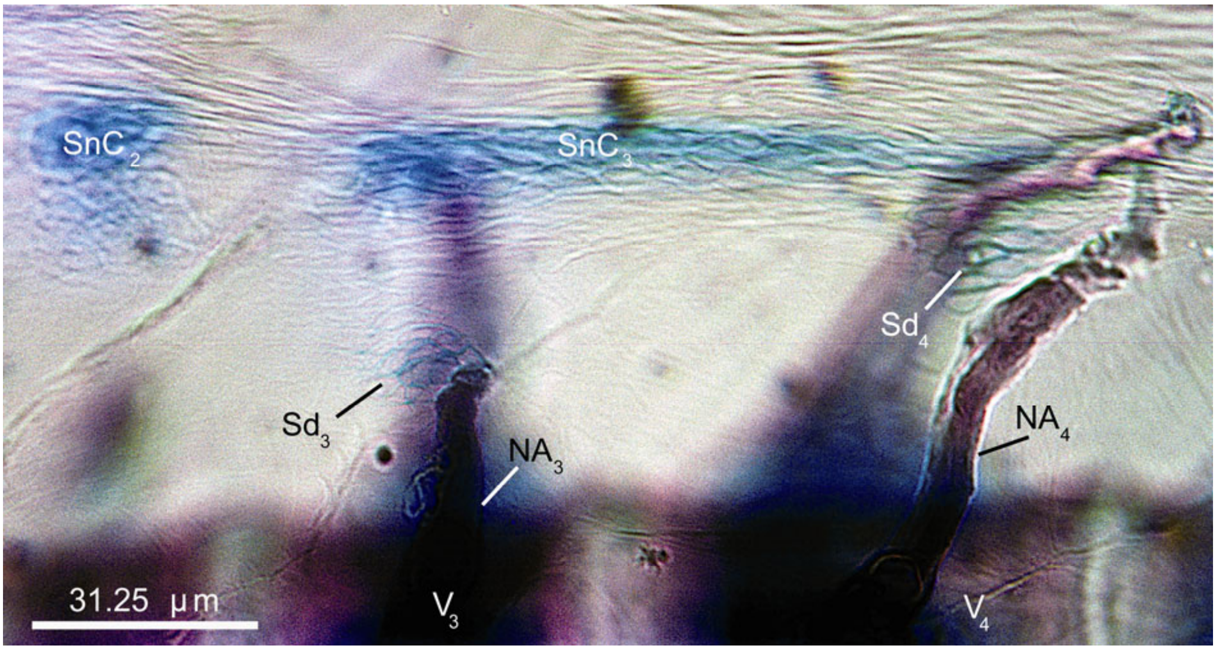

Fig. 21 Developmental stages of the neural complex in Cypriniformes.

Devario aequipinnatus, 7.1 mm, same as Fig. 20 but in close up and slightly dorsolateral

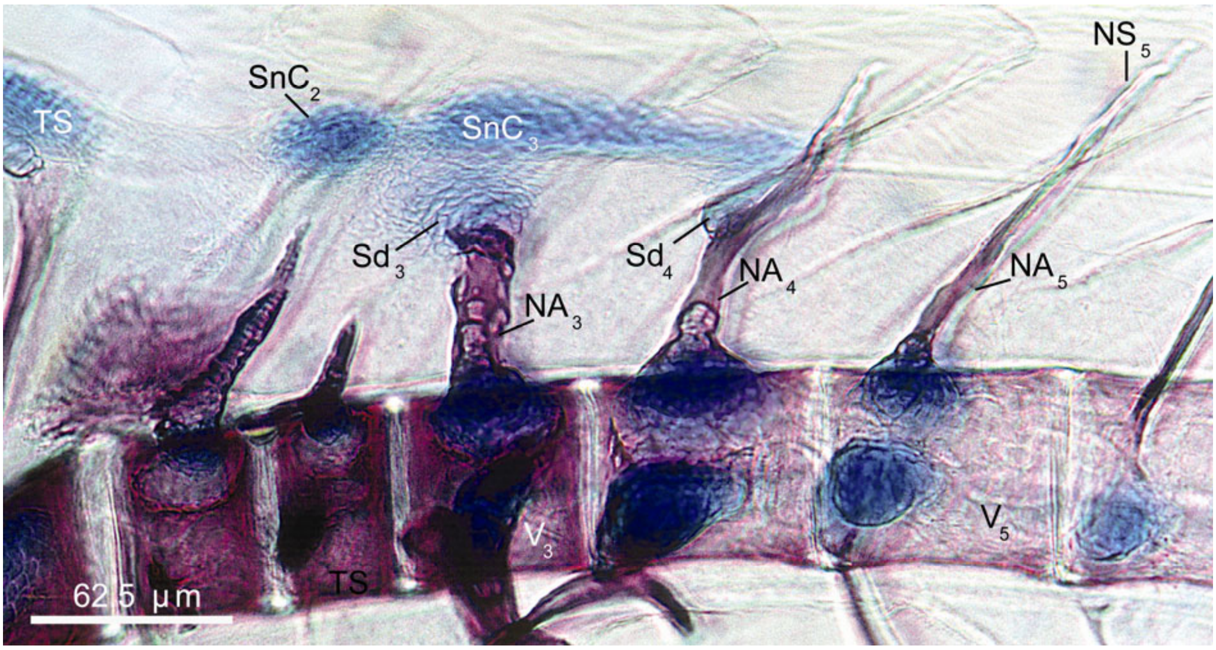

Fig. 22 Developmental stages of the neural complex in Cypriniformes.

Devario aequipinnatus, 7.6 mm, lateral view.

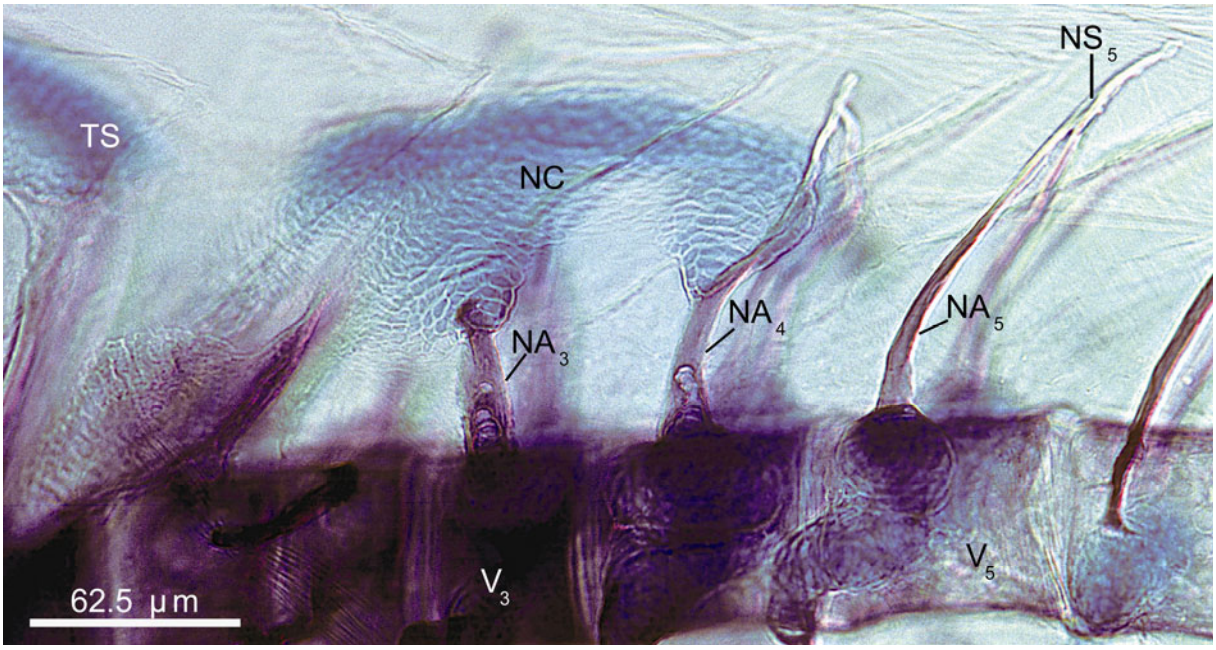

Fig. 23 Developmental stages of the neural complex in Cypriniformes. *Devario aequipinnatus*, 7.5 mm, lateral view.

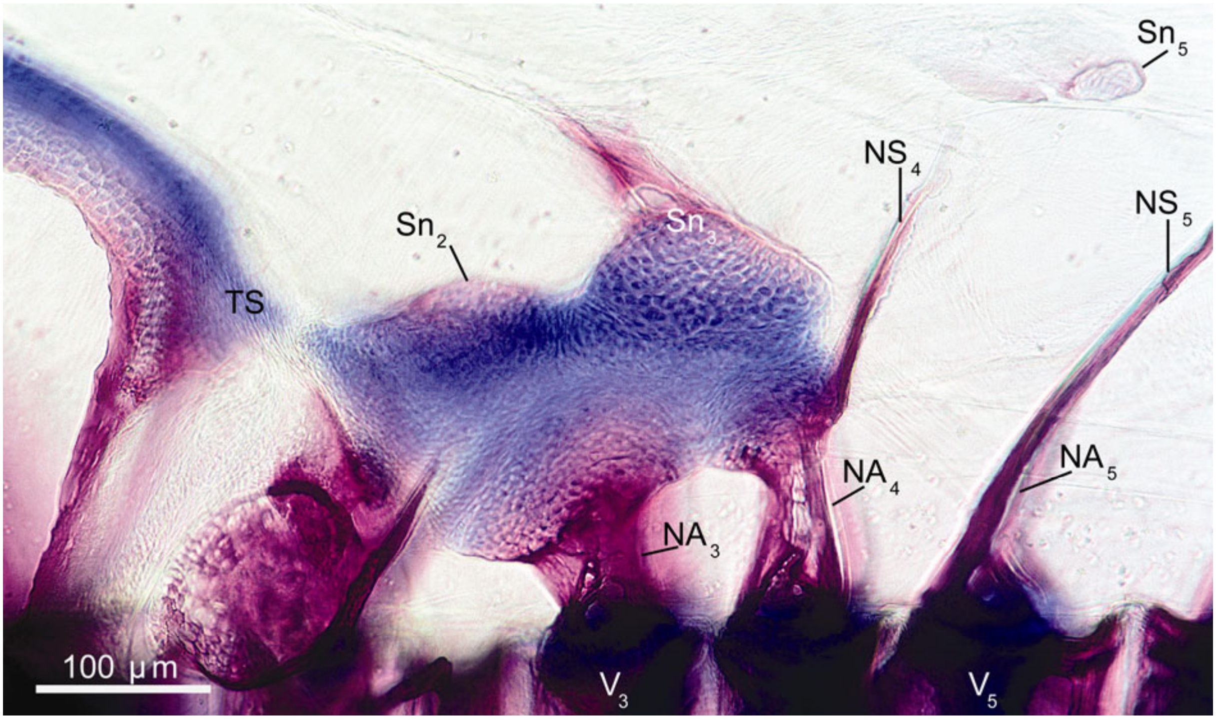

Fig. 24 Developmental stages of the neural complex in Cypriniformes. *Devario aequipinnatus*, 14.5 mm, lateral view.

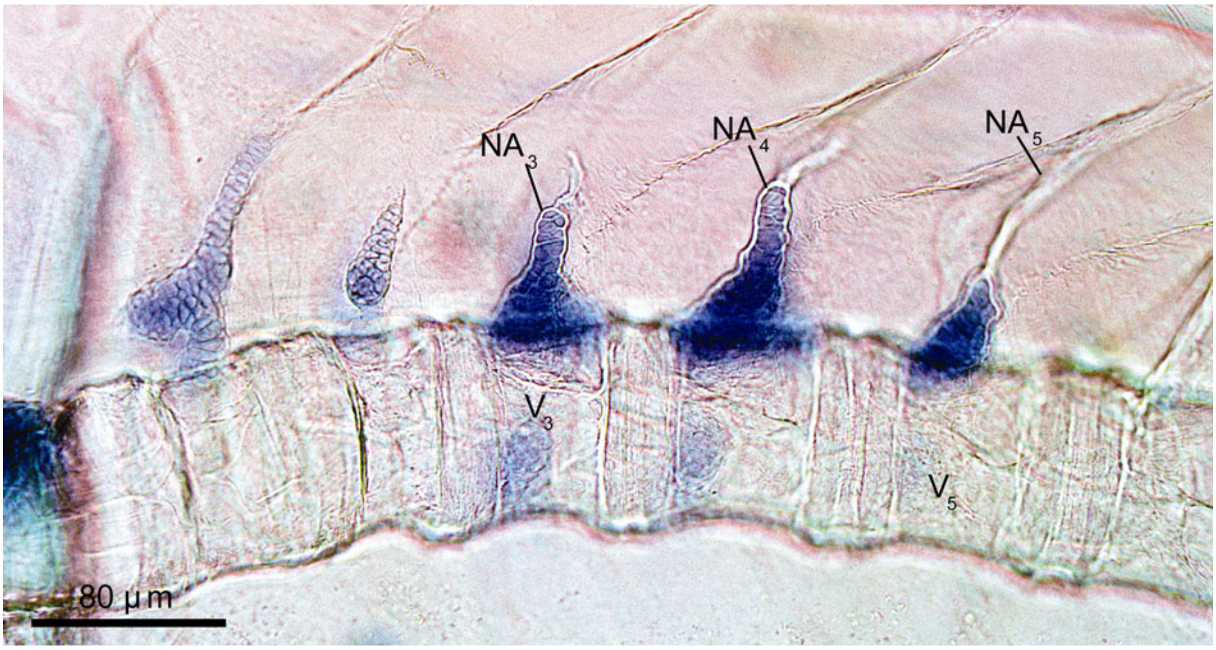

Fig. 25 Developmental stages of the neural complex in Cypriniformes. *Cyprinus carpio*, 8.6 mm, lateral view.

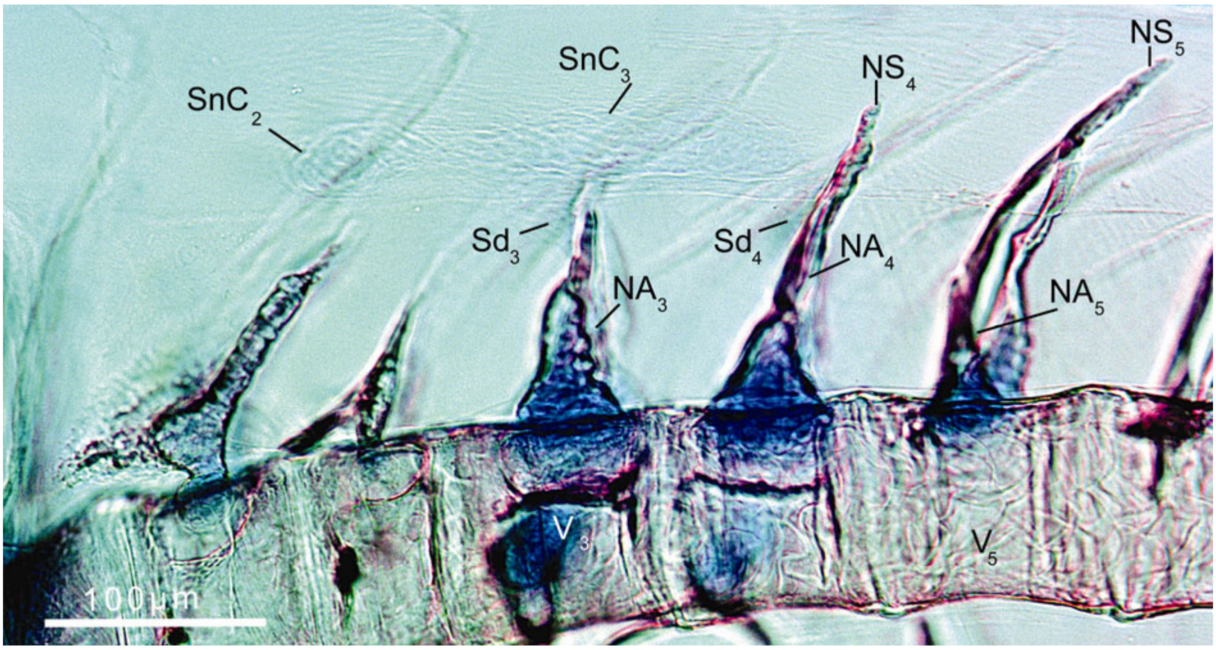

Fig. 26 Developmental stages of the neural complex in Cypriniformes. *Cyprinus carpio*, 9.1 mm, lateral view.

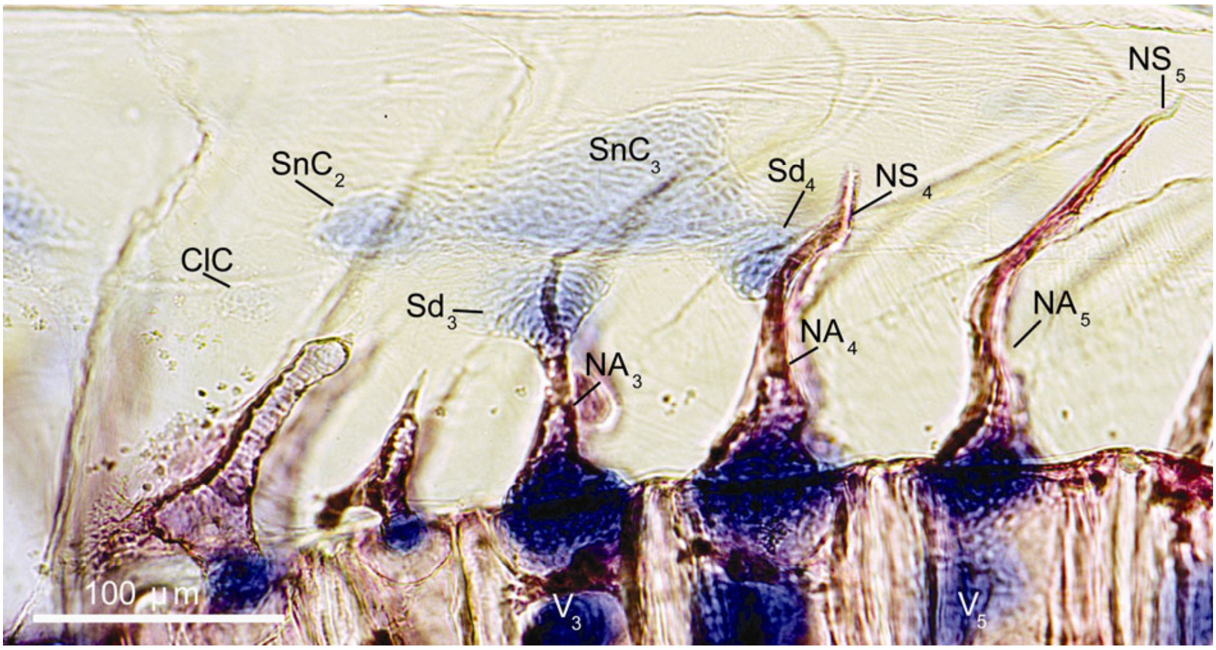

Fig. 27 Developmental stages of the neural complex in Cypriniformes. *Cyprinus carpio*, 9.8 mm, lateral view.

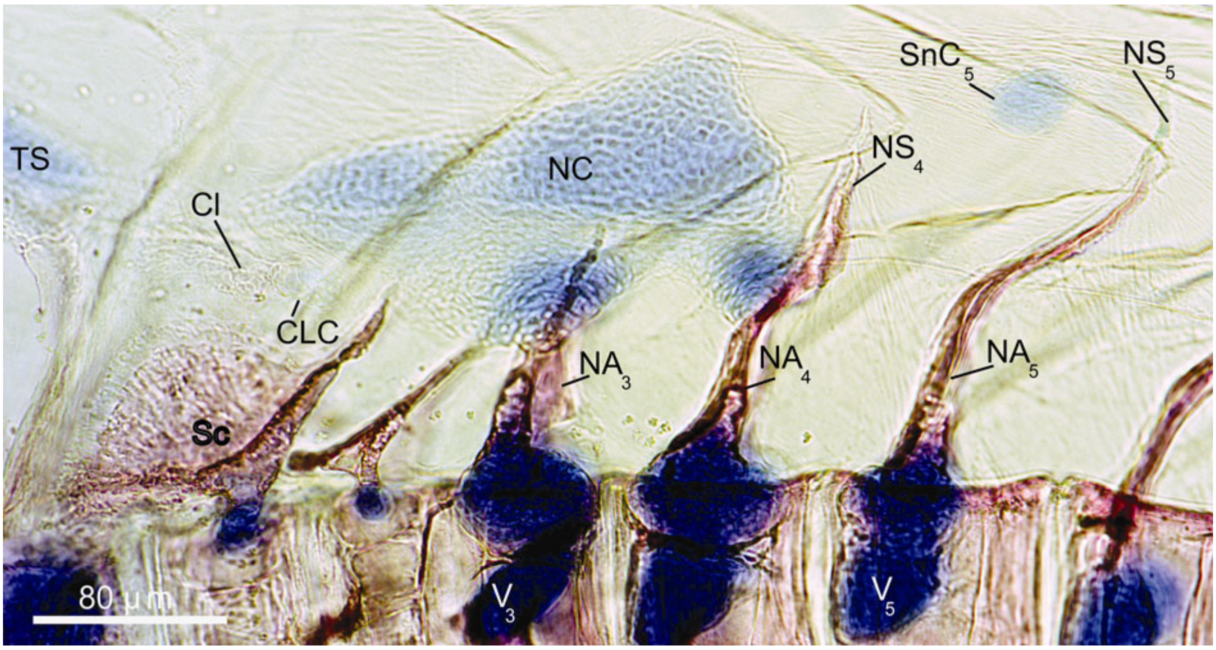

Fig. 28 Developmental stages of the neural complex in Cypriniformes. *Cyprinus carpio*, 11.1 mm, lateral view.

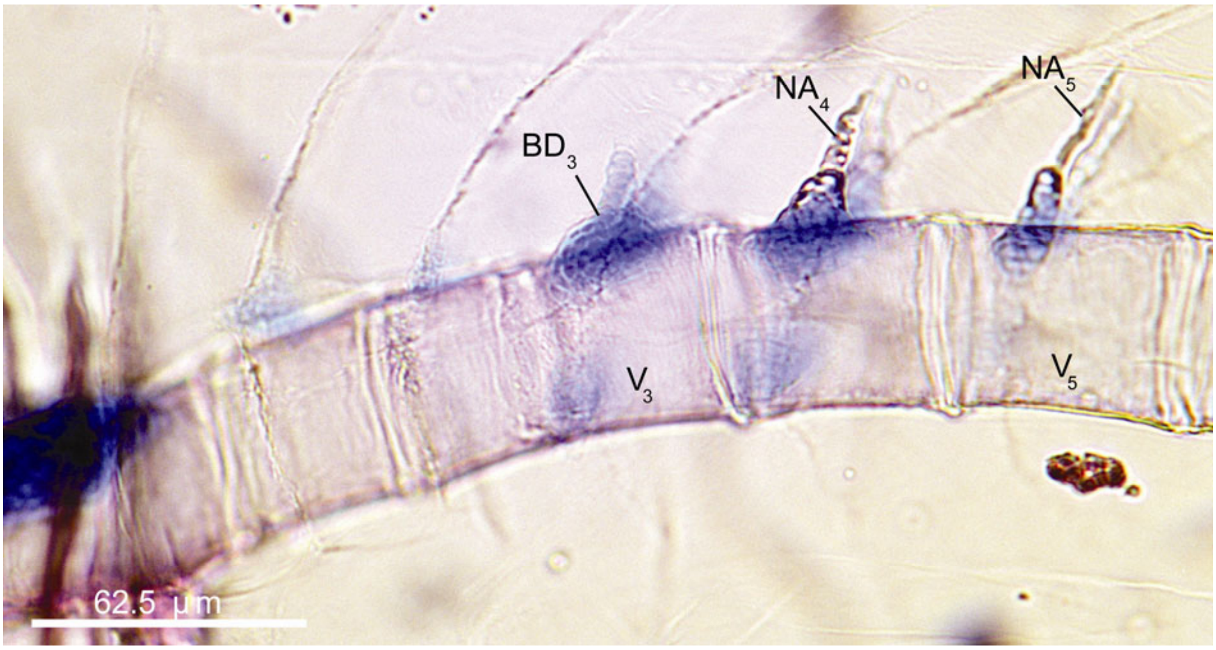

Fig. 29 Developmental stages of the neural complex in Cypriniformes. *Puntius* sp., 4.7 mm, slightly ventrolateral view.

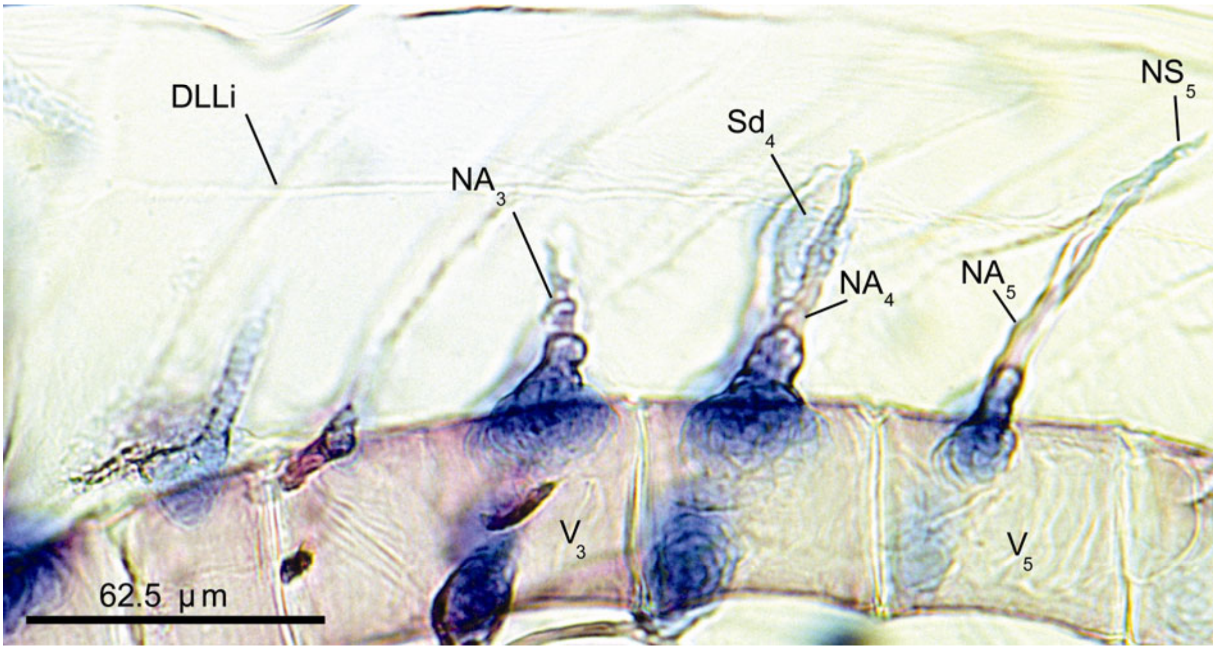

Fig. 30 Developmental stages of the neural complex in Cypriniformes. *Puntius* sp., 5.1 mm, slightly ventrolateral view.

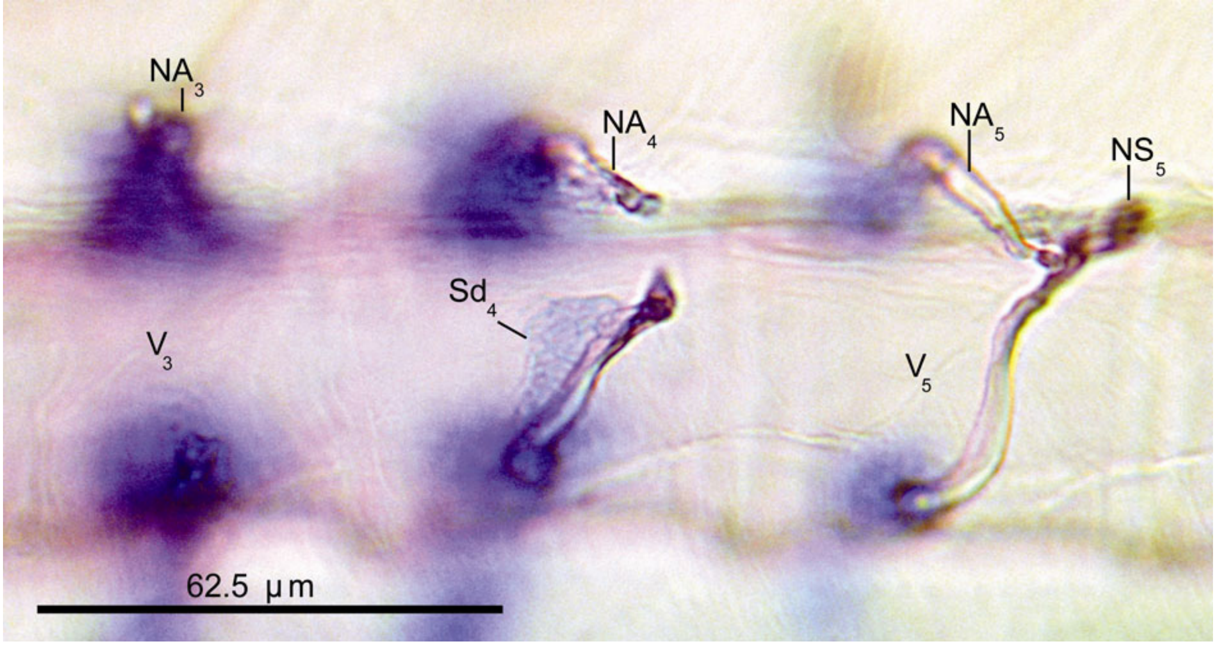

Fig. 31 Developmental stages of the neural complex in Cypriniformes. *Puntius* sp., 5.3 mm, dorsal view.

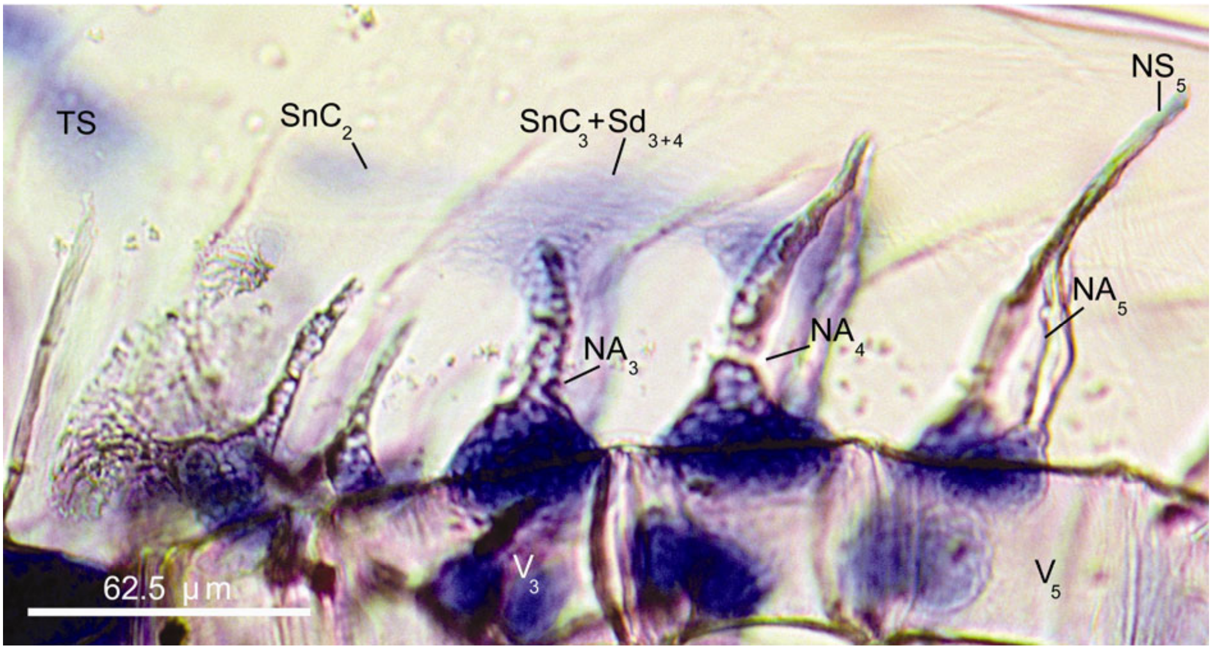

Fig. 32 Developmental stages of the neural complex in Cypriniformes. *Puntius* sp., 5.1 mm, lateral view.

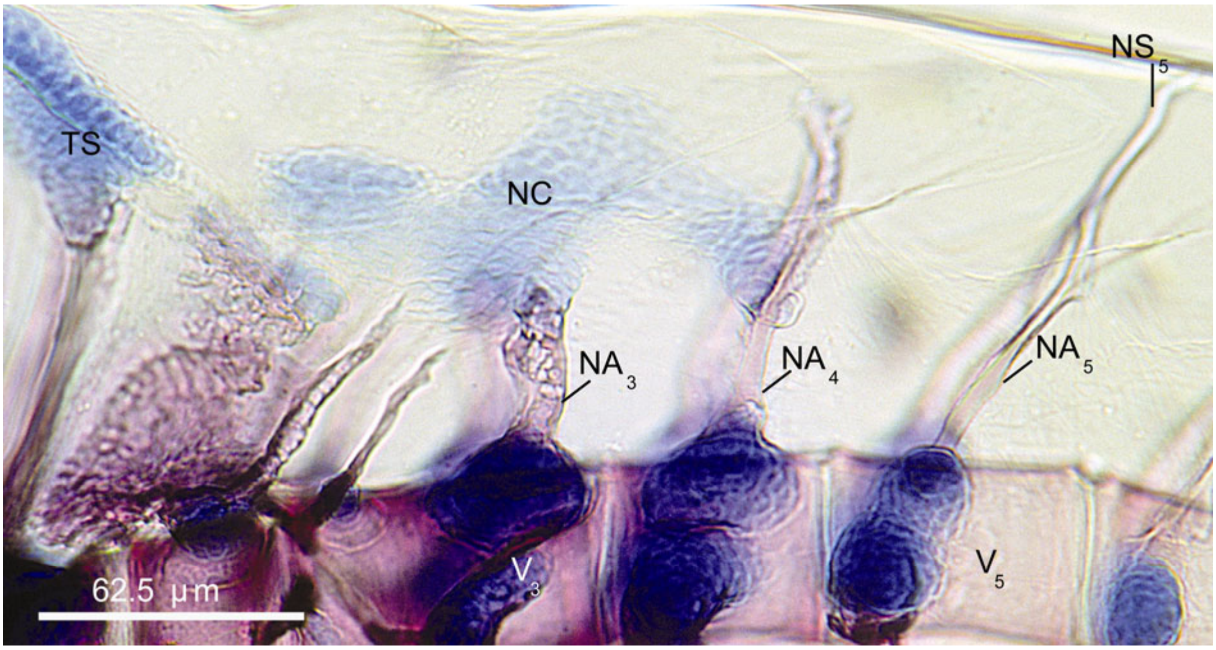

Fig. 33 Developmental stages of the neural complex in Cypriniformes. *Puntius* sp., 5.4 mm, lateral view.

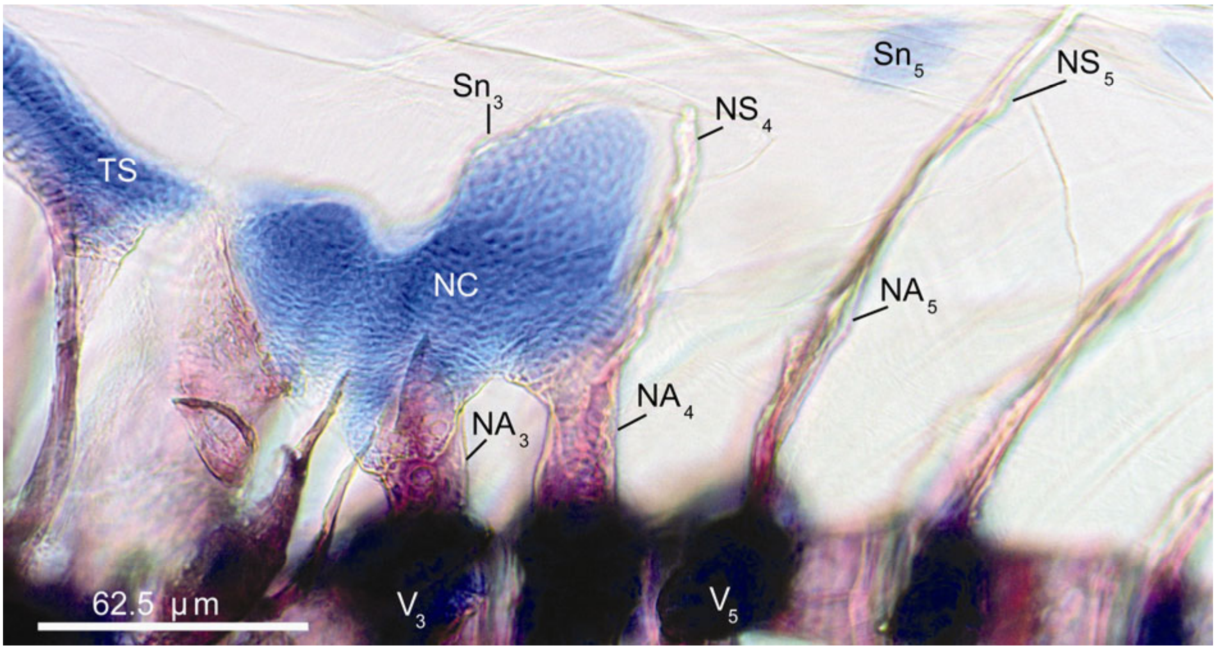

Fig. 34 Developmental stages of the neural complex in Cypriniformes. *Puntius* sp., 7.3 mm, lateral view.

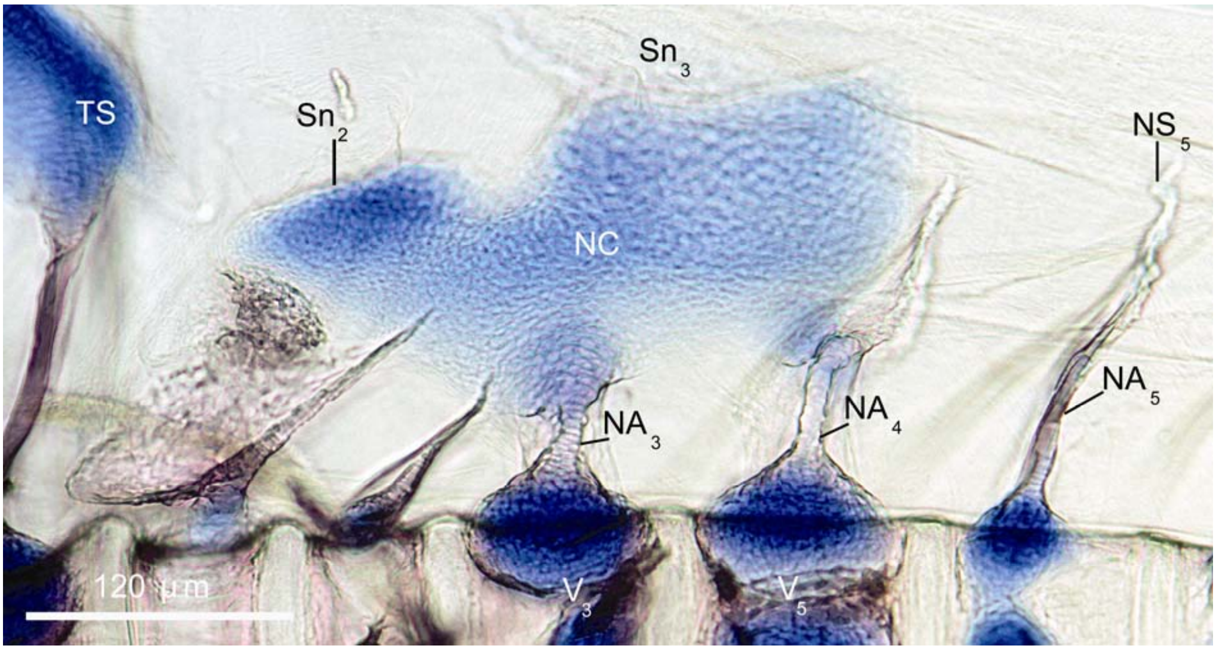

Fig. 35 Developmental stages of the neural complex in Cypriniformes. *Myxocyprinus asiaticus*, 16.3 mm, lateral view.

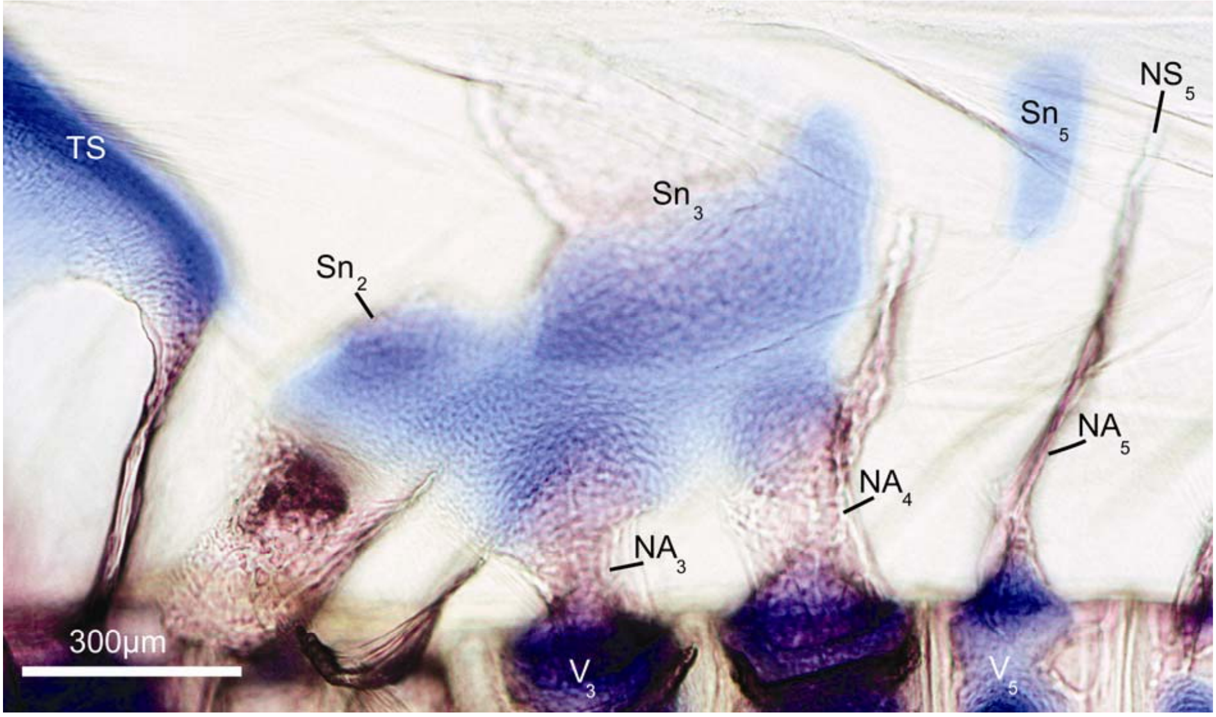

Fig. 36 Developmental stages of the neural complex in Cypriniformes. *Myxocyprinus asiaticus*, 16.8 mm, lateral view.

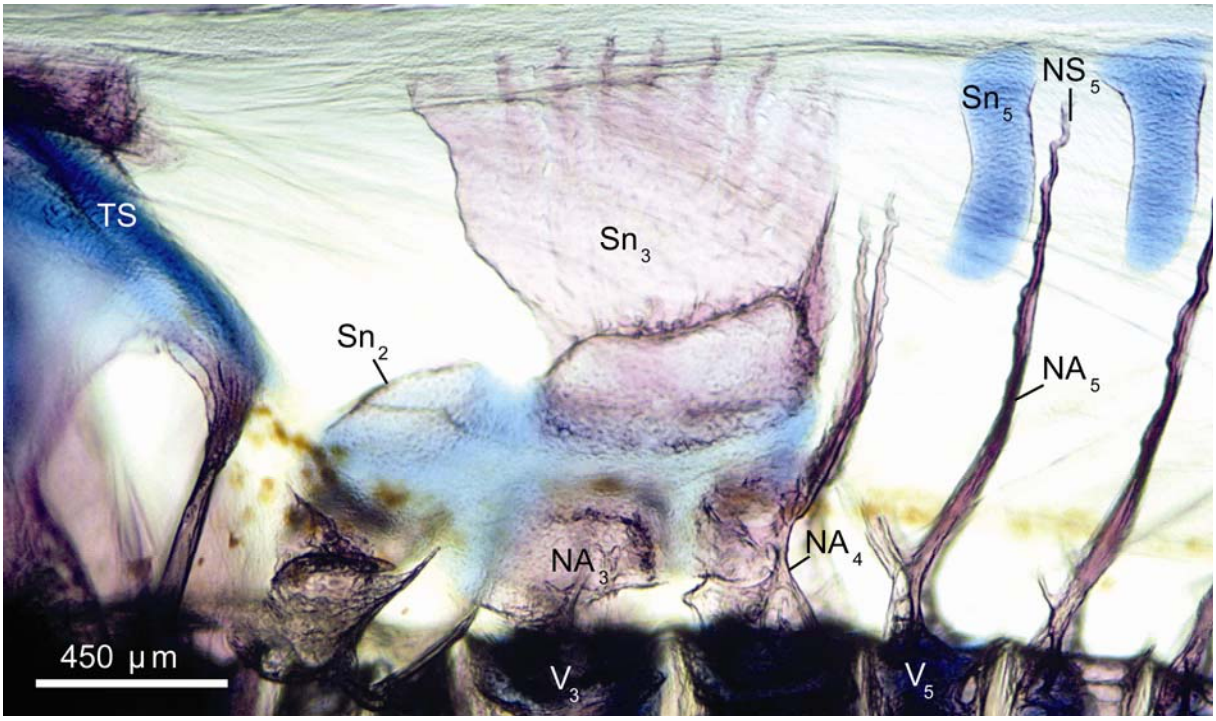

Fig. 37 Developmental stages of the neural complex in Cypriniformes.
Myxocyprinus asiaticus, 20.1 mm, lateral view.

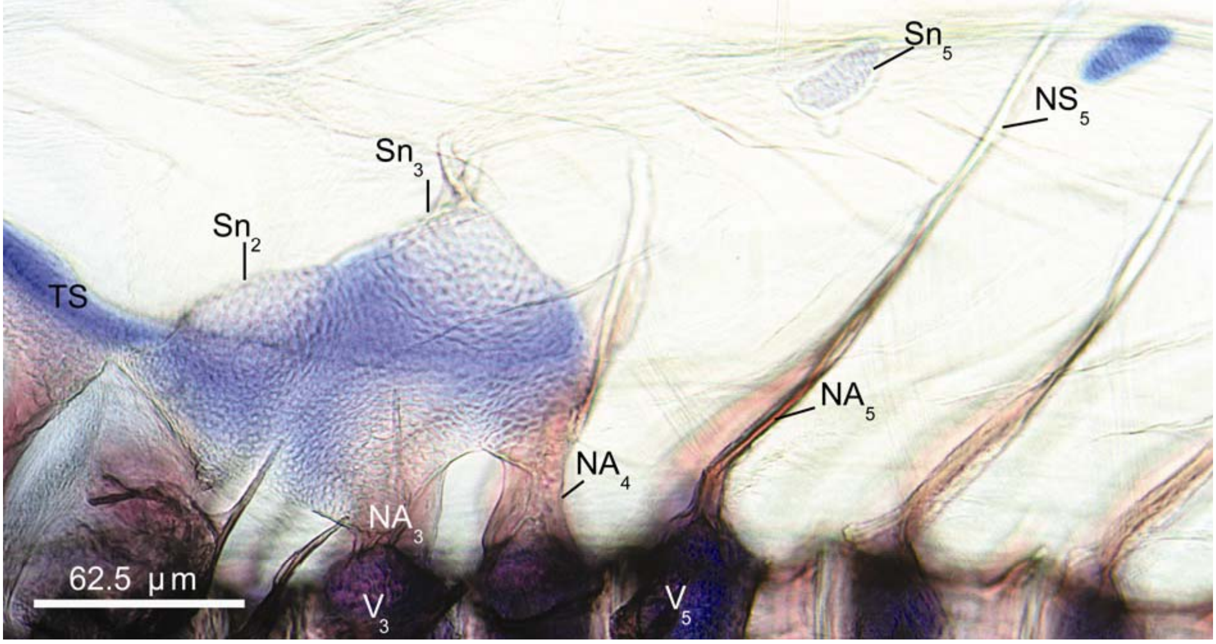

Fig. 38 Developmental stages of the neural complex in Cypriniformes.
Rasbora daniconius, 11.9 mm, lateral view.

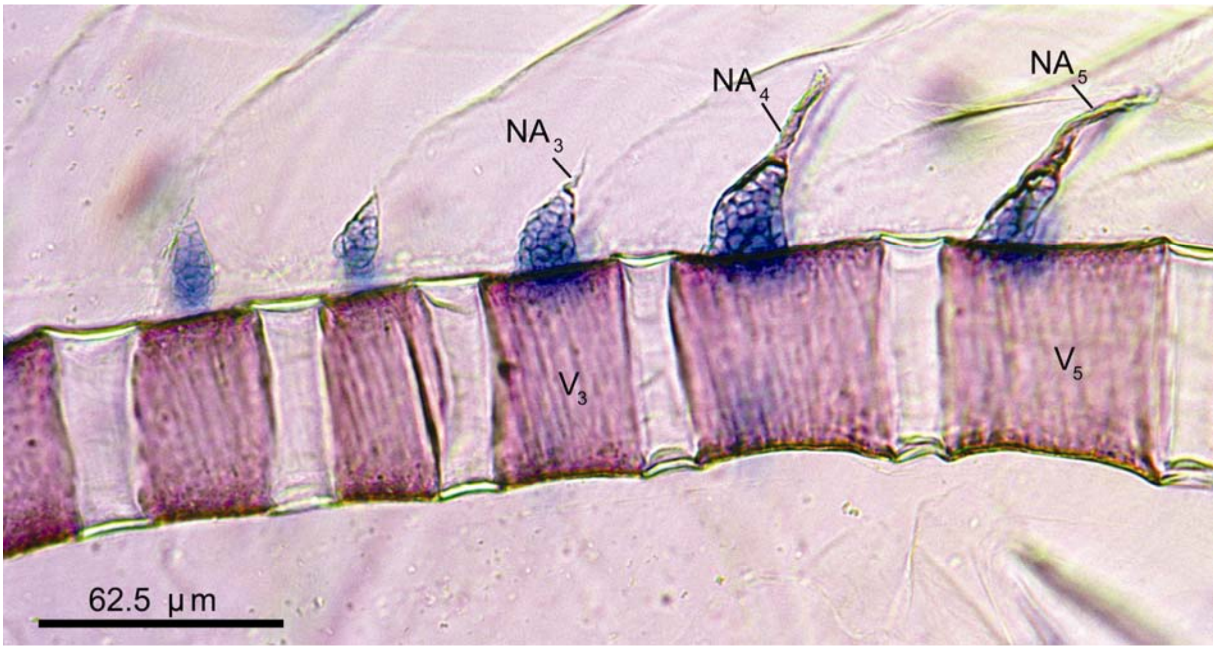

Fig. 39 Developmental stages of the neural complex in Characiformes. *Rhabdalestes septentrionalis*, 7.1 mm, lateral view.

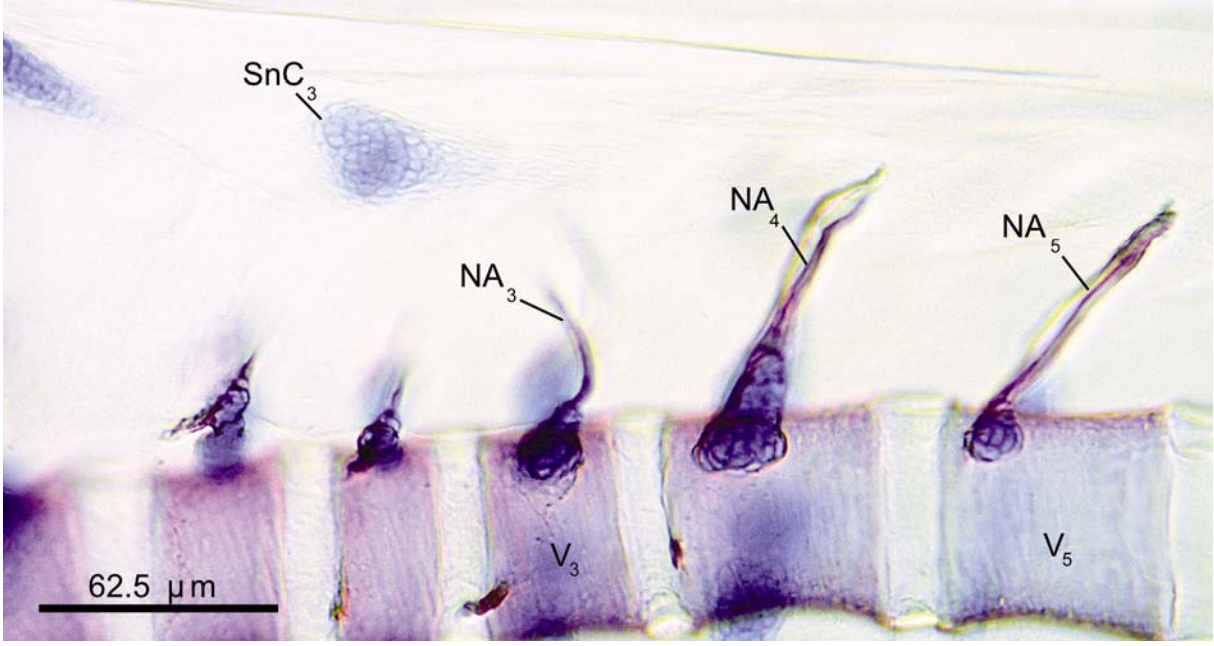

Fig. 40 Developmental stages of the neural complex in Characiformes. *Rhabdalestes septentrionalis*, 7.3 mm, lateral view.

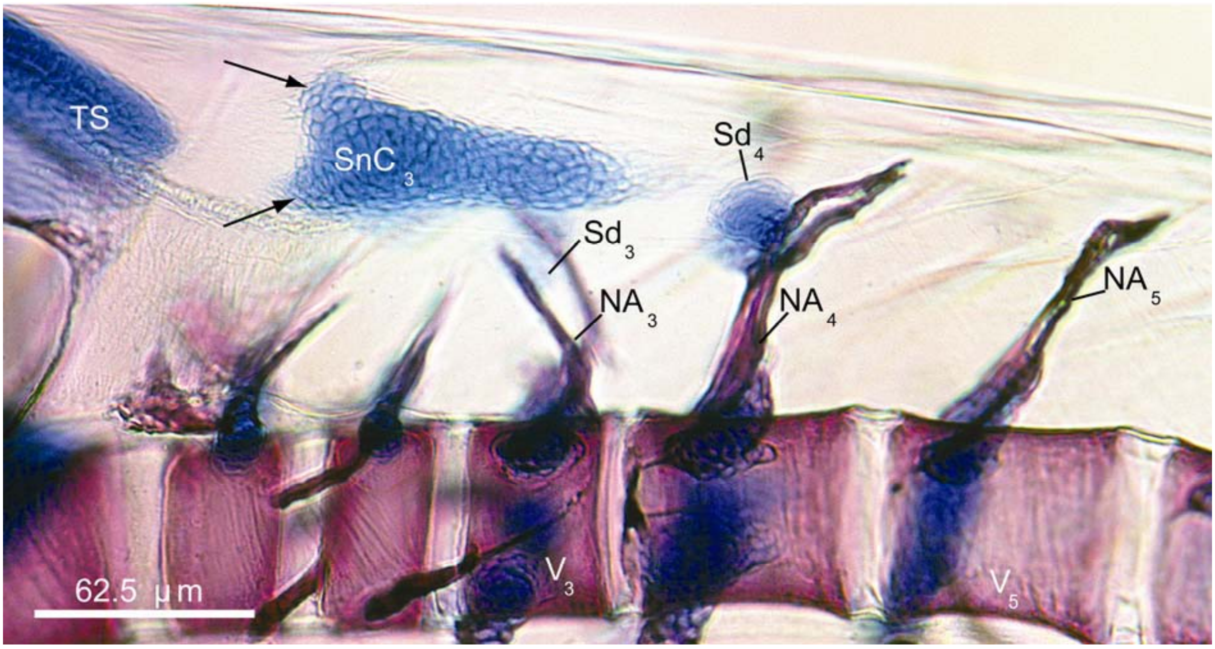

Fig. 41 Developmental stages of the neural complex in Characiformes. *Rhabdalestes septentrionalis,* 7.5 mm, lateral view. Arrows mark median anterodorsal and anterventral process of left side.

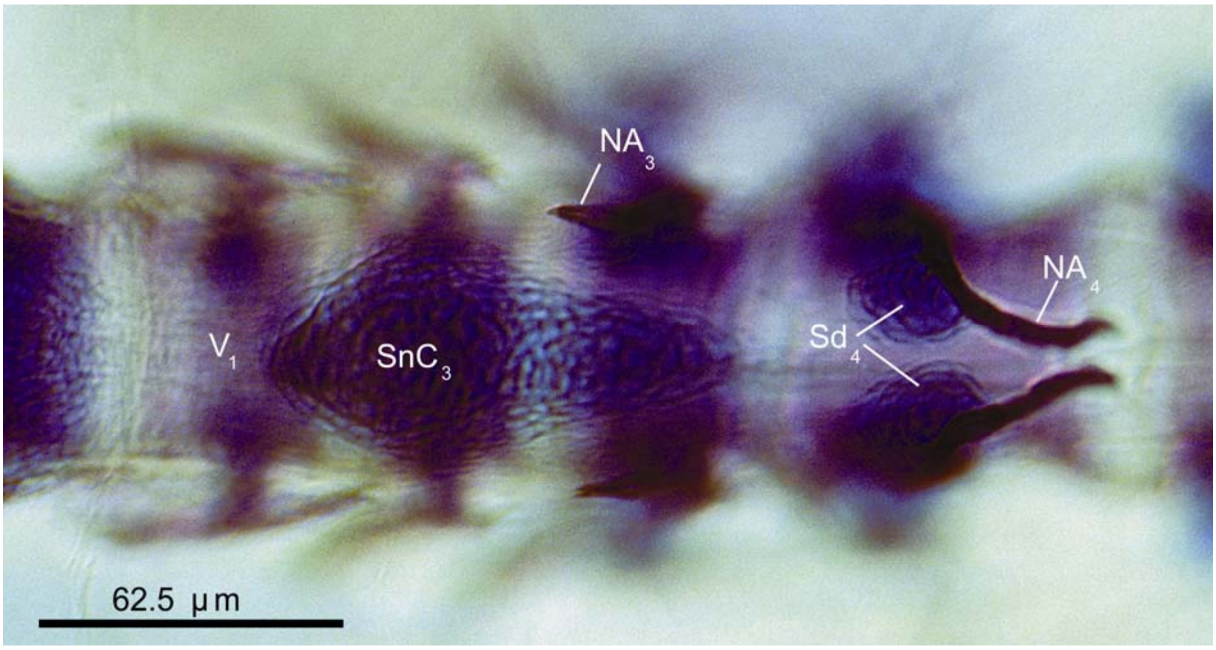

Fig. 42 Developmental stages of the neural complex in Characiformes. *Rhabdalestes septentrionalis*, 7.5 mm, same as Fig. 41; dorsal view.

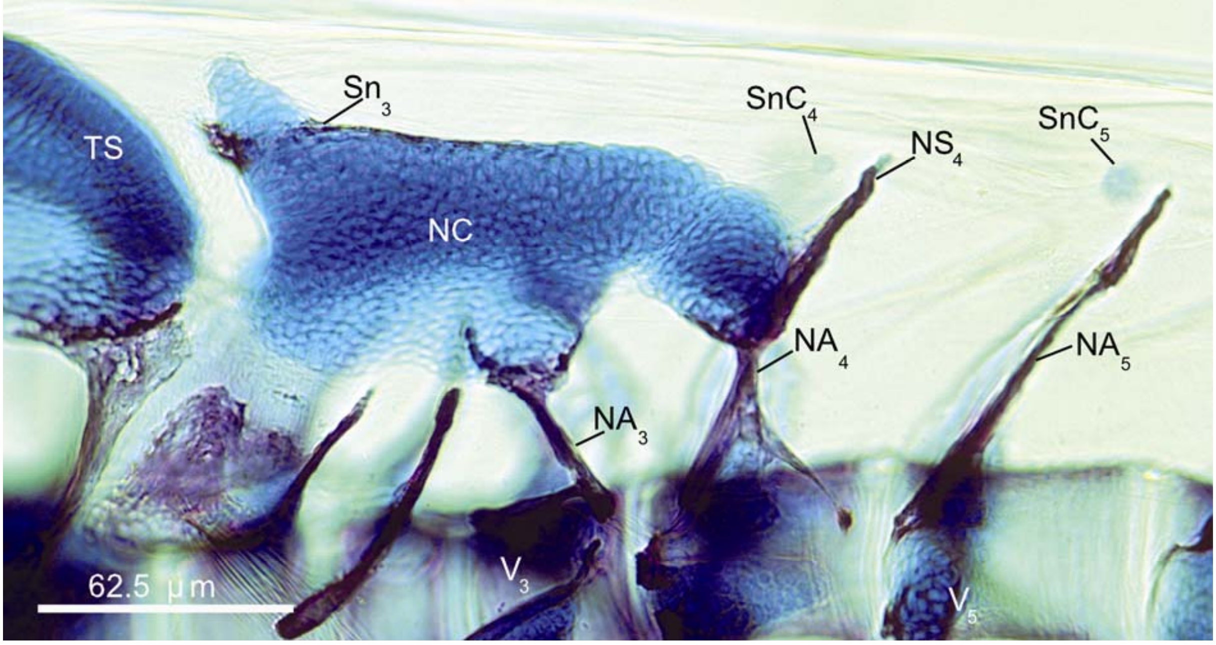

Fig. 43 Developmental stages of the neural complex in Characiformes. *Rhabdalestes septentrionalis*, 8.0 mm, lateral view.

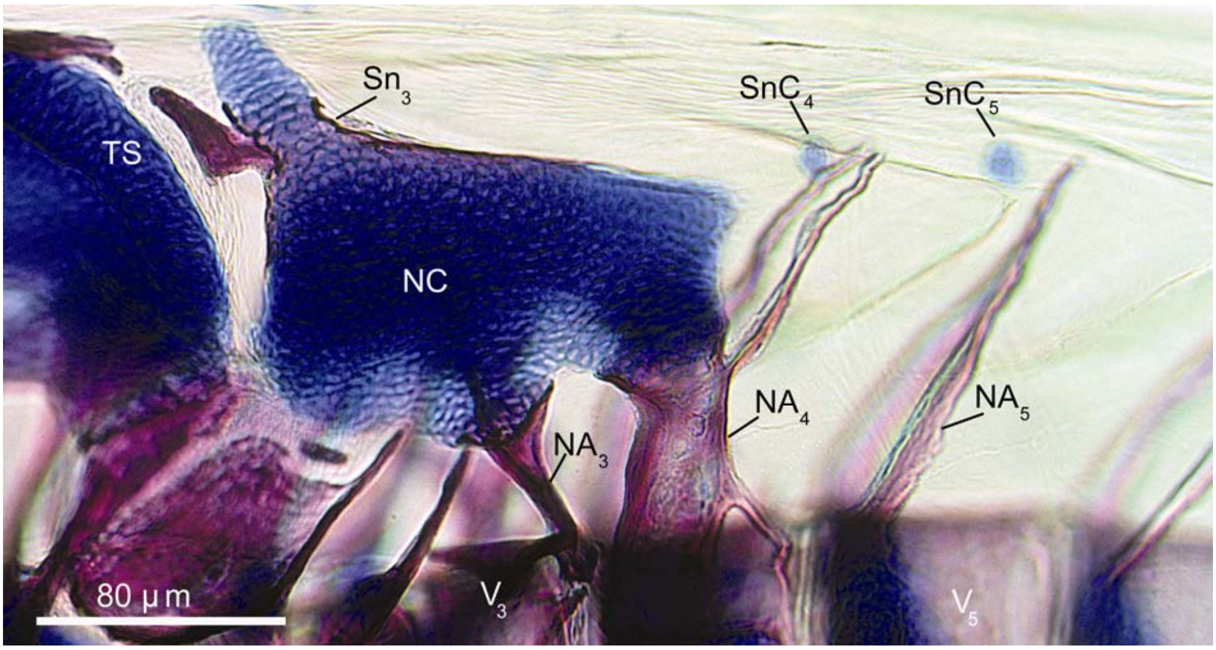

Fig. 44 Developmental stages of the neural complex in Characiformes. *Rhabdalestes septentrionalis,* 8.4 mm, lateral view.

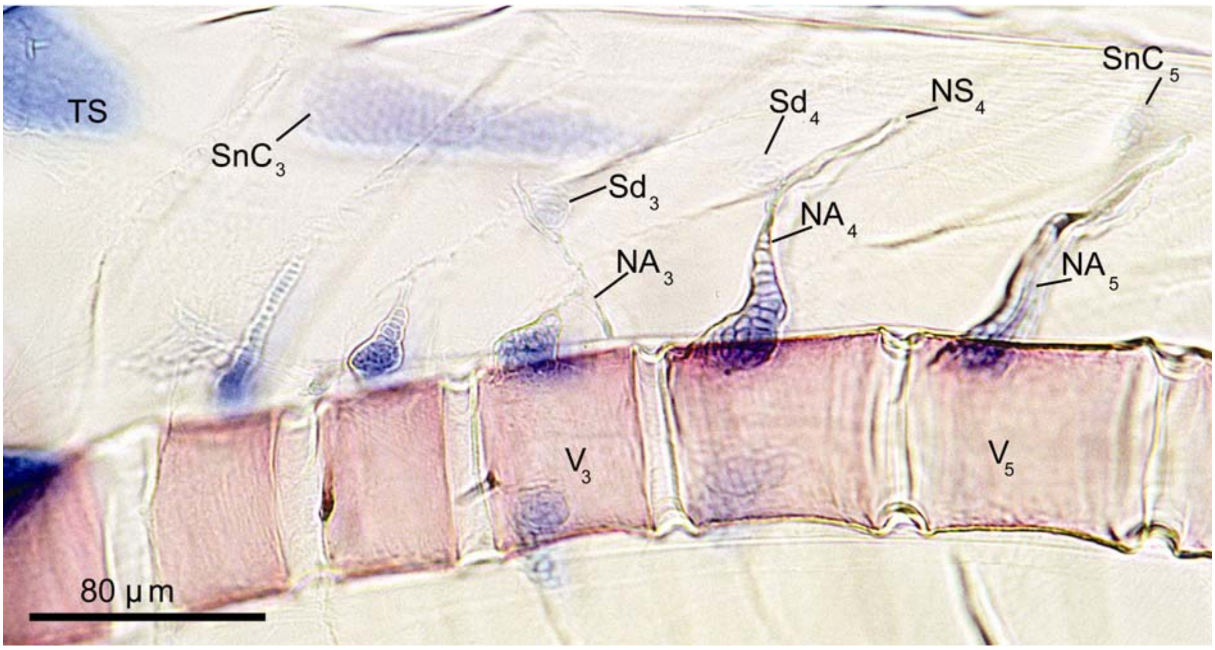

Fig. 45 Developmental stages of the neural complex in Characiformes. *Alestopetersius smykalai*, 8.3 mm, lateral view.

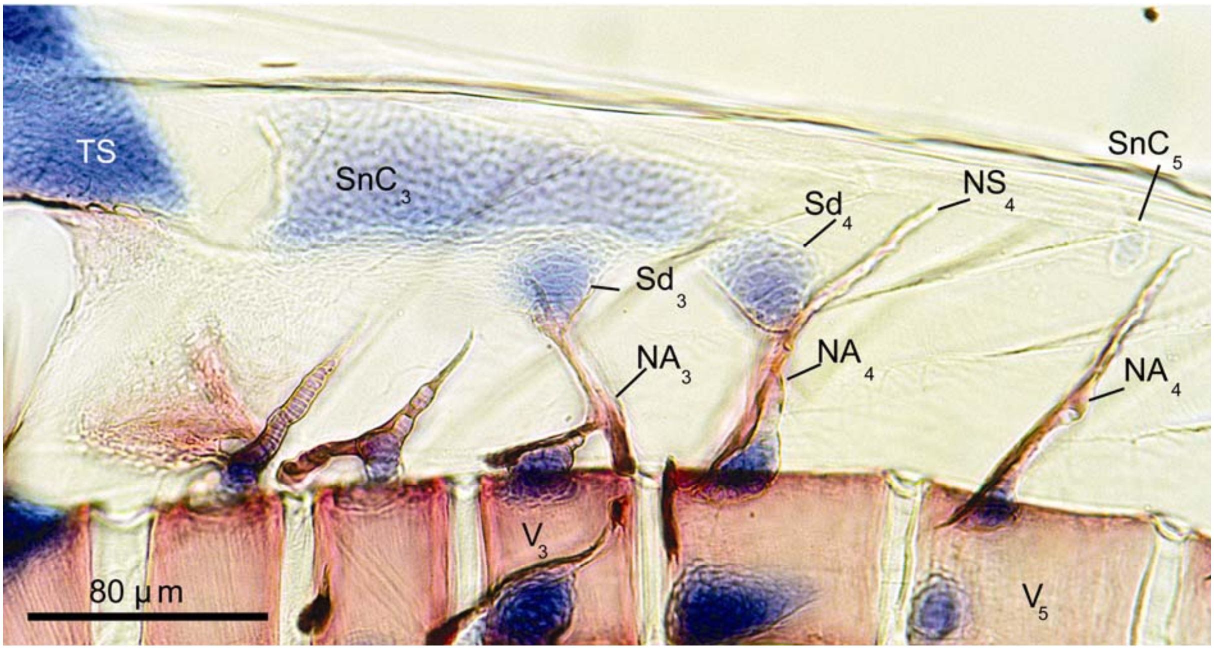

Fig. 46 Developmental stages of the neural complex in Characiformes. *Alestopetersius smykalai*, 8.7 mm, lateral view.

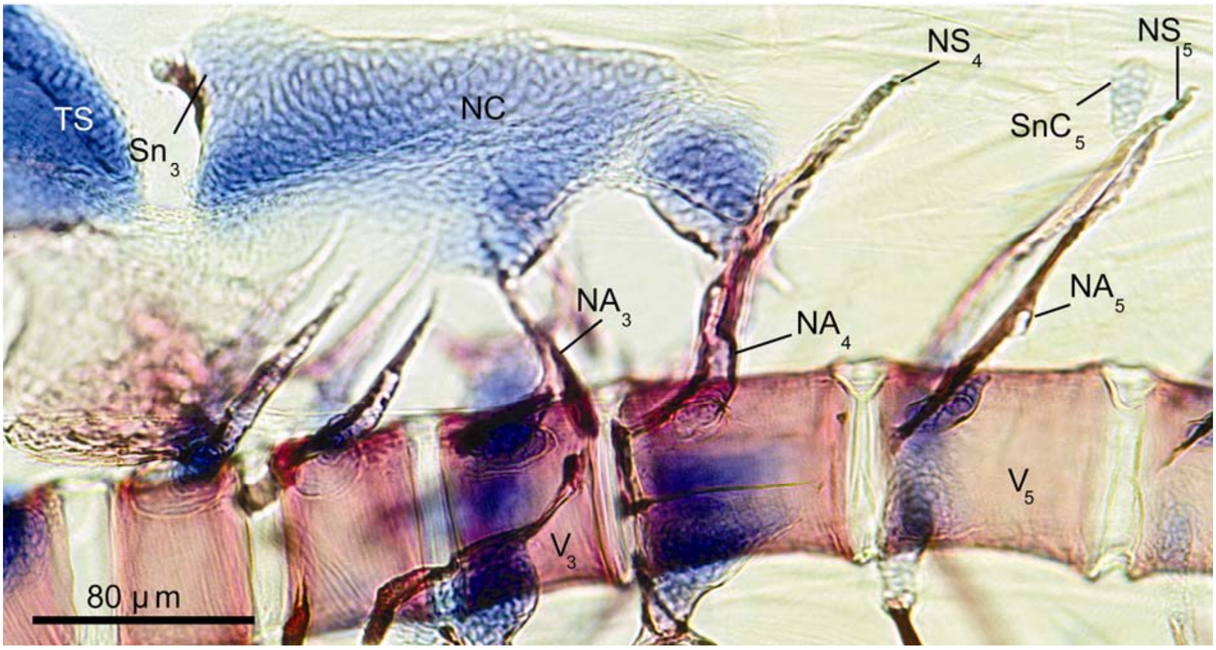

Fig. 47 Developmental stages of the neural complex in Characiformes. *Alestopetersius smykalai*, 8.6 mm, lateral view.

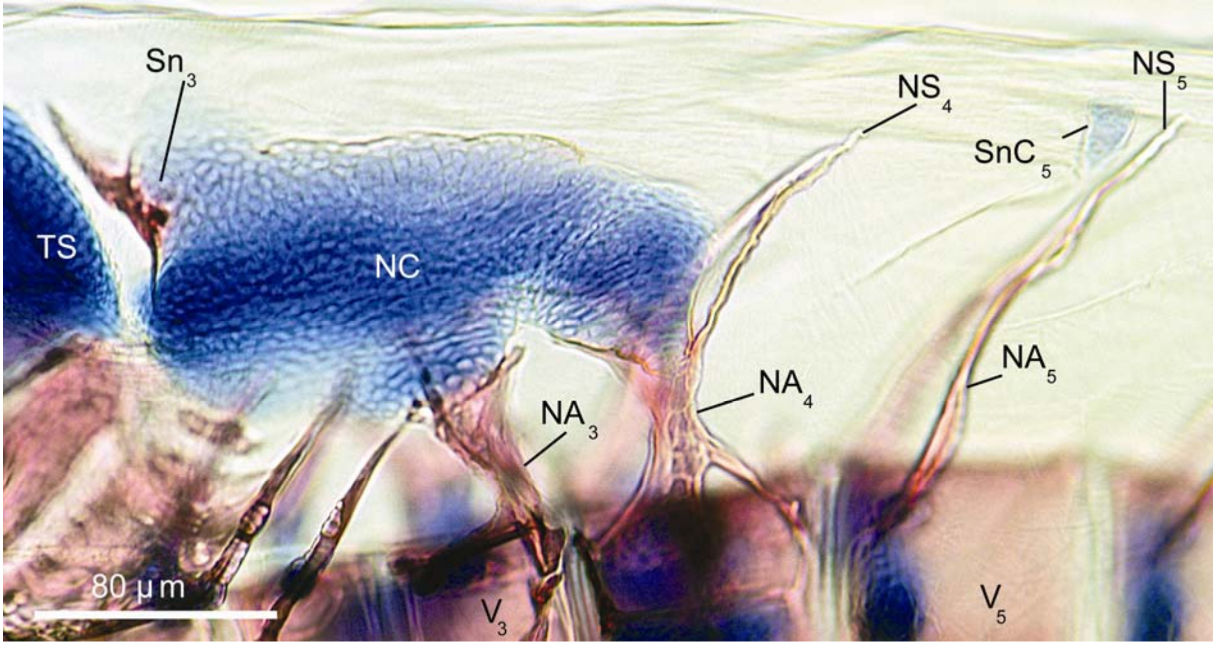

Fig. 48 Developmental stages of the neural complex in Characiformes. *Alestopetersius smykalai*, 9.1 mm, lateral view.

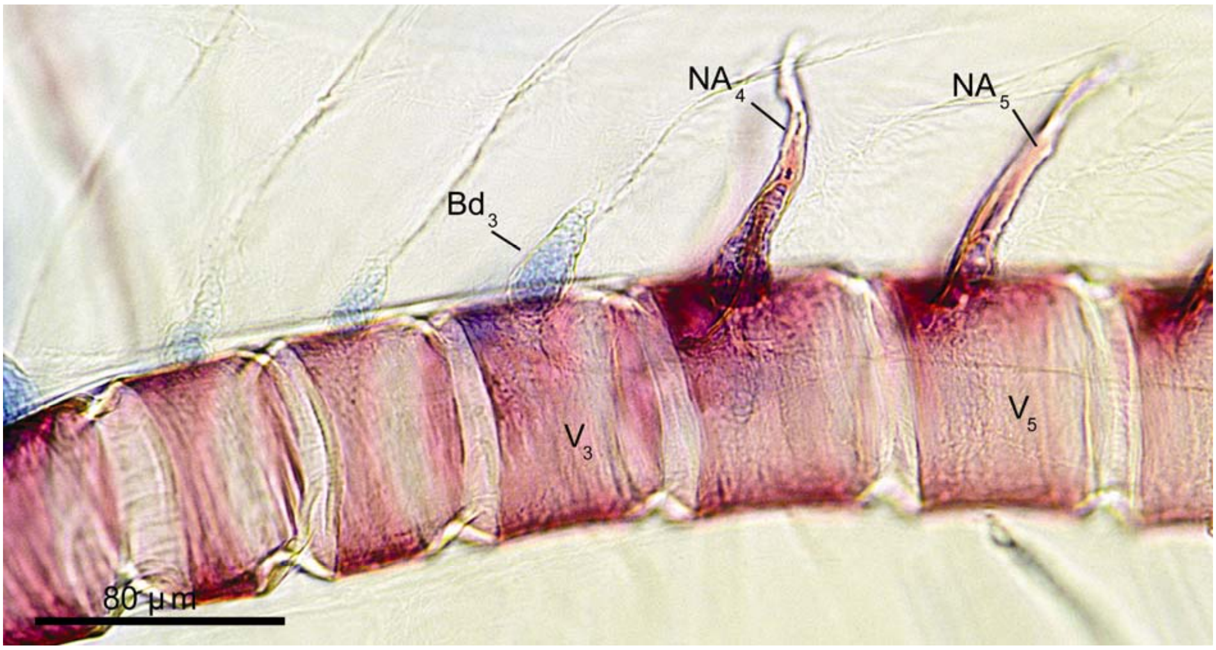

Fig. 49 Developmental stages of the neural complex in Characiformes.
Lebiasina bimaculata, 7.7 mm, lateral view.

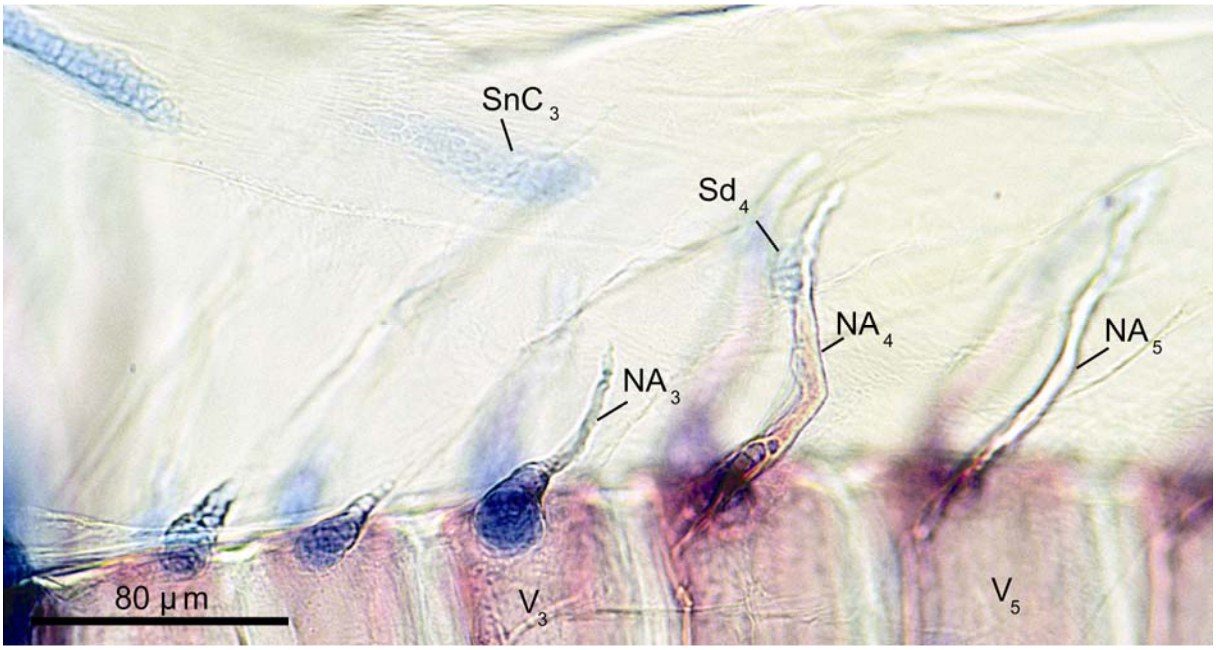

Fig. 50 Developmental stages of the neural complex in Characiformes.
Lebiasina bimaculata, 8.0 mm, lateral view.

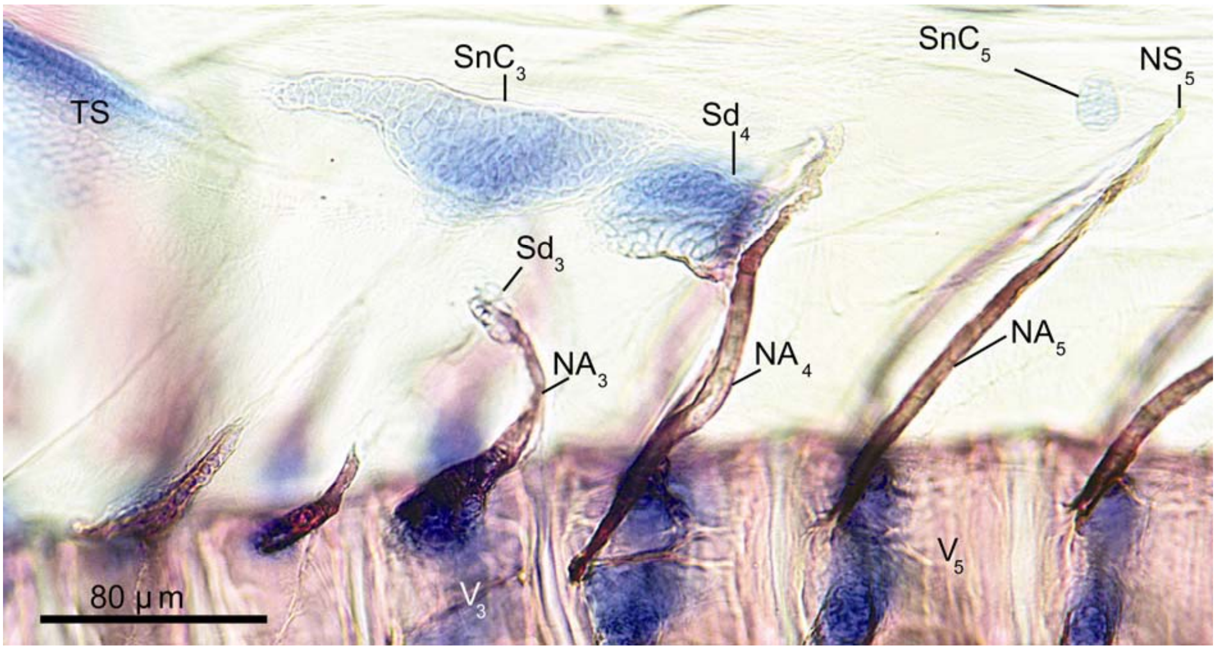

Fig. 51 Developmental stages of the neural complex in Characiformes. *Lebiasina bimaculata*, 9.0 mm, slightly dorsolateral view.

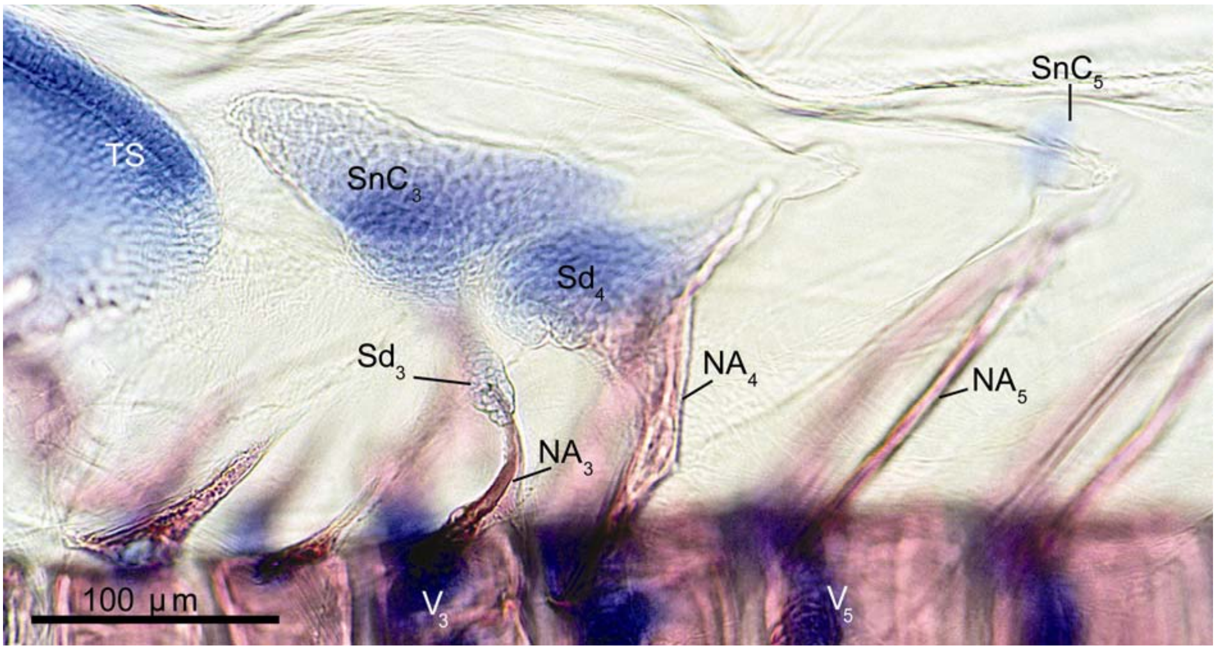

Fig. 52 Developmental stages of the neural complex in Characiformes. *Lebiasina bimaculata,* 9.9 mm, lateral view.

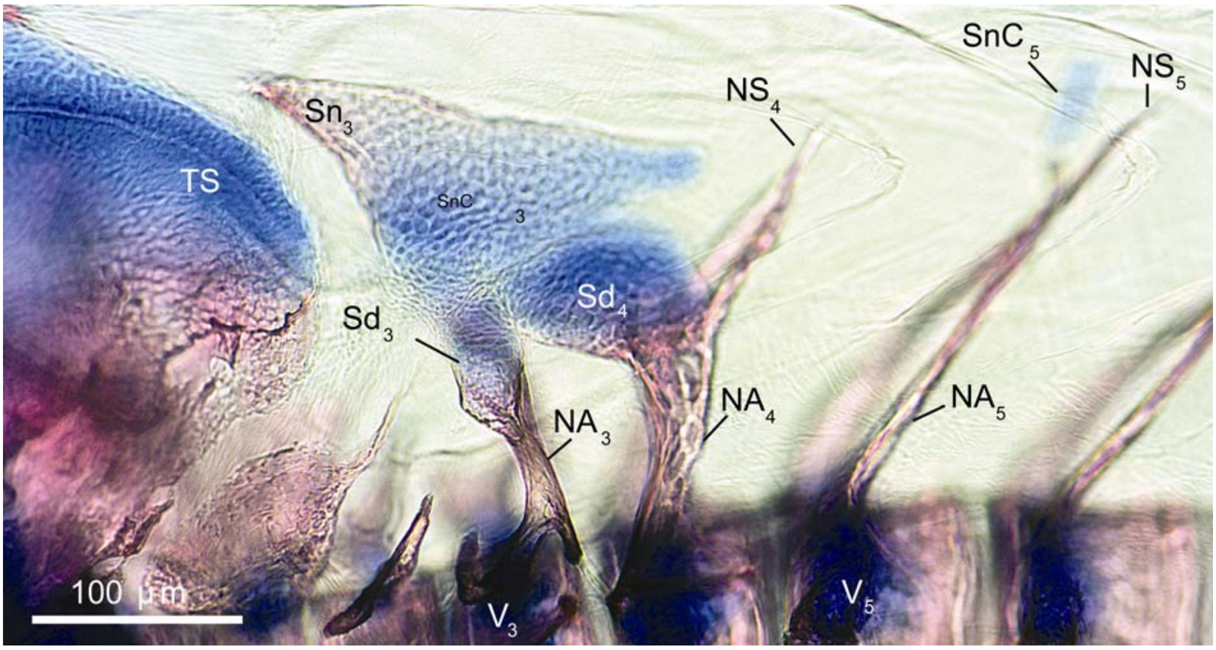

Fig. 53 Developmental stages of the neural complex in Characiformes. *Lebiasina bimaculata*, 11.2 mm, lateral view.

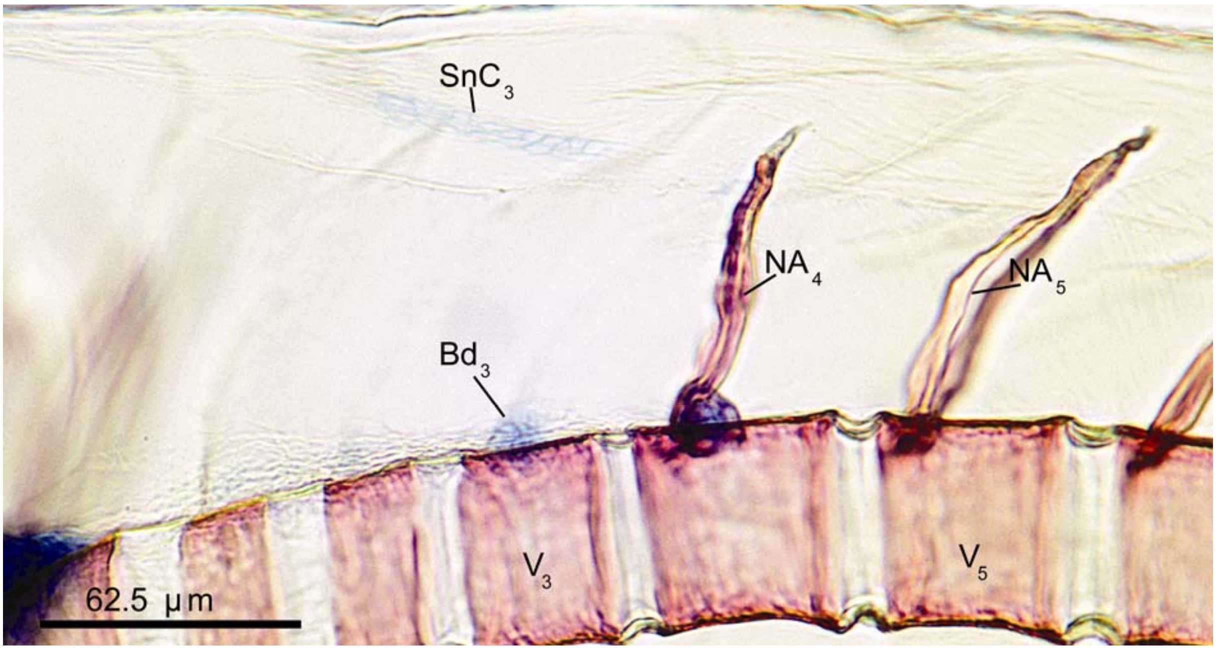

Fig. 54 Developmental stages of the neural complex in Characiformes. *Pyrrhulina spilota*, 6.0 mm, lateral view.

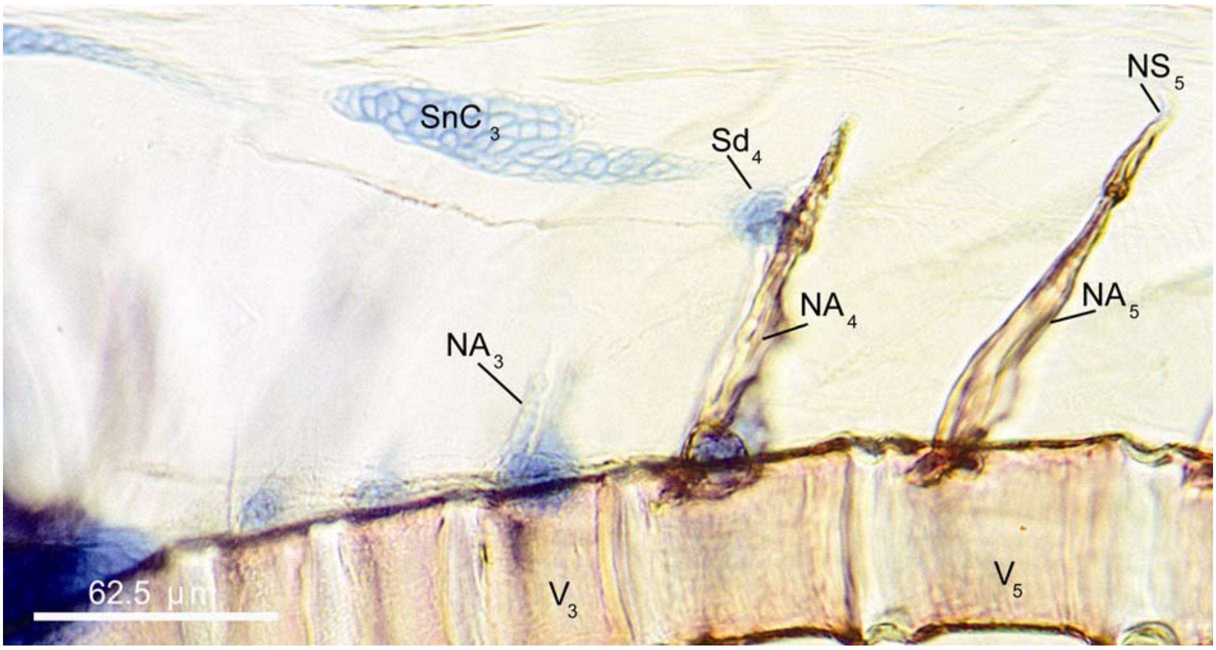

Fig. 55 Developmental stages of the neural complex in Characiformes. *Pyrrhulina spilota*, 6.2 mm, lateral view.

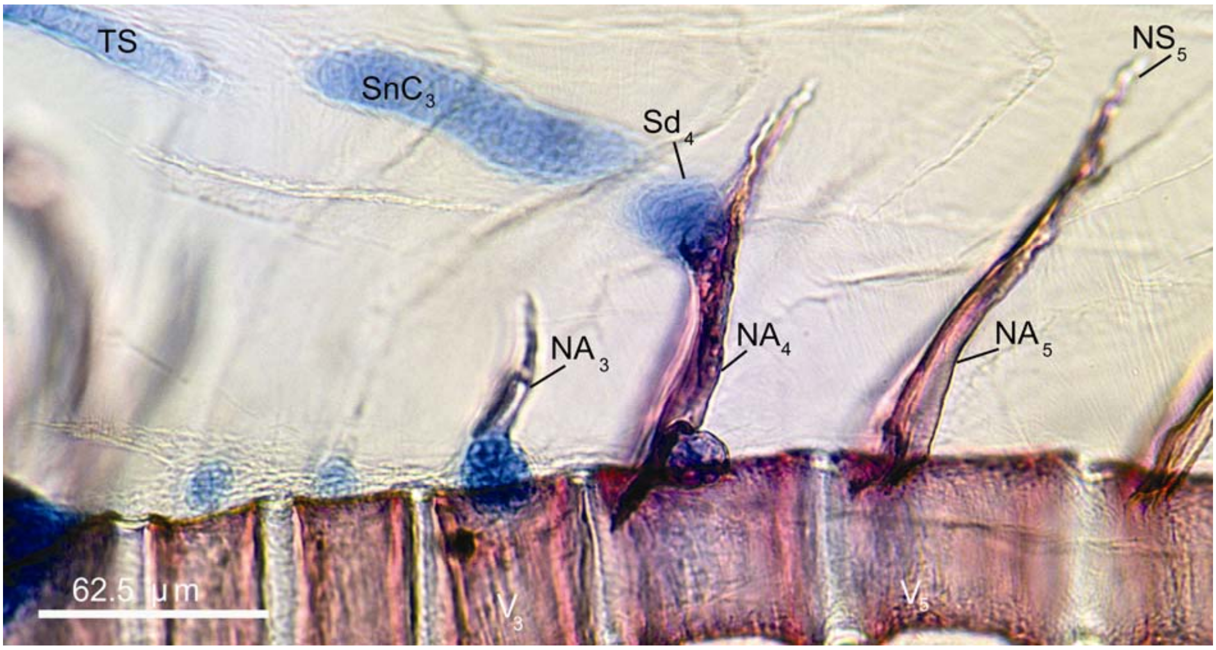

Fig. 56 Developmental stages of the neural complex in Characiformes. *Pyrrhulina spilota*, 6.4 mm, lateral view.

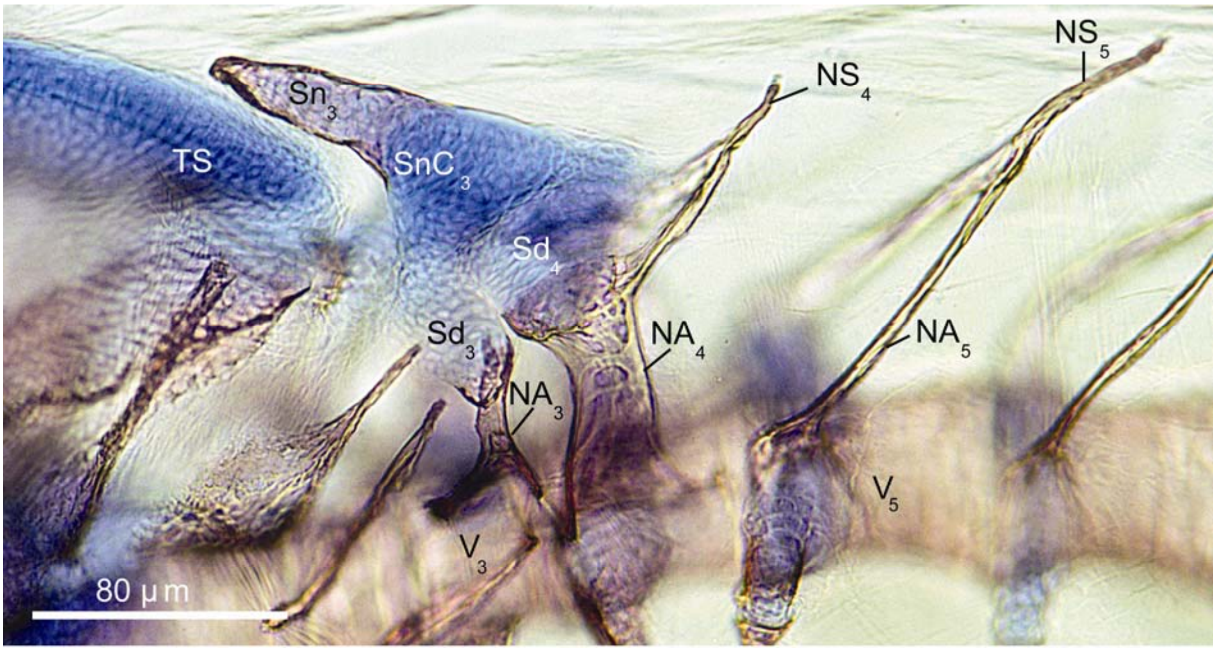

Fig. 57 Developmental stages of the neural complex in Characiformes.
Pyrrhulina spilota, 7.4 mm, slightly dorsolateral view.

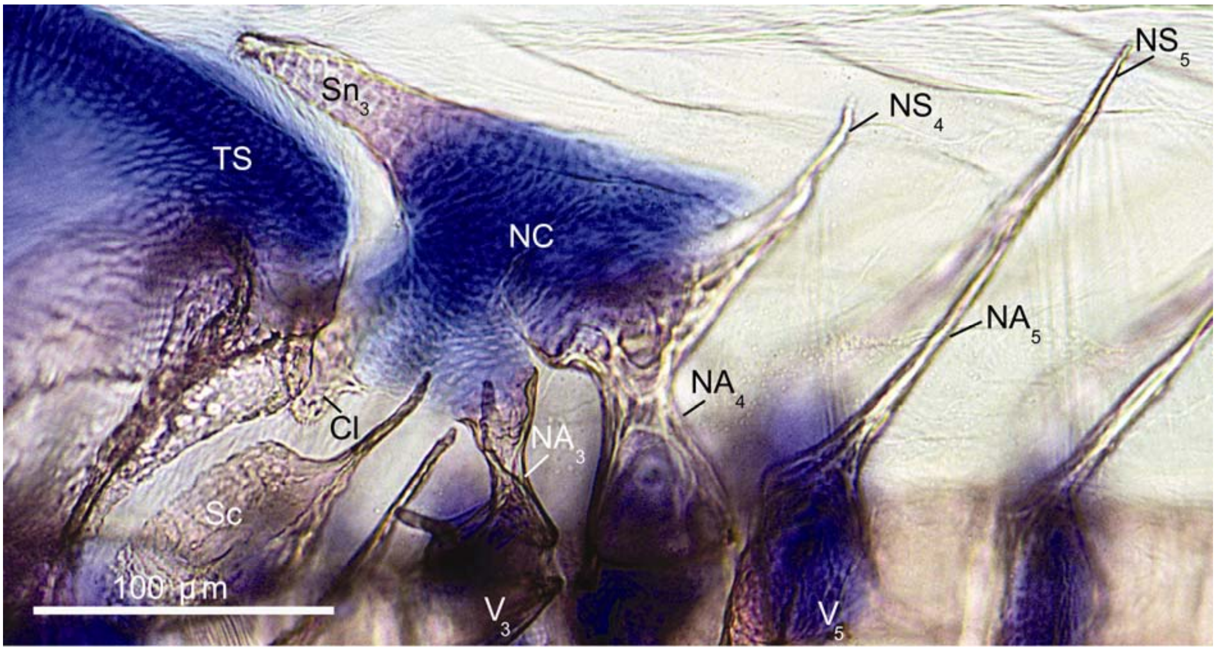

Fig. 58 Developmental stages of the neural complex in Characiformes.
Pyrrhulina spilota, 8.2 mm, lateral view.

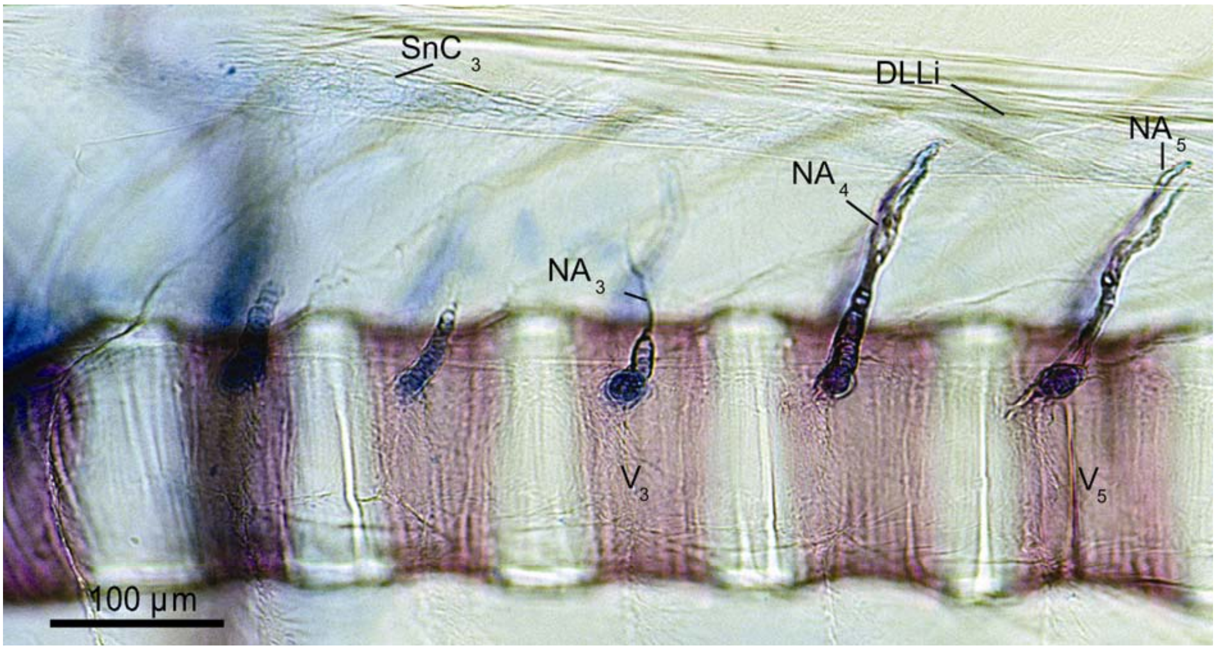

Fig. 59 Developmental stages of the neural complex in Characiformes. *Ctenolucius hujeta*, 10.2 mm, lateral view.

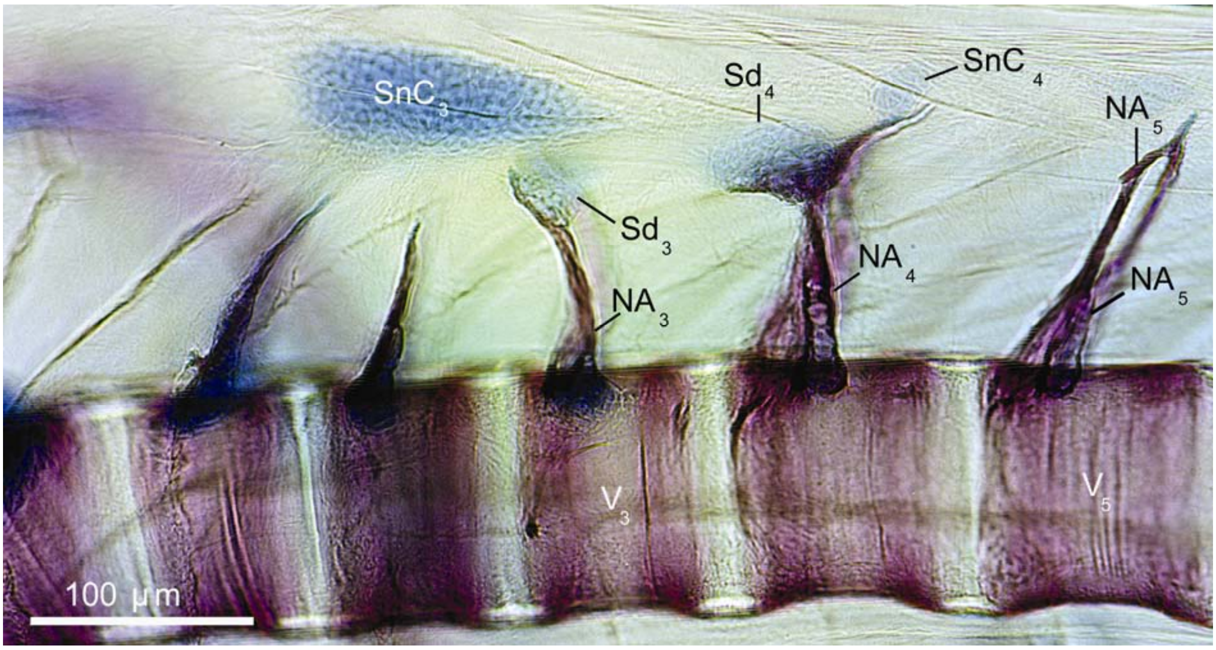

Fig. 60 Developmental stages of the neural complex in Characiformes. *Ctenolucius hujeta*, 13.5 mm, lateral view.

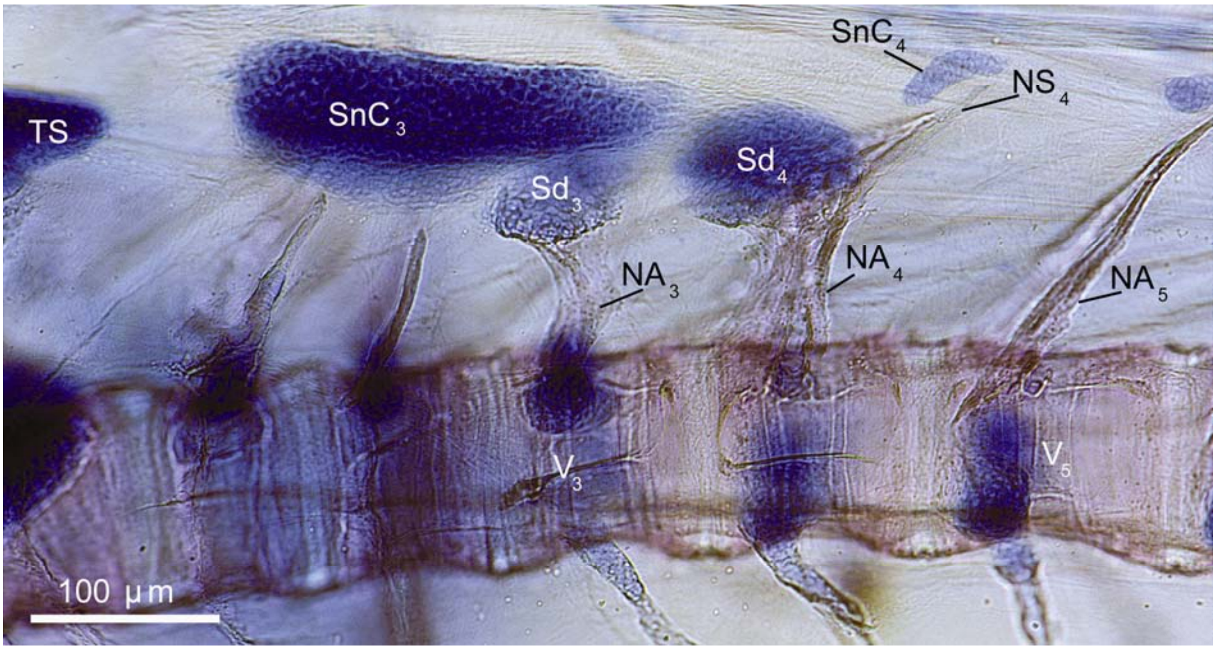

Fig. 61 Developmental stages of the neural complex in Characiformes. *Ctenolucius hujeta*, 16.2 mm, lateral view.

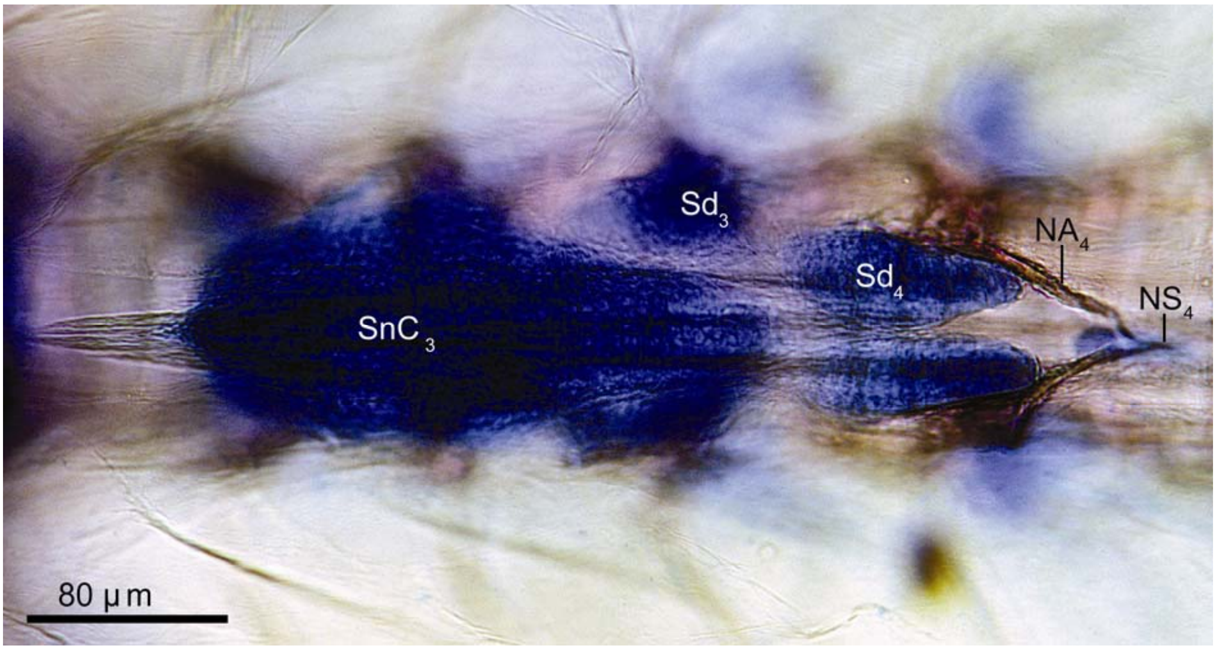

Fig. 62 Developmental stages of the neural complex in Characiformes. *Ctenolucius hujeta*, 16.2 mm, same as Fig. 61 but in close up and dorsal view.

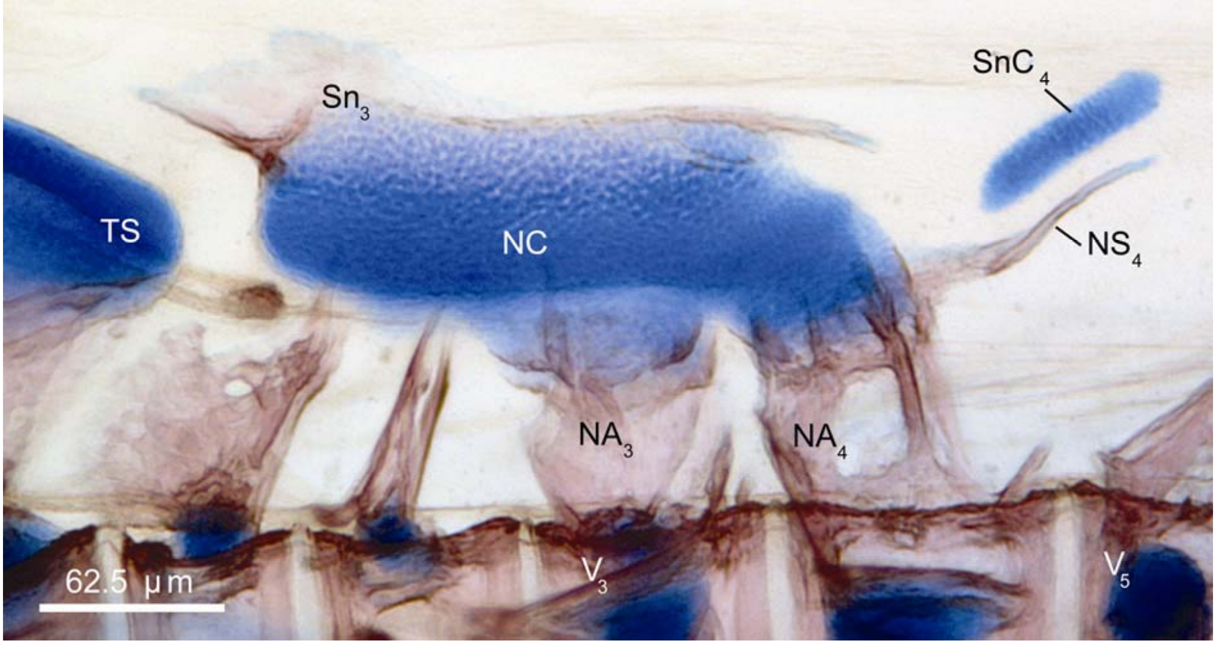

Fig. 63 Developmental stages of the neural complex in Characiformes. *Ctenolucius hujeta*, 23.3 mm, lateral view.

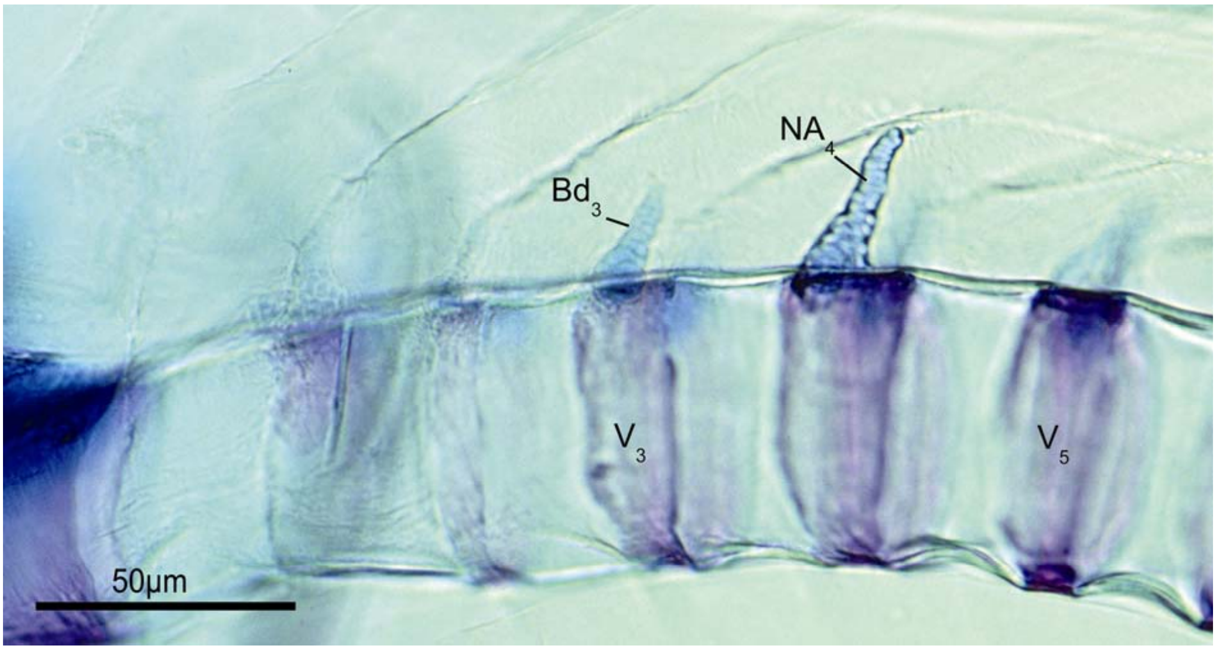

Fig. 64 Developmental stages of the neural complex in Characiformes. *Hoplias malabaricus*, 7.4 mm, lateral view.

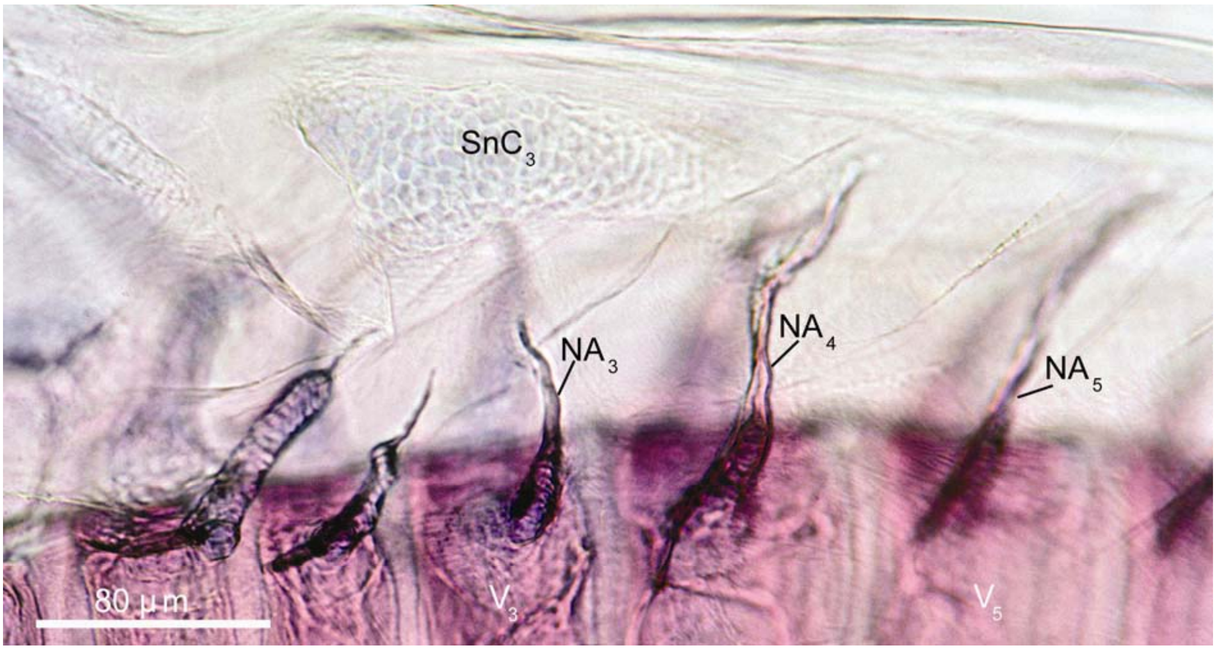

Fig. 65 Developmental stages of the neural complex in Characiformes. *Hoplias malabaricus*, 7.7 mm, lateral view.

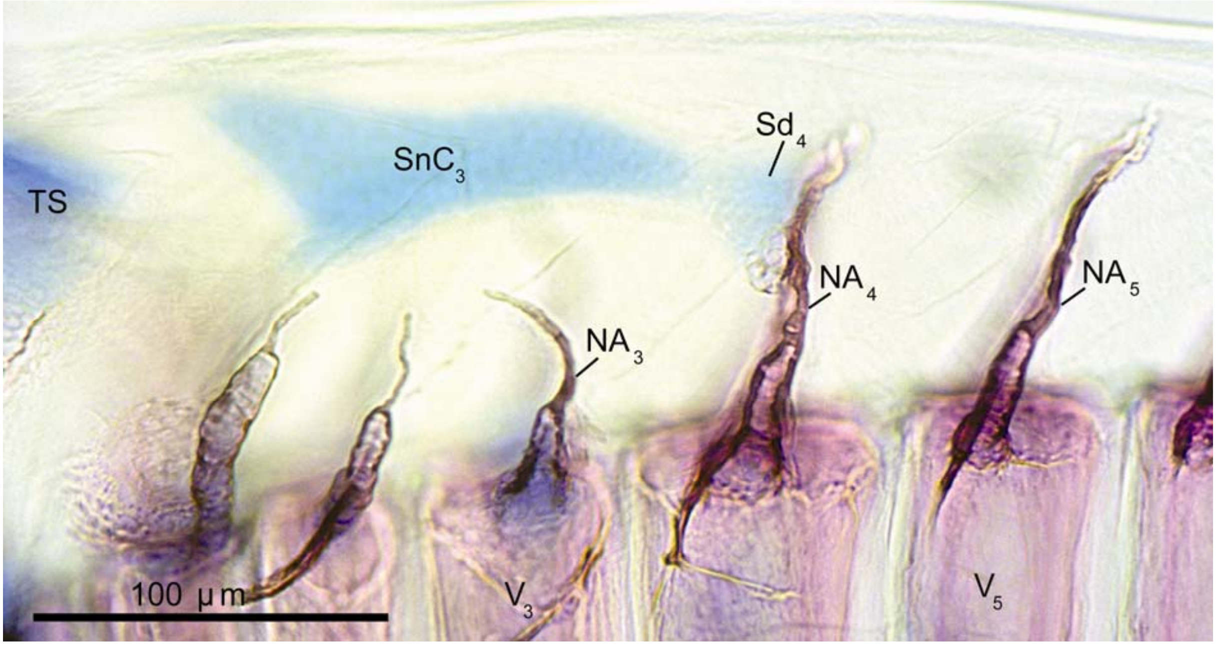

Fig. 66 Developmental stages of the neural complex in Characiformes. *Hoplias malabaricus*, 8.1 mm, lateral view.

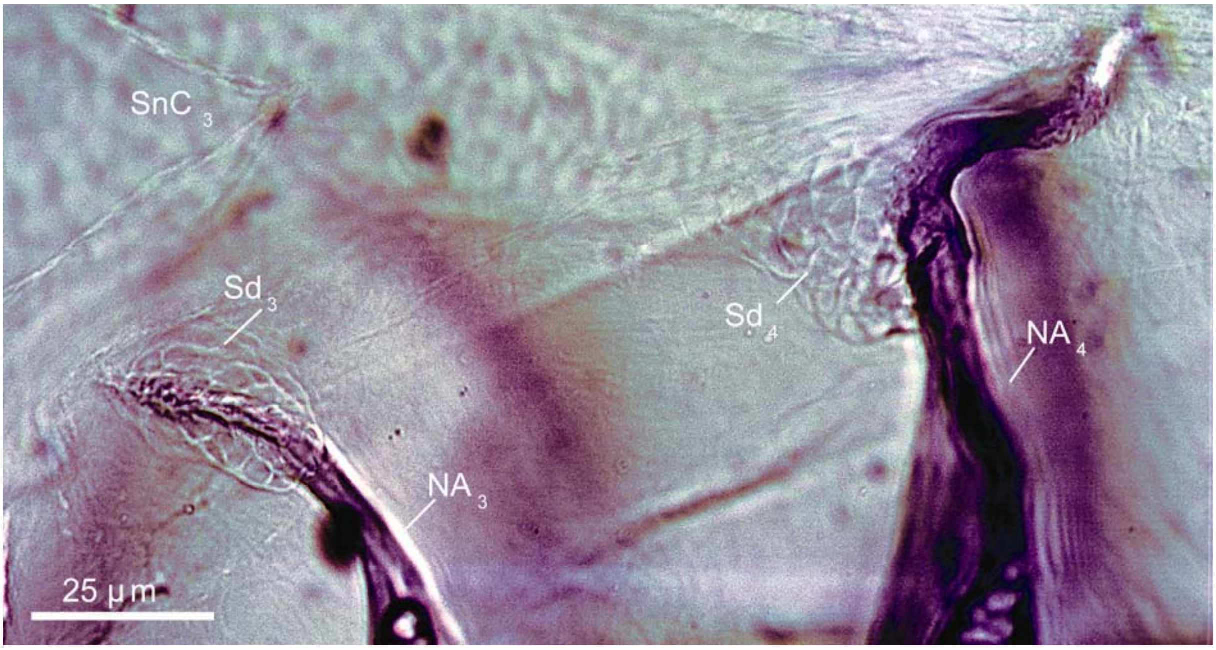

Fig. 67 Developmental stages of the neural complex in Characiformes. *Hoplias malabaricus*, 8.5 mm, close up and slightly dorsolateral view.

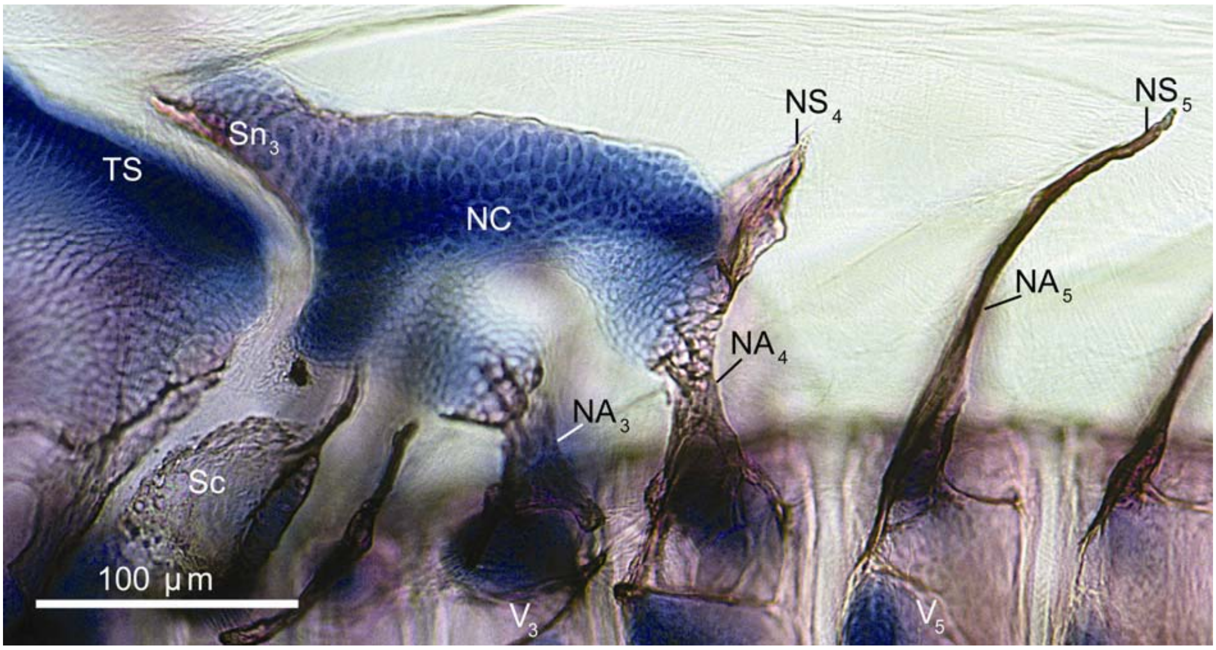

Fig. 68 Developmental stages of the neural complex in Characiformes. *Hoplias malabaricus*, 9.7 mm, dorsolateral view.

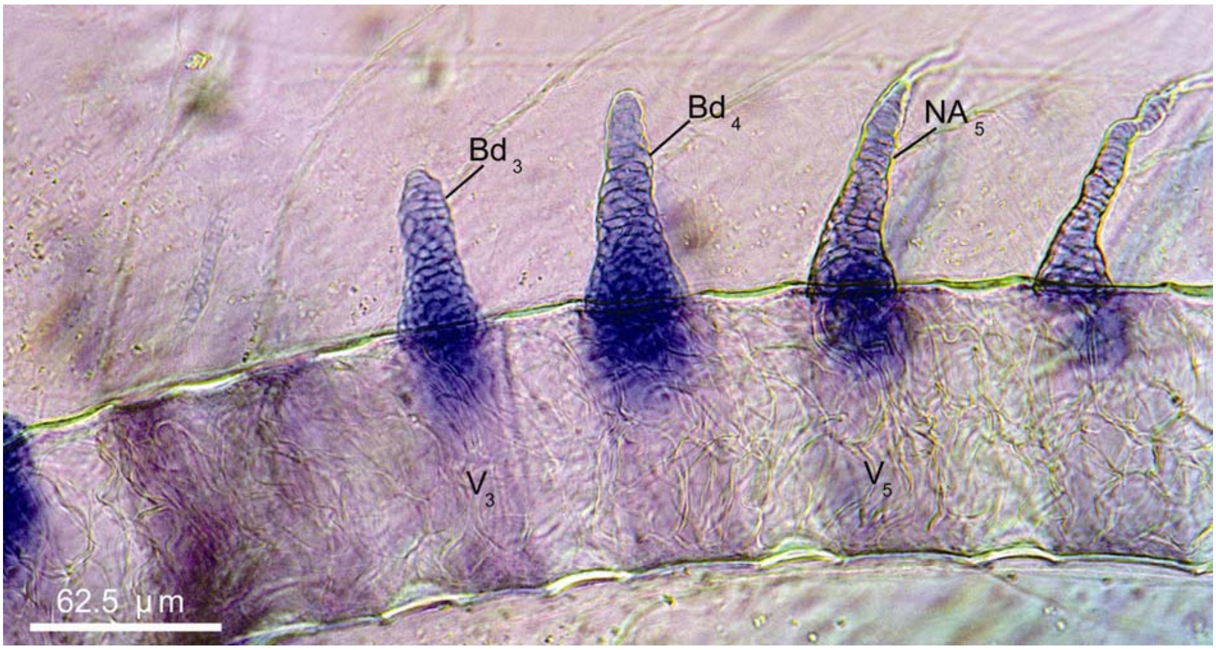

Fig. 69 Developmental stages of the neural complex in Gymnotiformes.
Apteronotus leptorhynchus, 9.0 mm, lateral view.

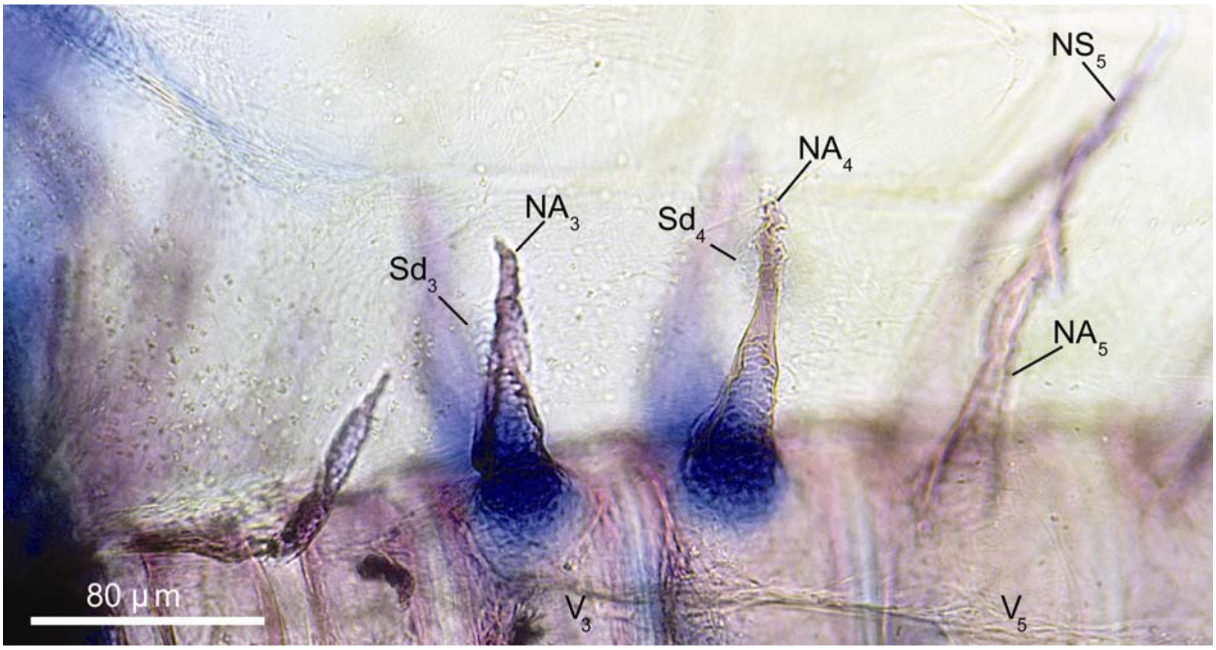

Fig. 70 Developmental stages of the neural complex in Gymnotiformes.
Apteronotus leptorhynchus, 10.6 mm, lateral view.

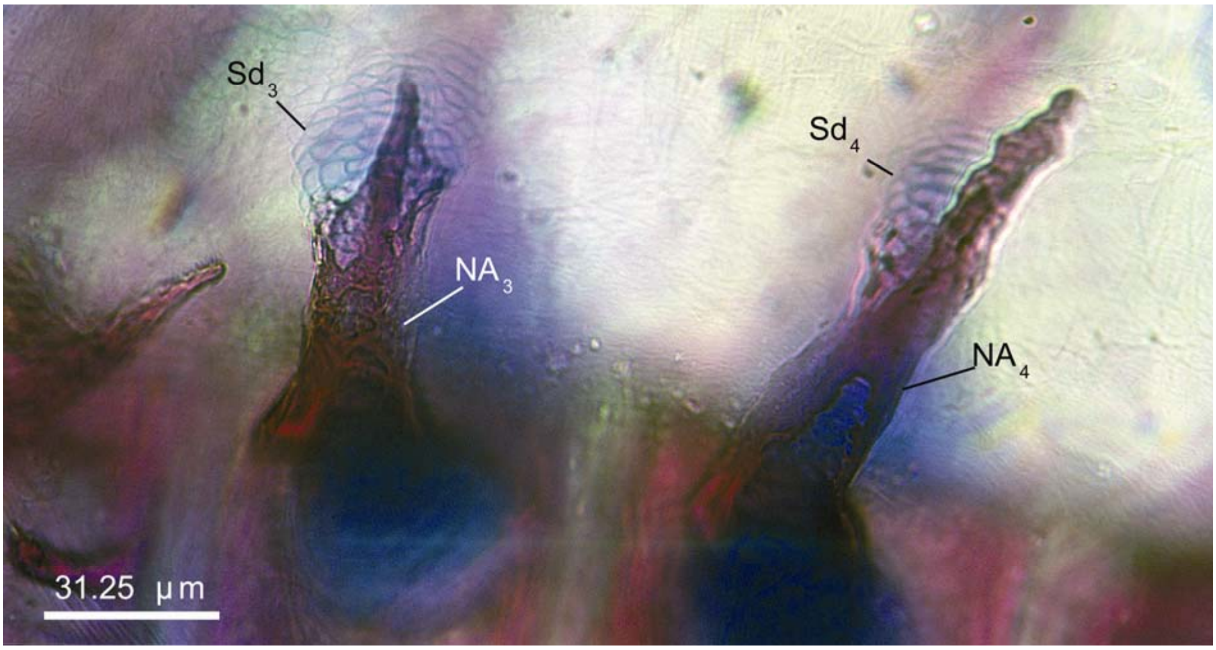

Fig. 71 Developmental stages of the neural complex in Gymnotiformes. *Apteronotus leptorhynchus*, 10.8 mm, close up and dorsolateral view.

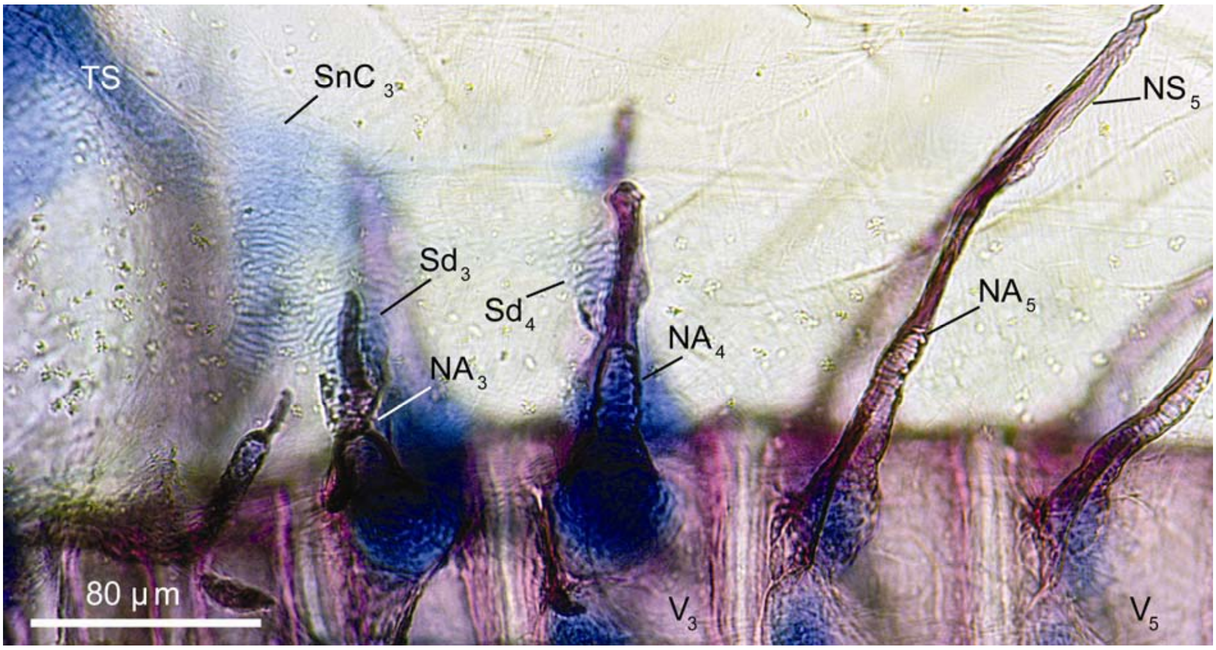

Fig. 72 Developmental stages of the neural complex in Gymnotiformes. *Apteronotus leptorhynchus*, 11.2 mm, lateral view.

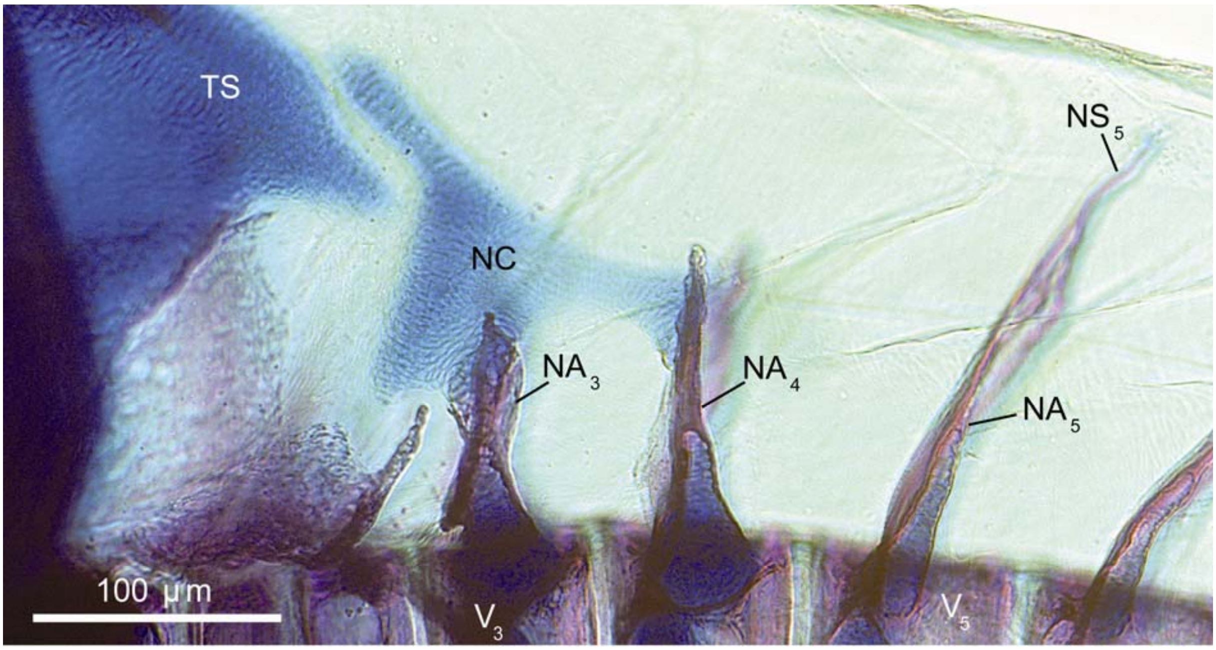

Fig. 73 Developmental stages of the neural complex in Gymnotiformes. *Apteronotus leptorhynchus*, 11.9 mm, lateral view.

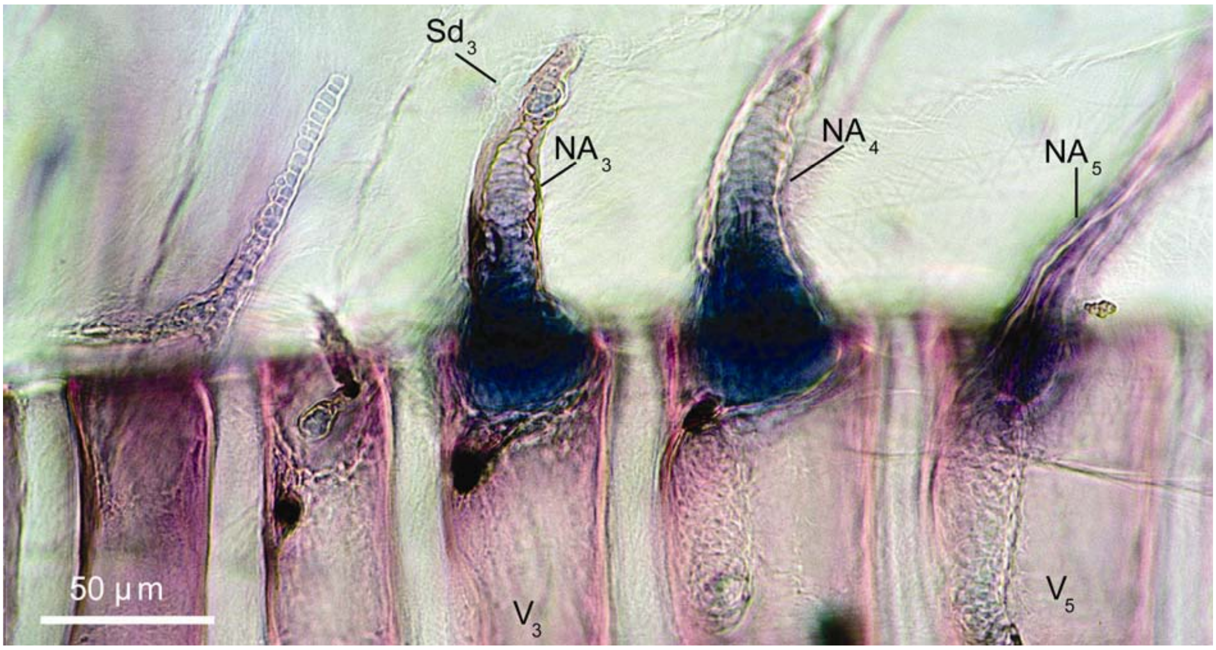

Fig. 74 Developmental stages of the neural complex in Gymnotiformes. *Apteronotus albifrons*, 11.0 mm, lateral view.

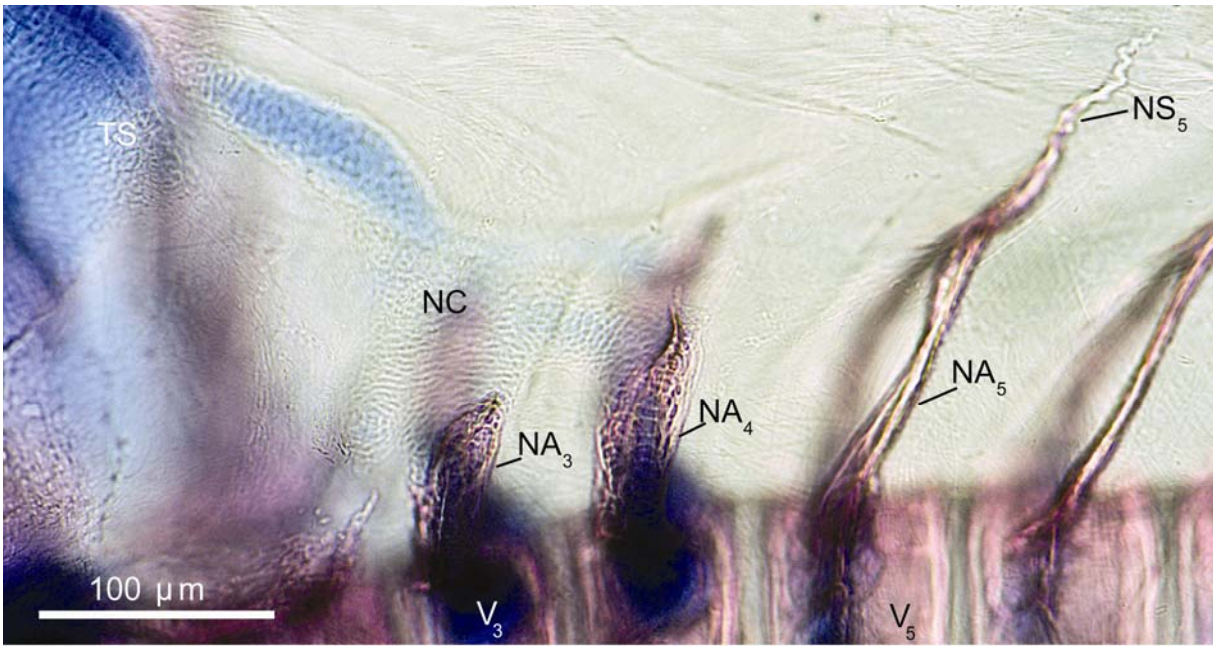

Fig. 75 Developmental stages of the neural complex in Gymnotiformes. *Apteronotus albifrons*, 12.0 mm, lateral view.

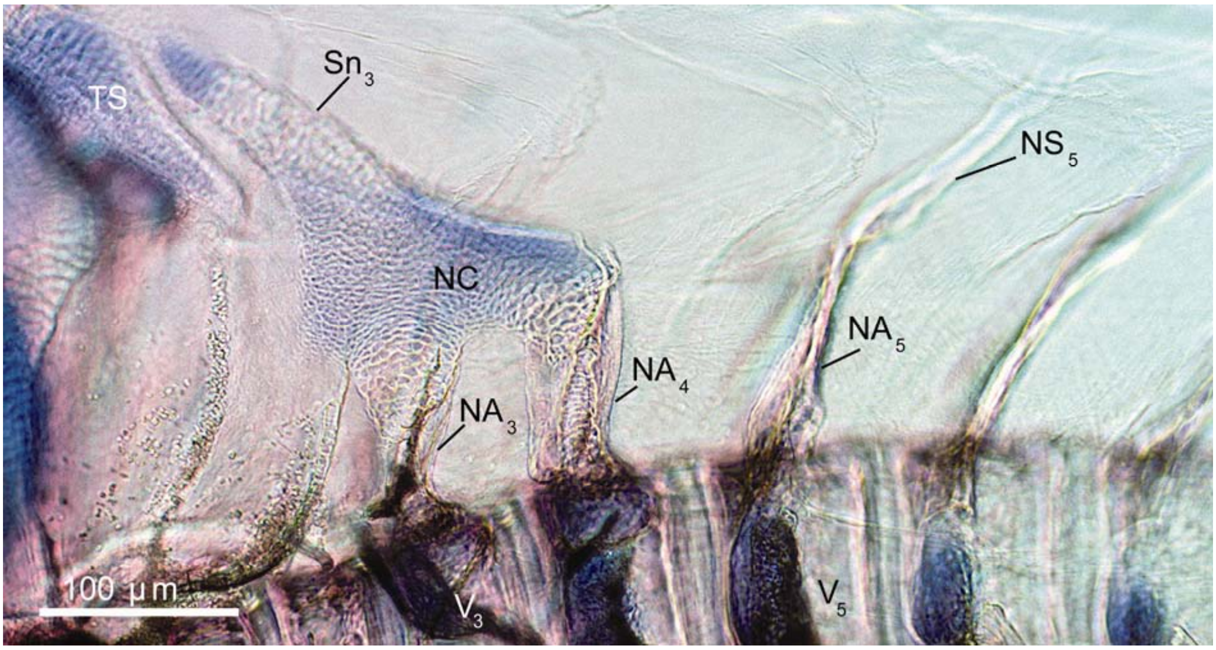

Fig. 76 Developmental stages of the neural complex in Gymnotiformes. *Apteronotus albifrons*, 16.0 mm, lateral view.

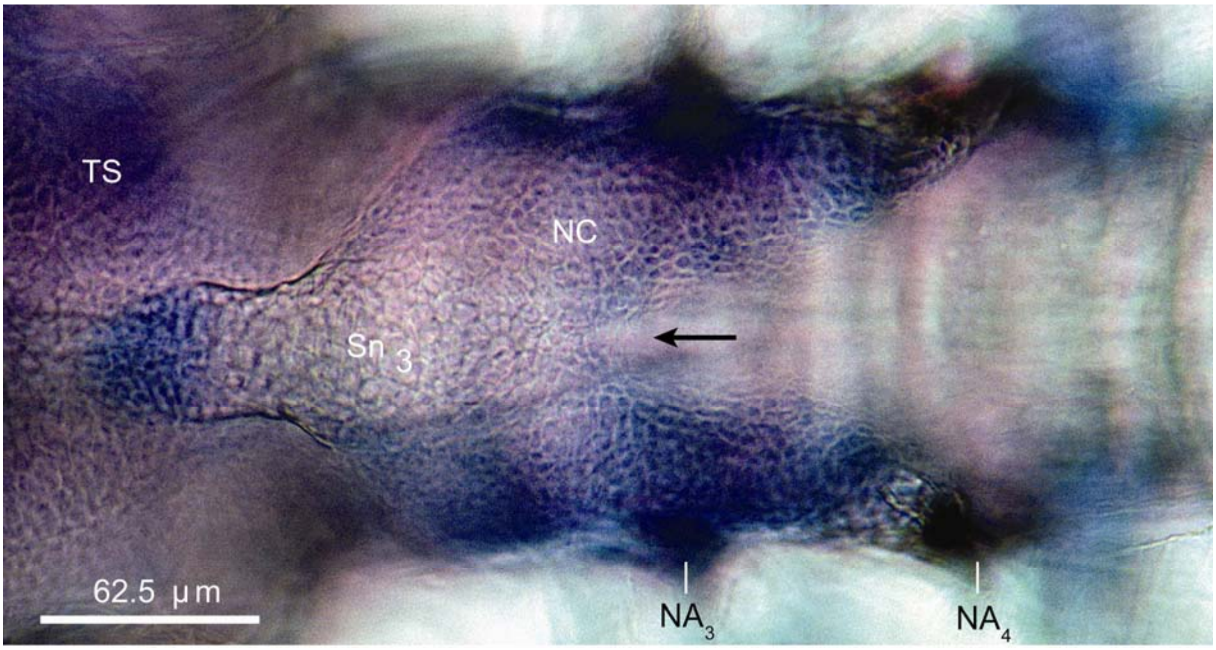

Fig. 77 Developmental stages of the neural complex in Gymnotiformes. *Apteronotus albifrons*, 16.0 mm, same as in Fig. 76, but close up and dorsal view. Arrow points to incisure resulting from incomplete median fusion of supradorsals 4.

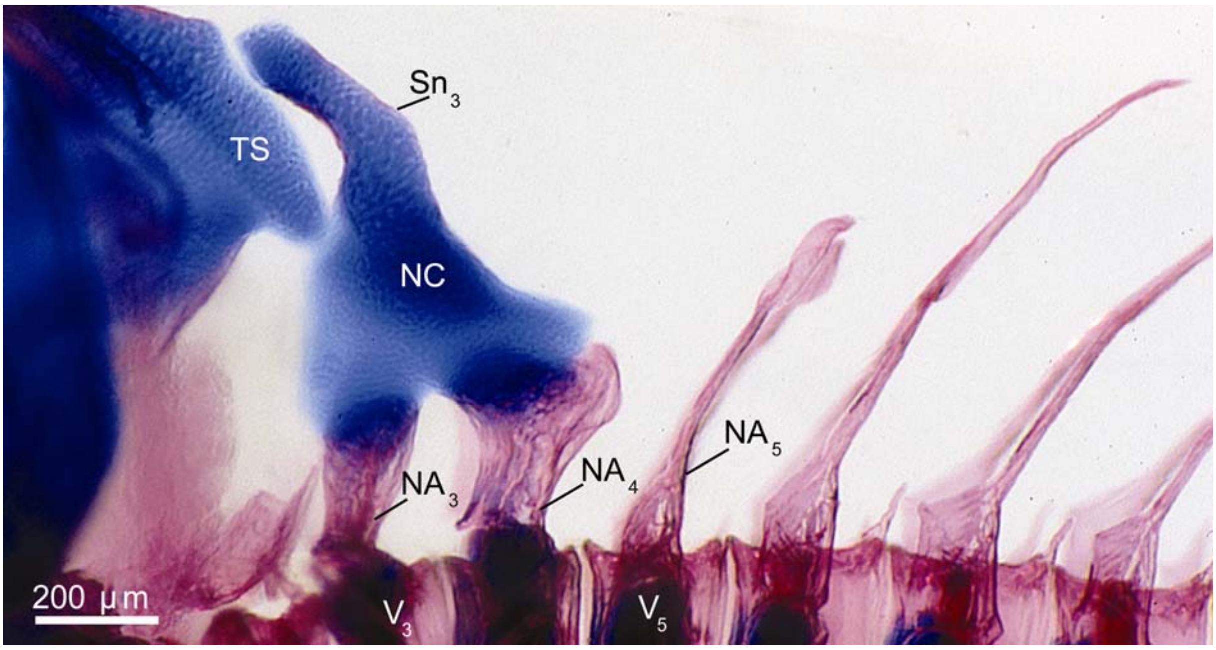

Fig. 78 Developmental stages of the neural complex in Gymnotiformes. *Apteronotus albifrons*, 19.8 mm, lateral view.

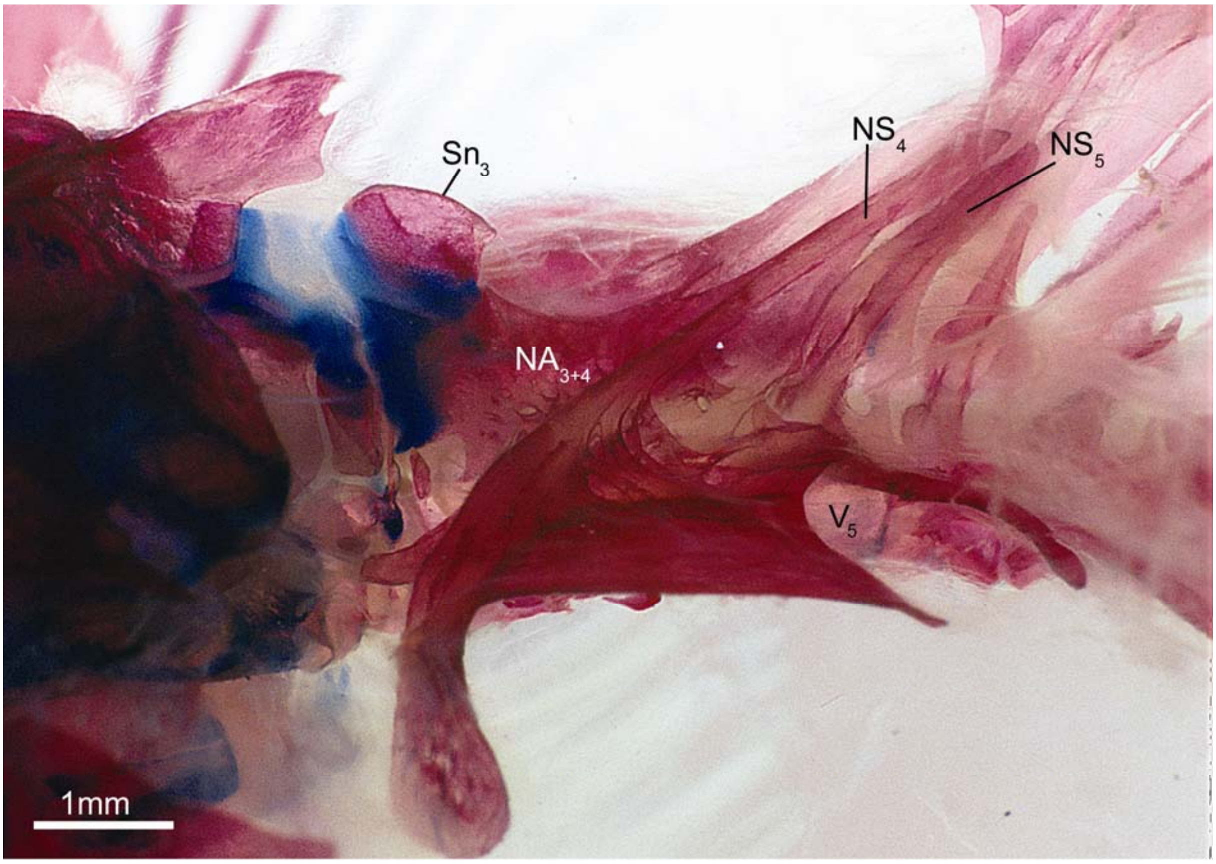

Fig. 79 Developmental stages of the neural complex in Siluriformes.
Diplomystes chilensis, 60.0 mm, lateral view.

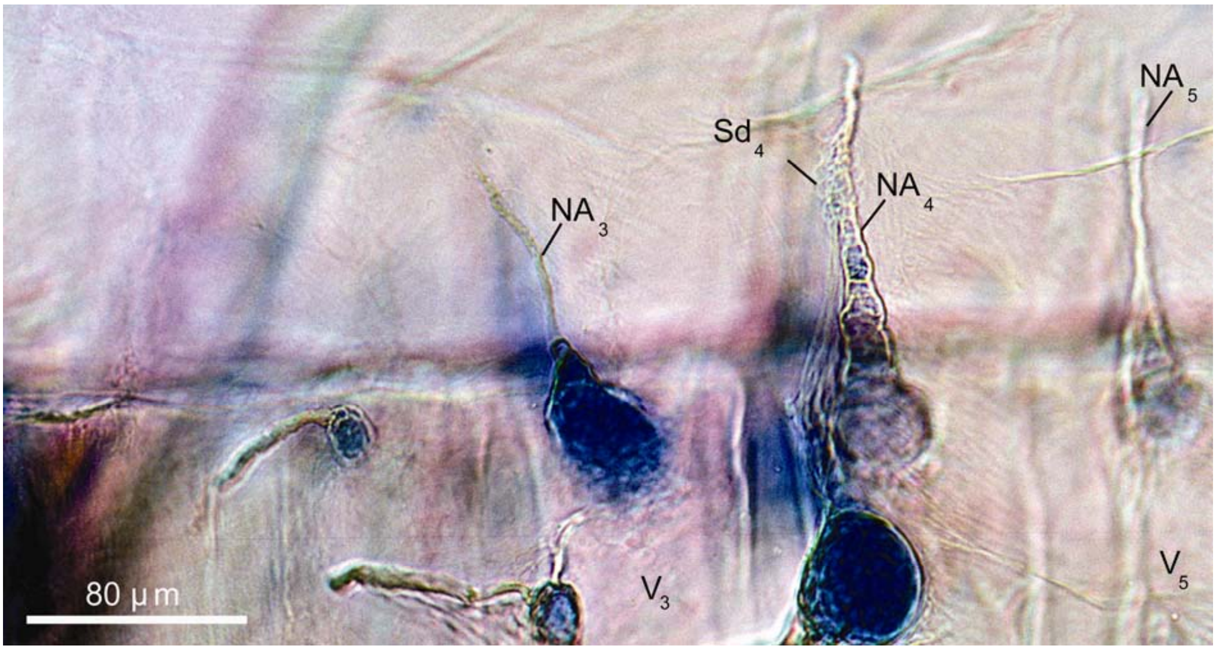

Fig. 80 Developmental stages of the neural complex in Siluriformes.
Silurus glanis, 11.6 mm, lateral view.

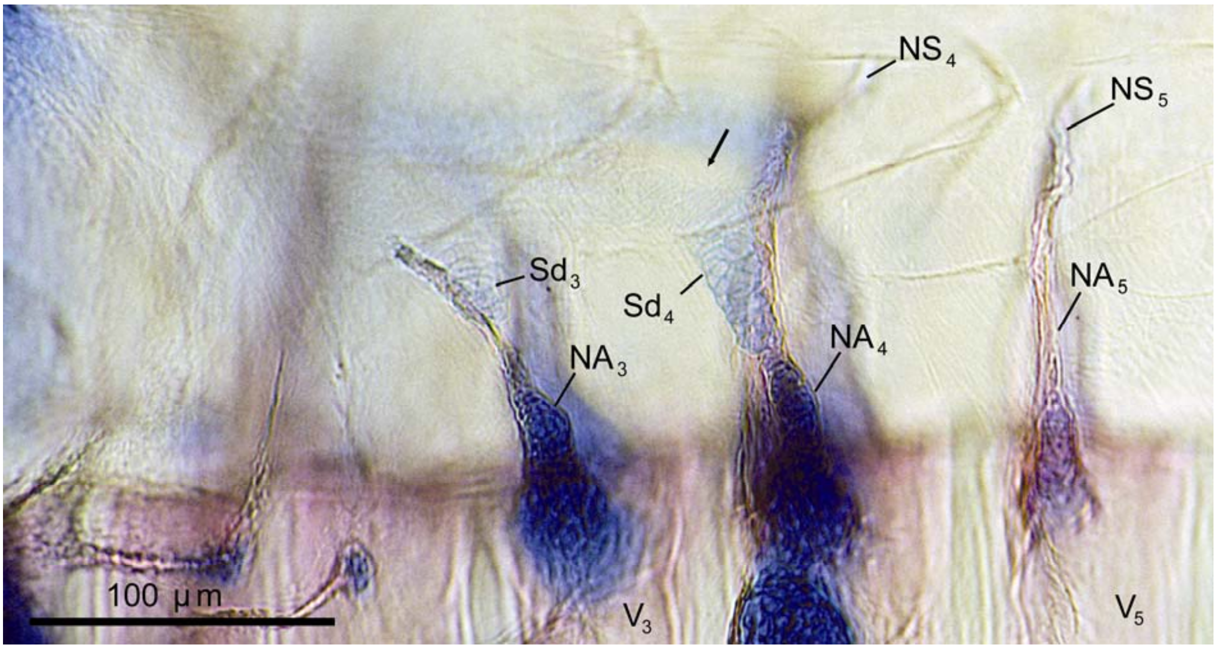

Fig. 81 Developmental stages of the neural complex in Siluriformes. *Silurus glanis*, 12.4 mm, lateral view. Arrow points to incisure resulting from incomplete median fusion of supradorsals 4.

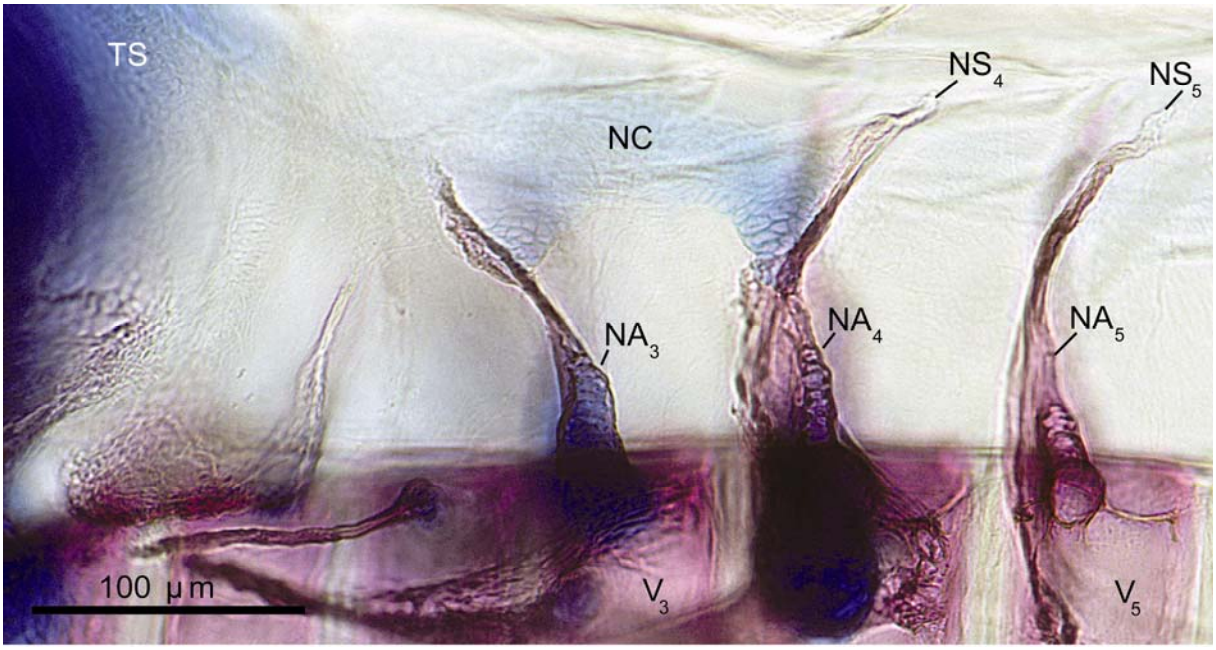

Fig. 82 Developmental stages of the neural complex in Siluriformes. *Silurus glanis*, 13.4 mm, lateral view.

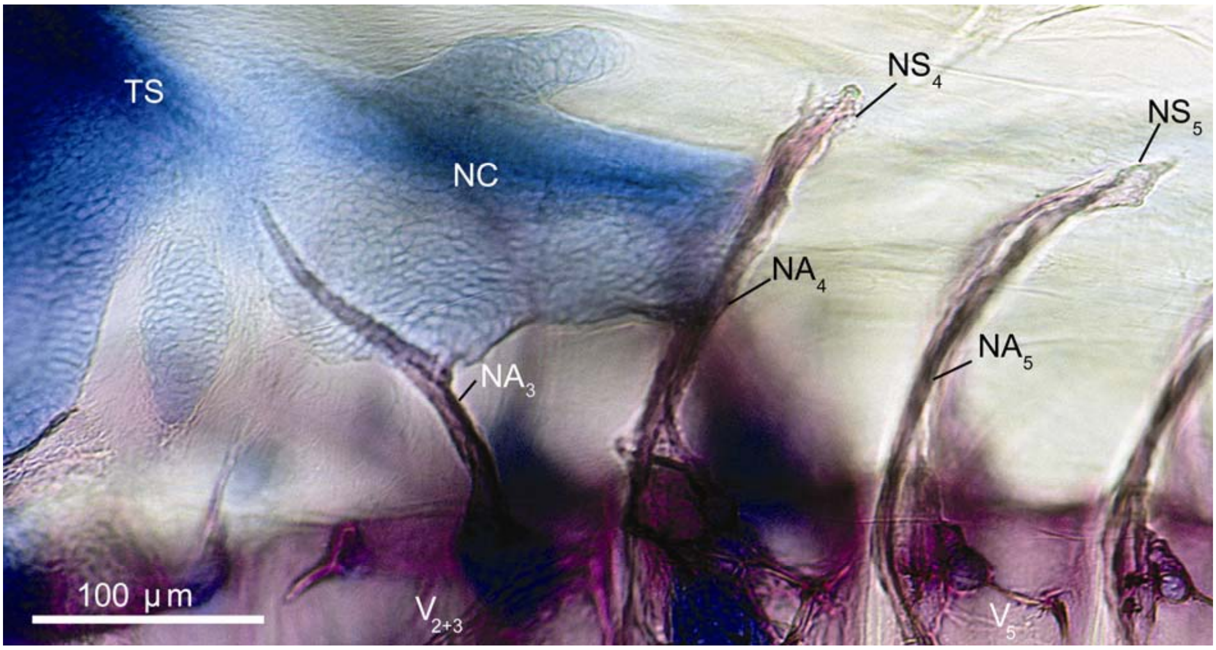

Fig. 83 Developmental stages of the neural complex in Siluriformes.
Silurus glanis, 15.4 mm, lateral view.

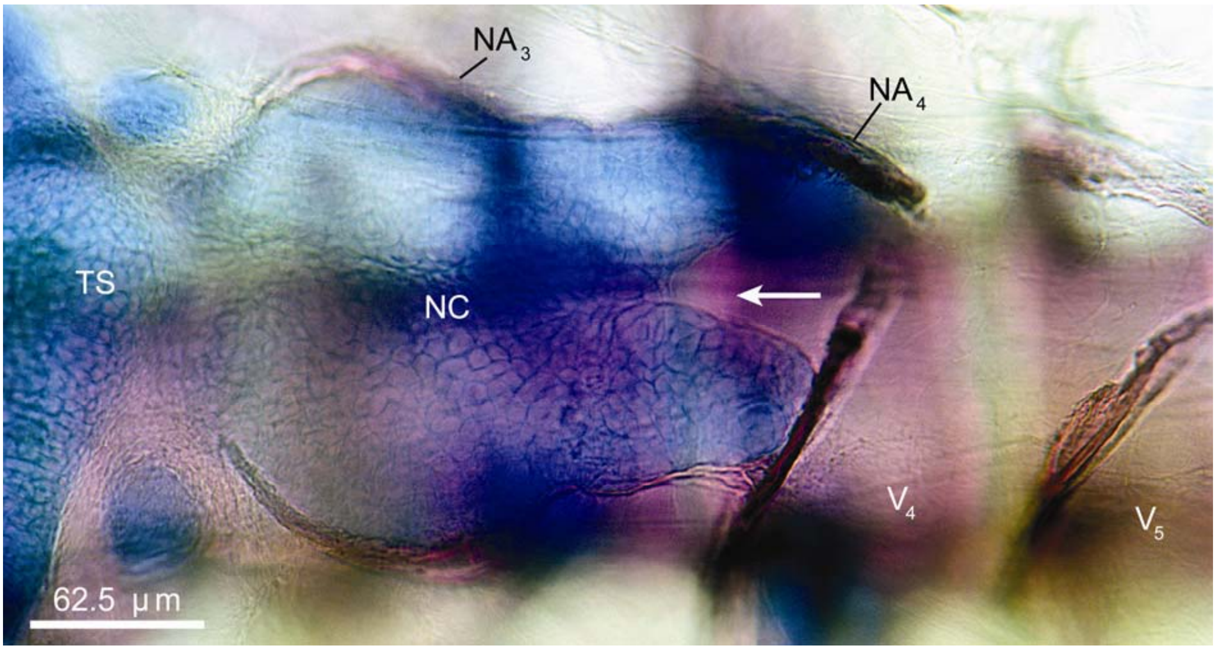

Fig. 84 Developmental stages of the neural complex in Siluriformes.
Silurus glanis, 15.4 mm, same as in Fig. 83, but close up and in dorsal view. Arrow points to incisure resulting from incomplete median fusion of supradorsals 4.

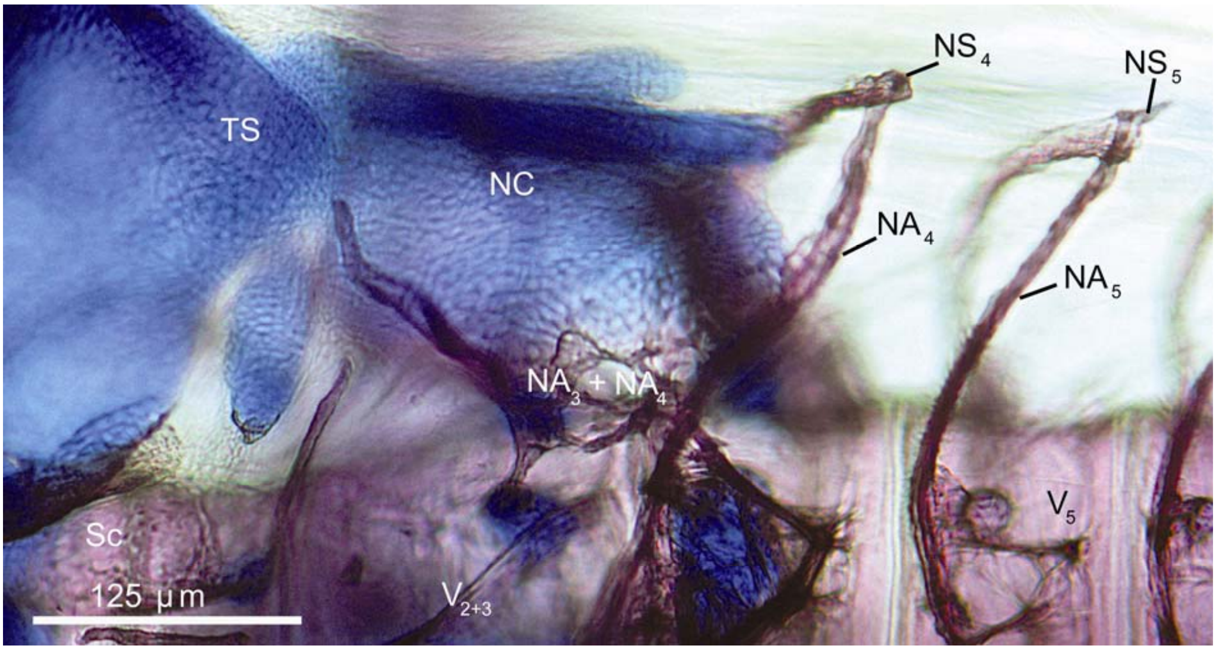

Fig. 85 Developmental stages of the neural complex in Siluriformes.
Silurus glanis, 16.6 mm, slightly dorsolateral view.

Fig. 86 Developmental stages of the neural complex in Siluriformes.
Ancistrus sp., 6.3 mm, lateral view.

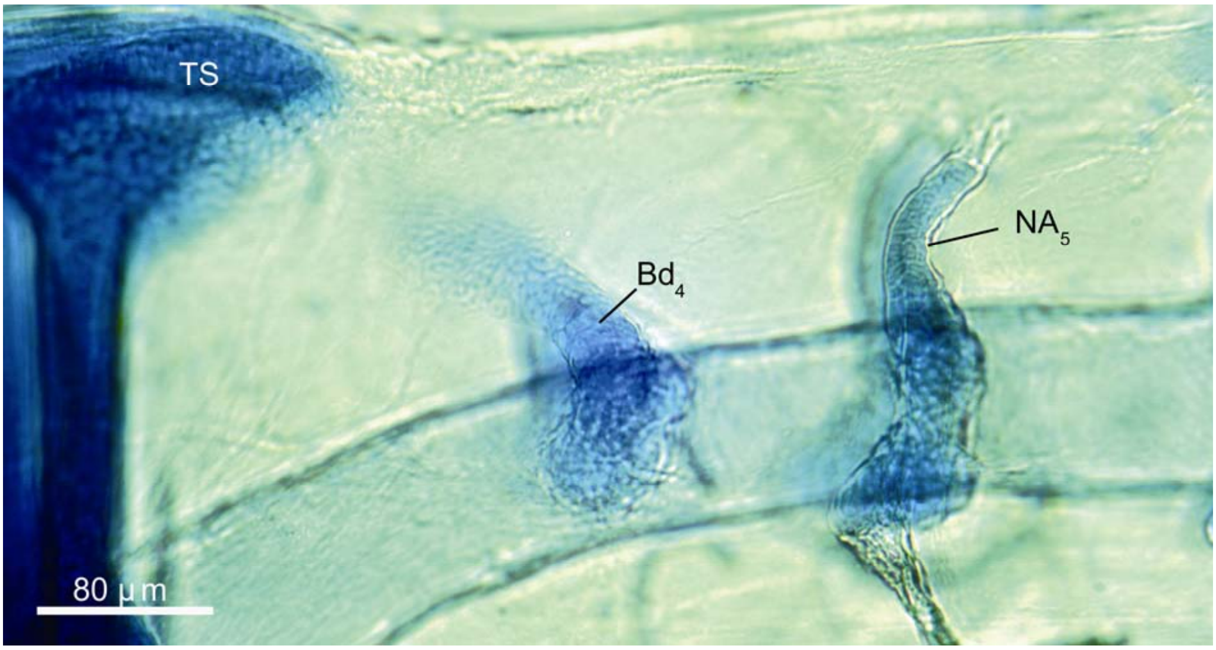

Fig. 87 Developmental stages of the neural complex in Siluriformes. *Ancistrus* sp., 6.5 mm, lateral view.

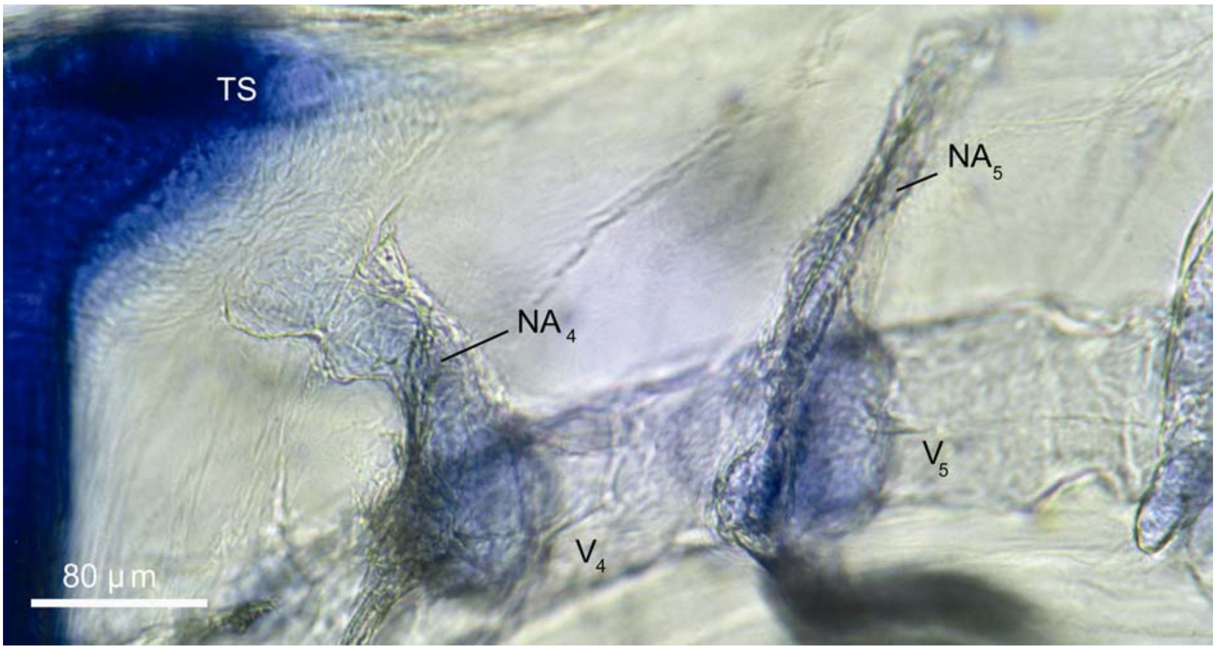

Fig. 88 Developmental stages of the neural complex in Siluriformes. *Ancistrus* sp., 7.5 mm, lateral view.

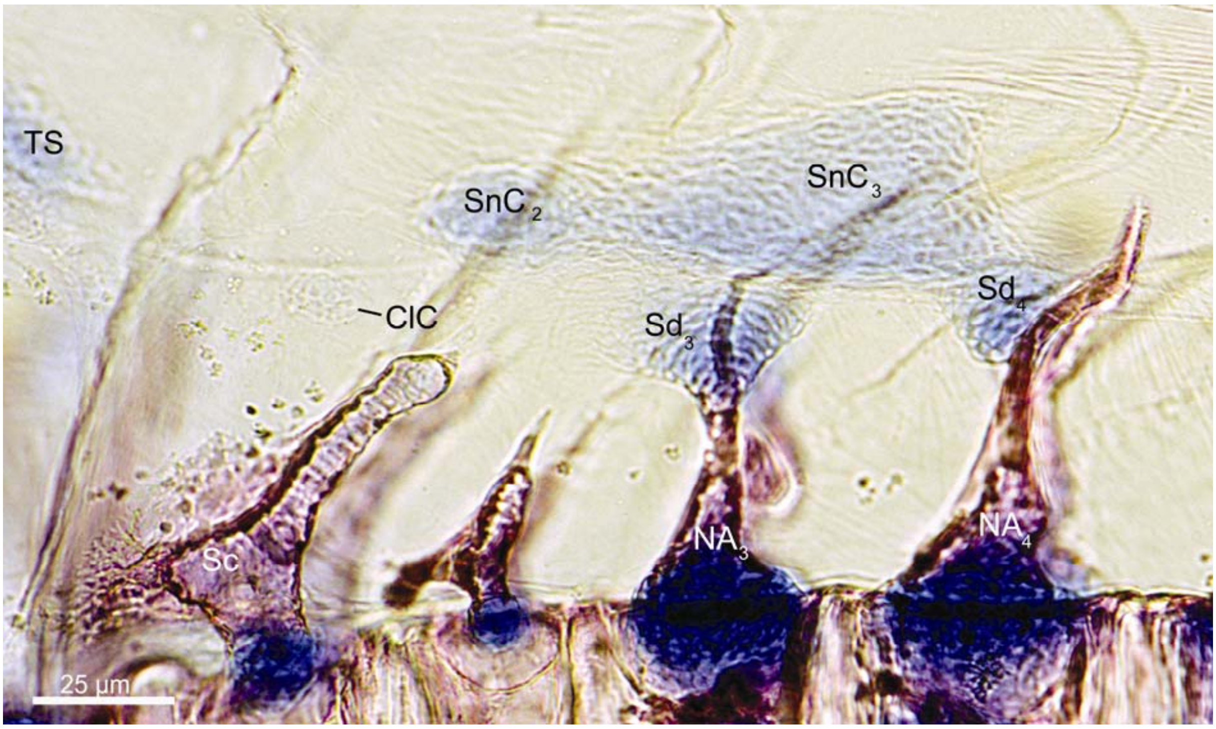

Fig. 89 Developmental stages of the claustrum in Cypriniformes. *Cyprinus carpio*, 9.8 mm, lateral view.

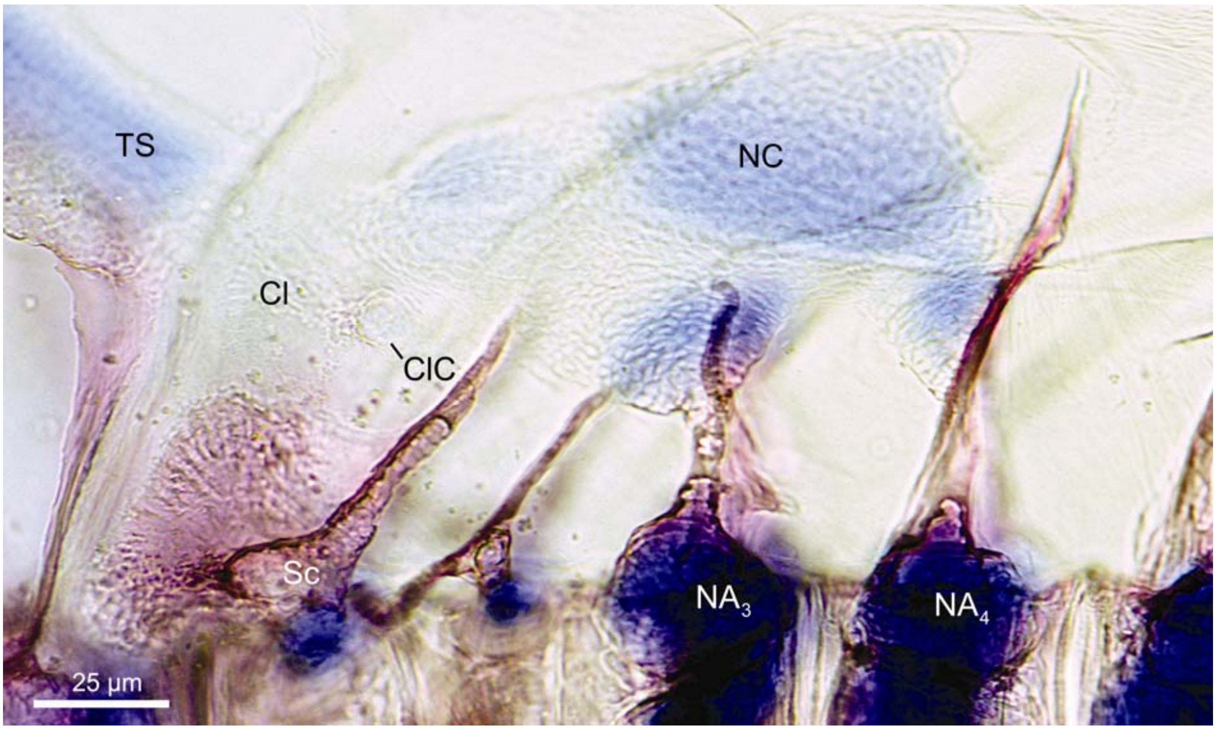

Fig. 90 Developmental stages of the claustrum in Cypriniformes. *Cyprinus carpio*, 11.1 mm, lateral view.

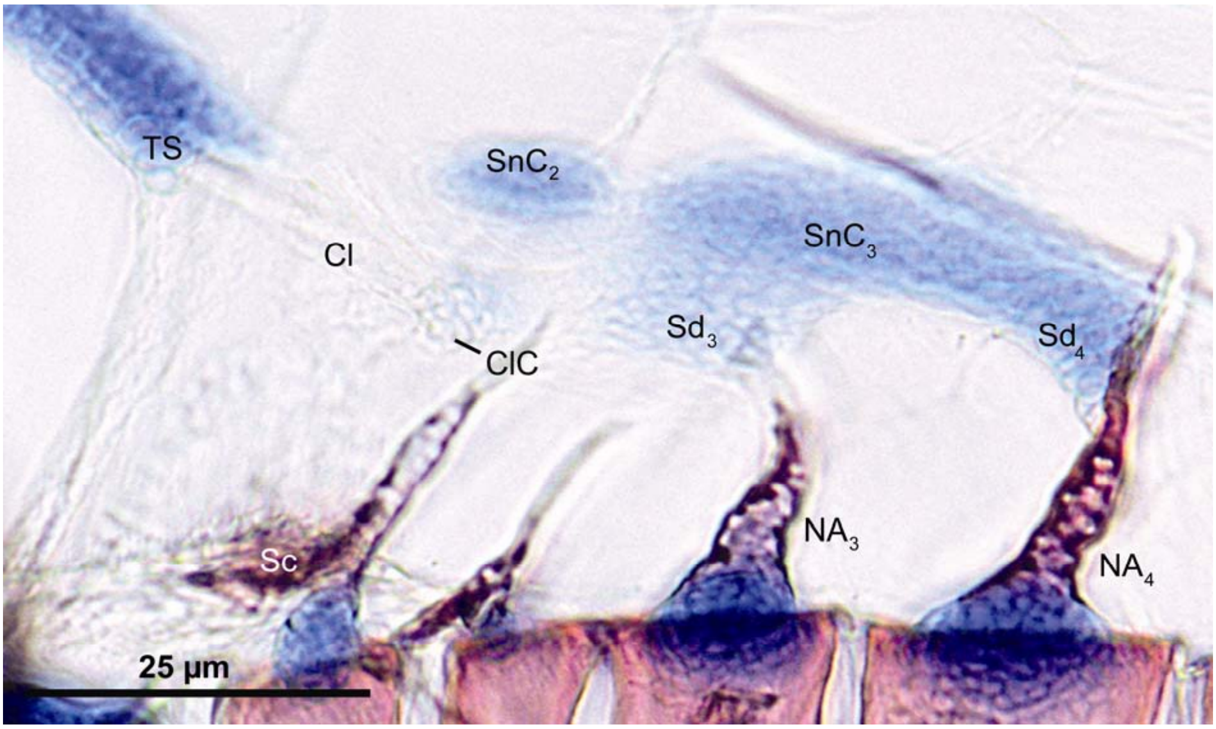

Fig. 91 Developmental stages of the claustrum in Cypriniformes. *Puntius fasciatus*, 4.7 mm, lateral view.

Fig. 92 Developmental stages of the claustrum in Cypriniformes. *Puntius fasciatus*, 5.6 mm, lateral view.

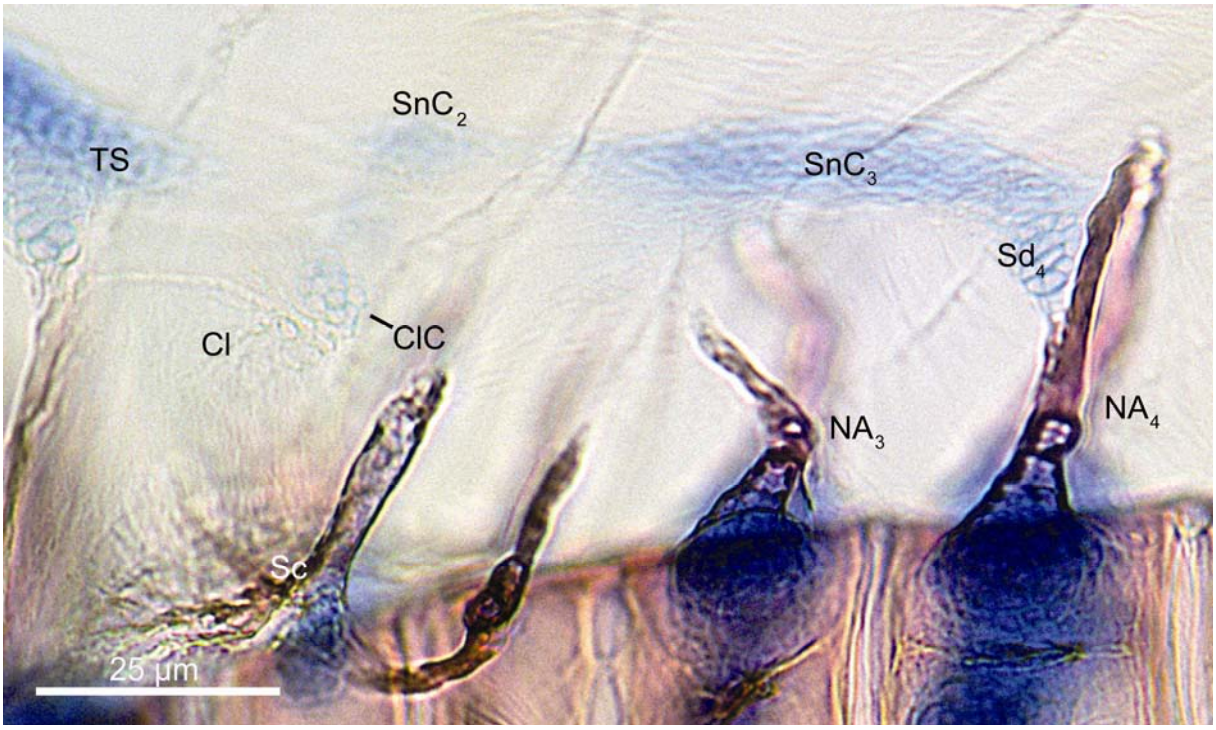

Fig.93 Developmental stages of the claustrum in Cypriniformes.
Puntius filamentosus, 5.7 mm, lateral view.

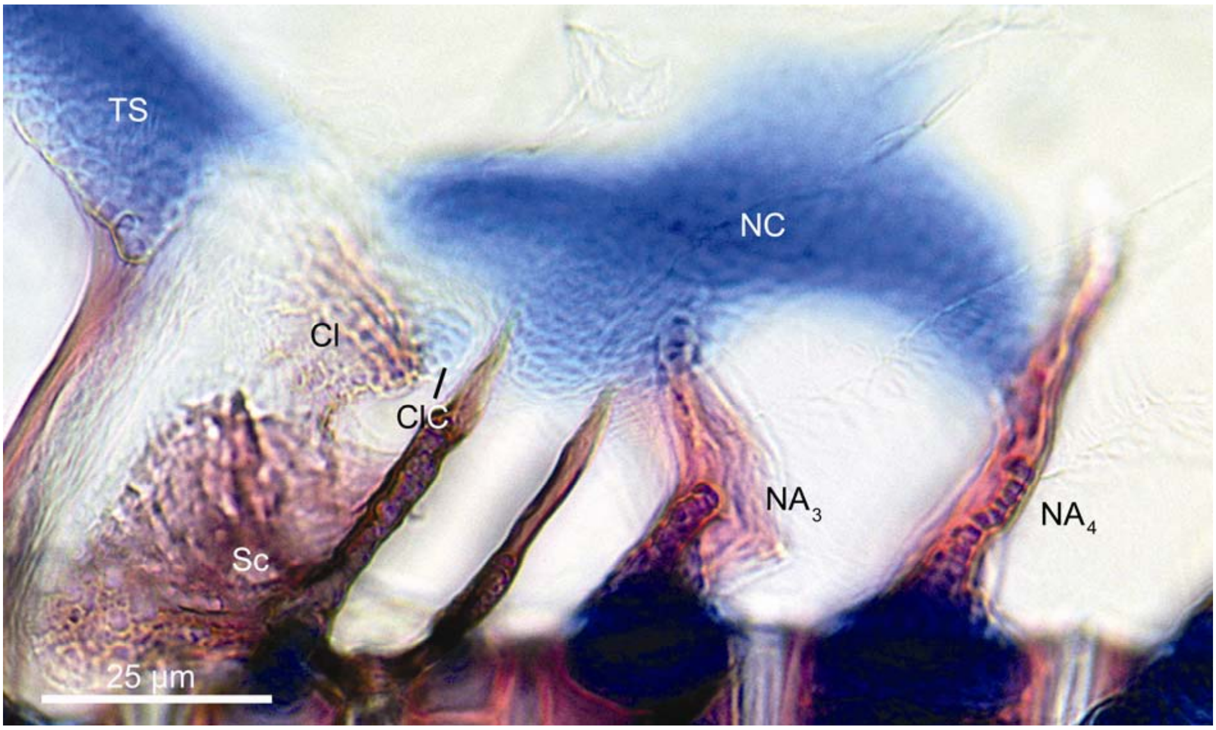

Fig.94 Developmental stages of the claustrum in Cypriniformes.
Puntius filamentosus, 6.3 mm, lateral view.

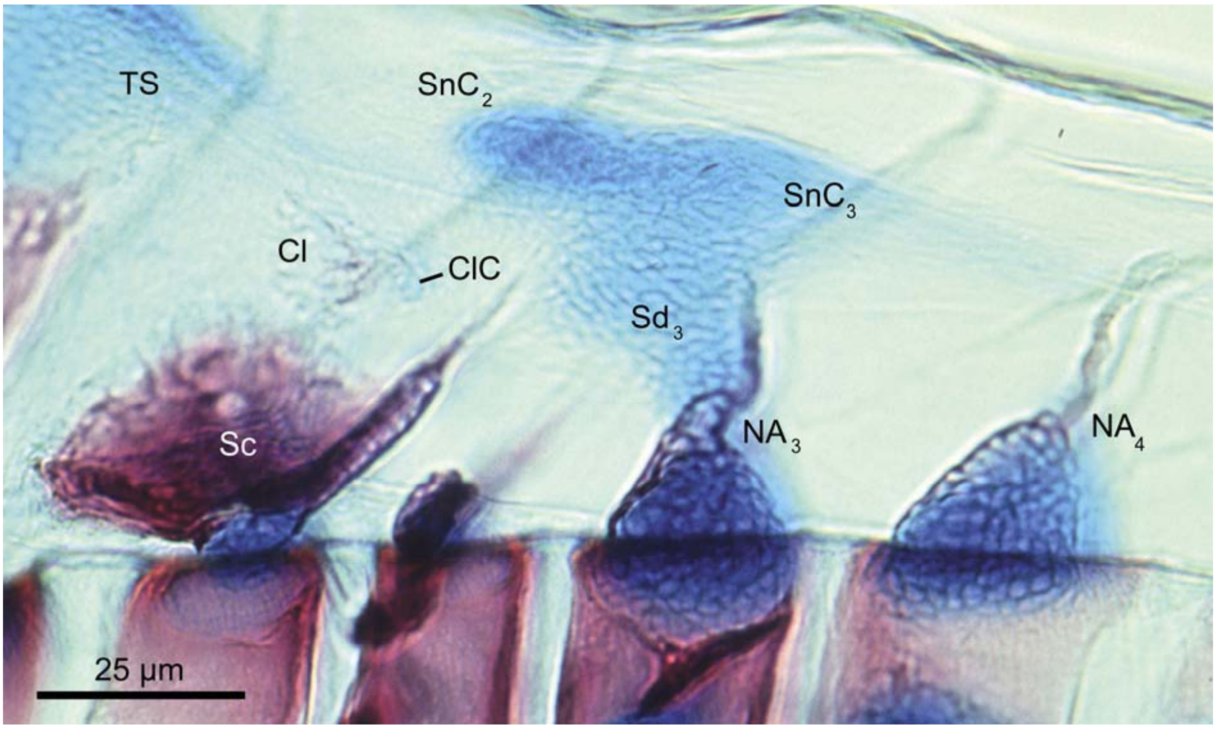

Fig.95 Developmental stages of the claustrum in Cypriniformes.
Candidia barbatus, 8.7 mm, lateral view.

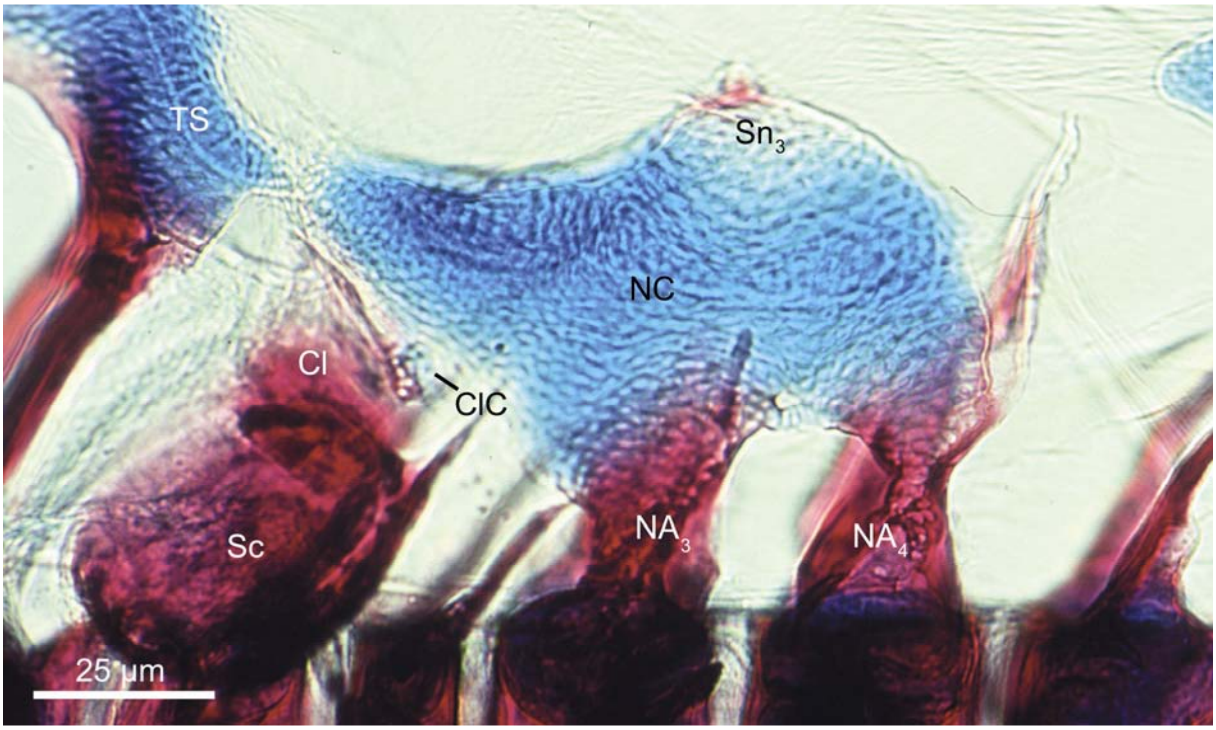

Fig.96 Developmental stages of the claustrum in Cypriniformes.
Candidia barbatus, 12.5 mm, lateral view.

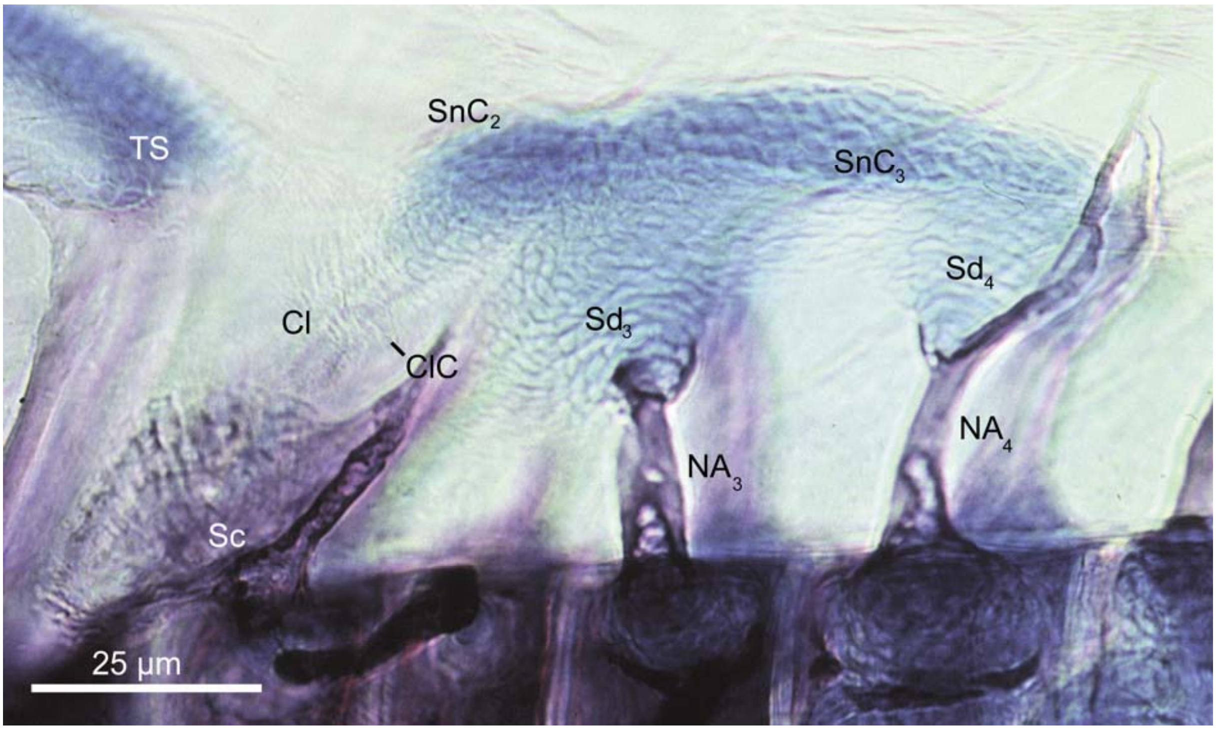

Fig. 97 Developmental stages of the claustrum in Cypriniformes.
Devario cf. *aequipinnatus*, 7.5 mm, lateral view.

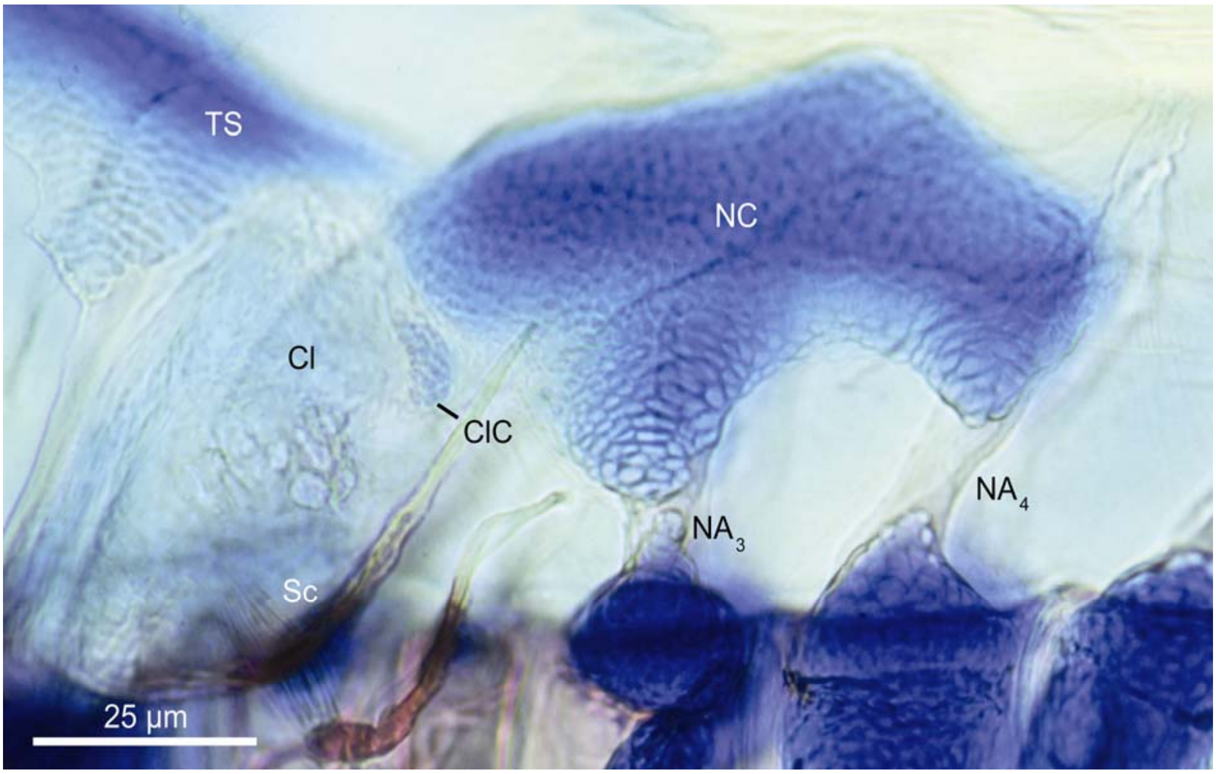

Fig. 98 Developmental stages of the claustrum in Cypriniformes.
Rasbora daniconius, 7.2 mm, lateral view.

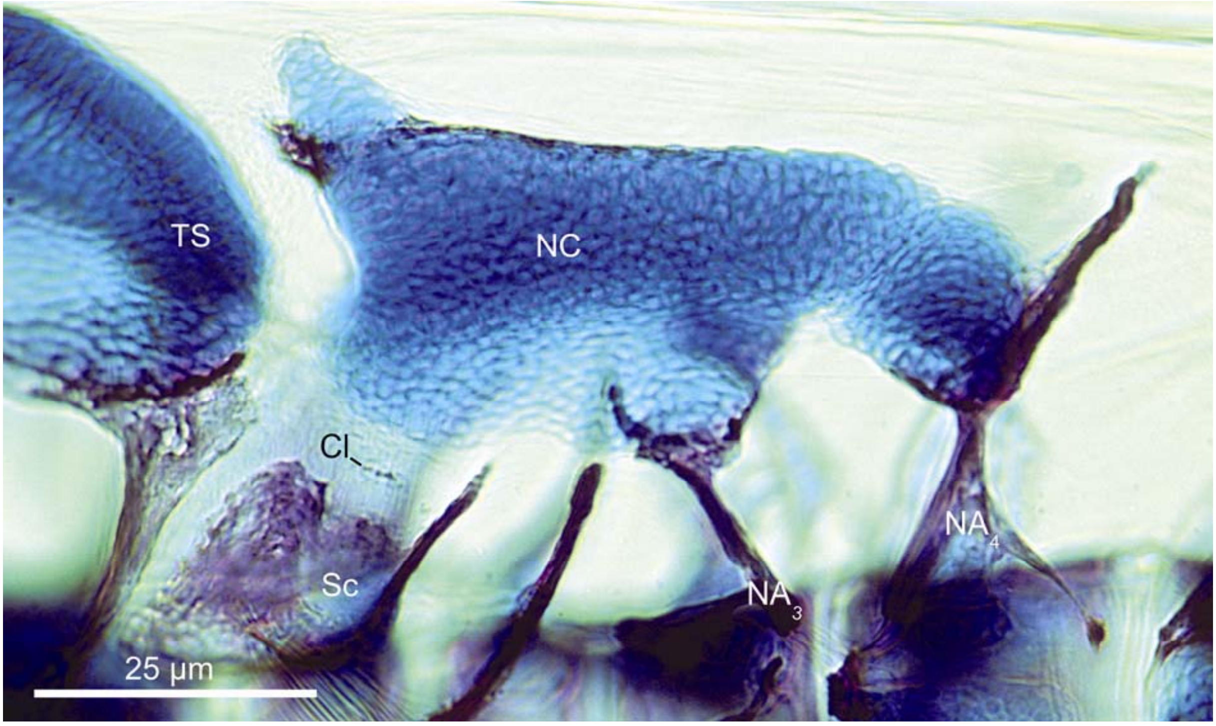

Fig. 99 Developmental stages of the claustrum in Characiformes. *Rhabdalestes septentrionalis*, 8.0 mm, lateral view.

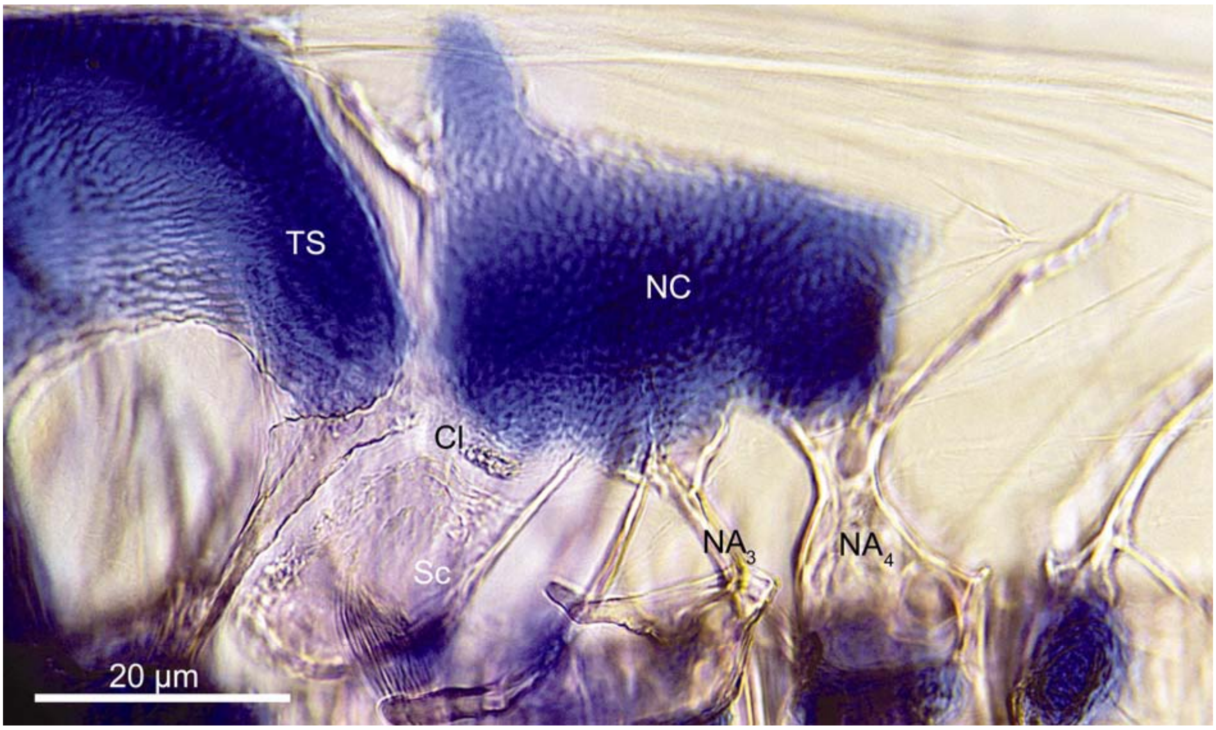

Fig. 100 Developmental stages of the claustrum in Characiformes. *Rhabdalestes septentrionalis*, 8.6 mm, lateral view.

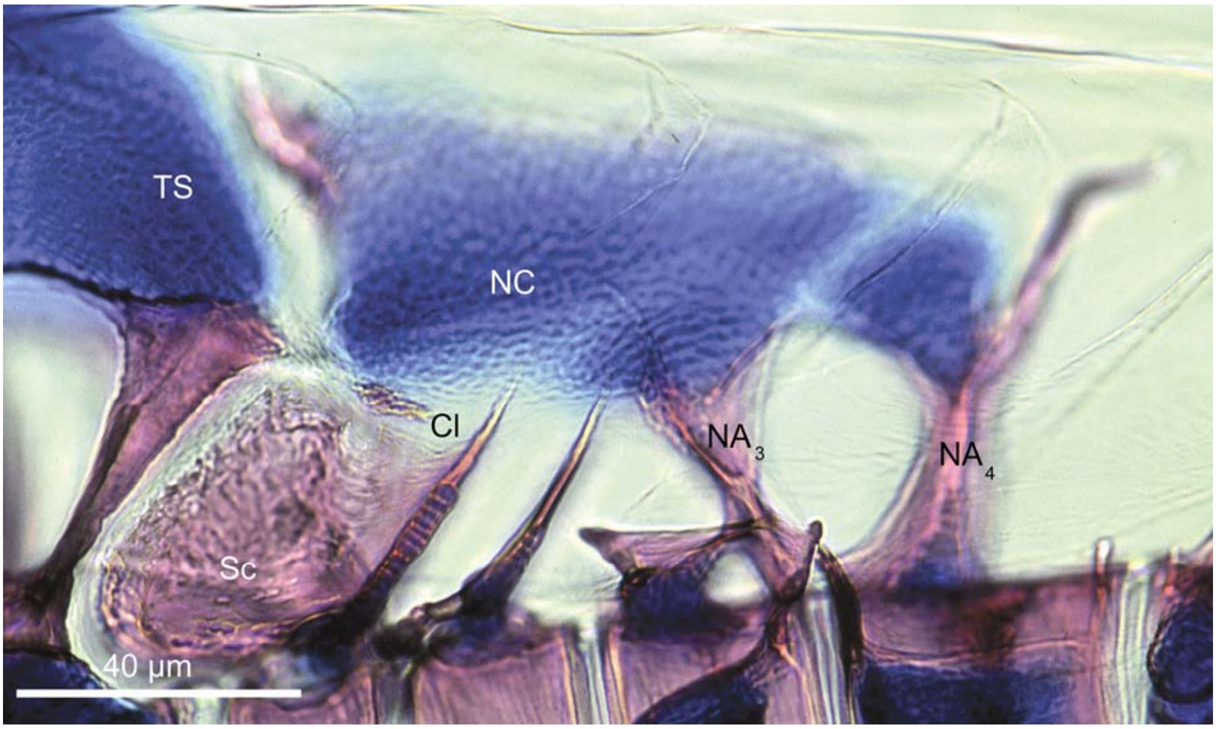

Fig.101 Developmental stages of the claustrum in Characiformes. *Alestopetersius smykalai*, 9.0 mm, lateral view.

Fig. 102 Developmental stages of the claustrum in Characiformes. *Alestopetersius smykalai*, 11.5 mm, lateral view.

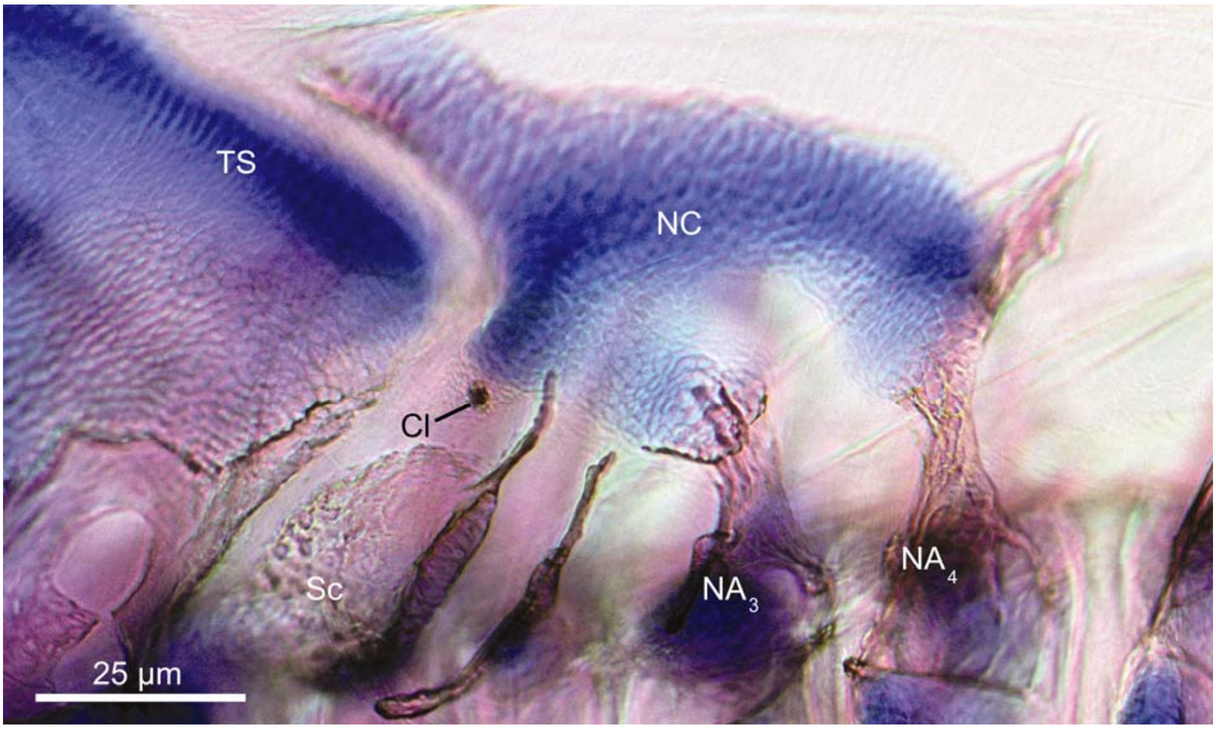

Fig. 103 Developmental stages of the claustrum in Characiformes. *Hoplias malabaricus*, 9.7 mm, lateral view.

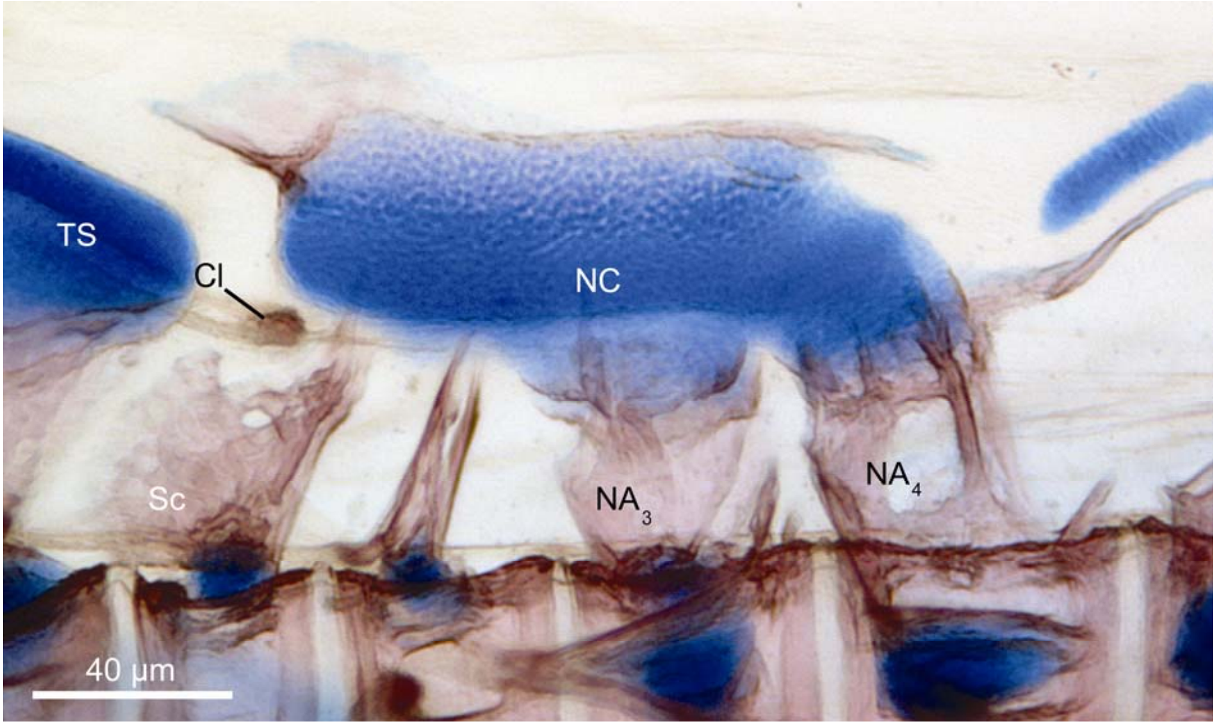

Fig. 104 Developmental stages of the claustrum in Characiformes. *Ctenolucius hujeta*, 20.0 mm, lateral view.

Fig. 105 Developmental stages of the claustrum in Characiformes. *Lebiasina bimaculata*, 12.1 mm, lateral view.

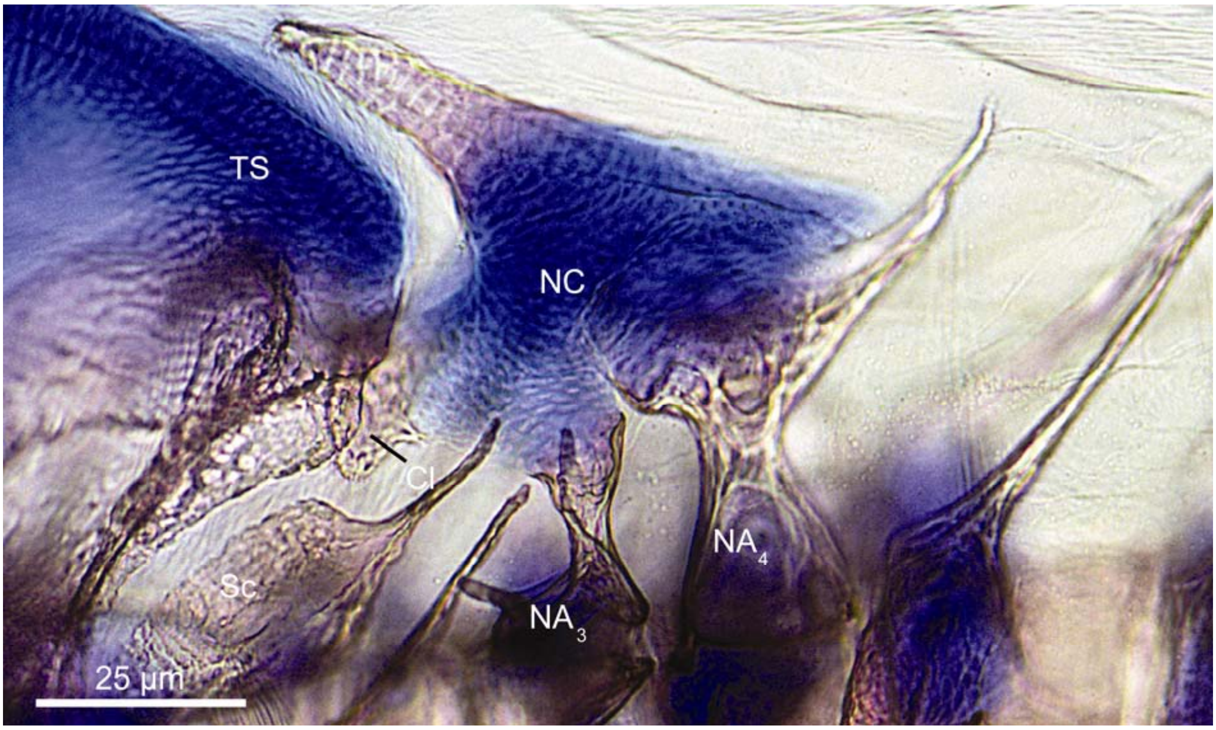

Fig. 106 Developmental stages of the claustrum in Characiformes. *Pyrrhulina spiloptera*, 8.2 mm, lateral view.

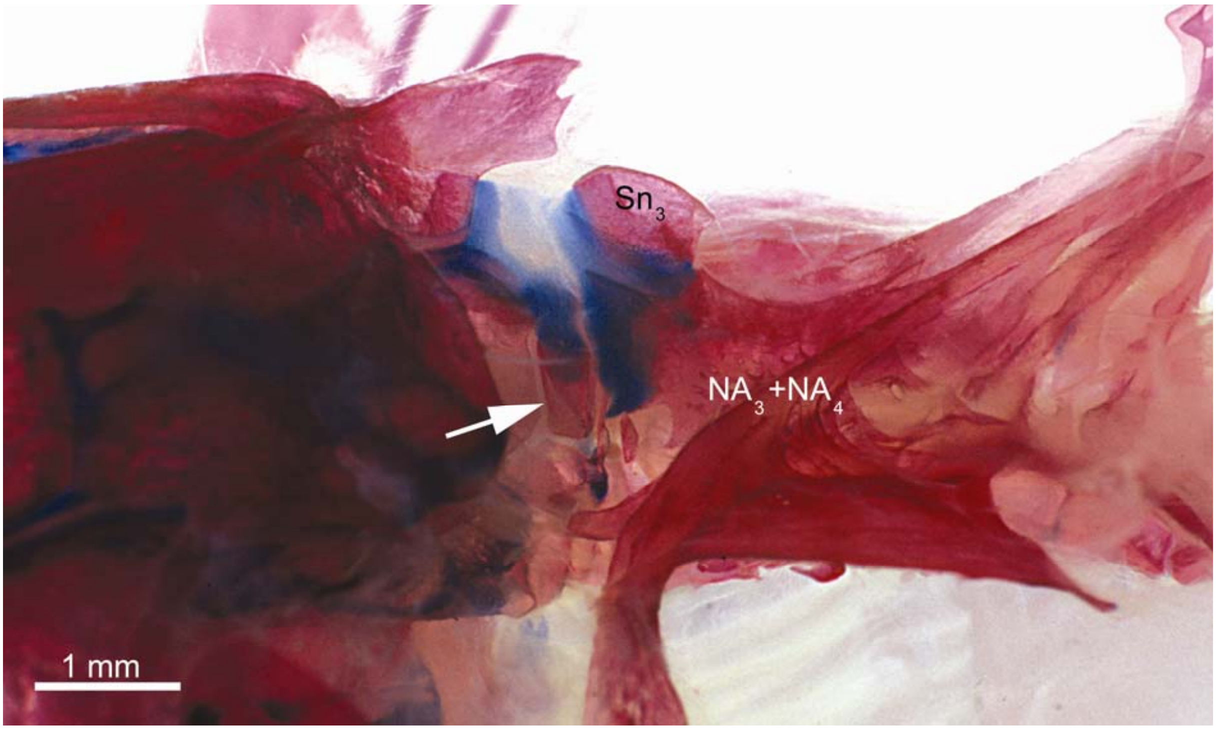

Fig. 107 Developmental stages of the claustrum in Siluriformes. *Diplomystes chilensis*, 60.0 mm, lateral view. Arrow points to the claustrum.

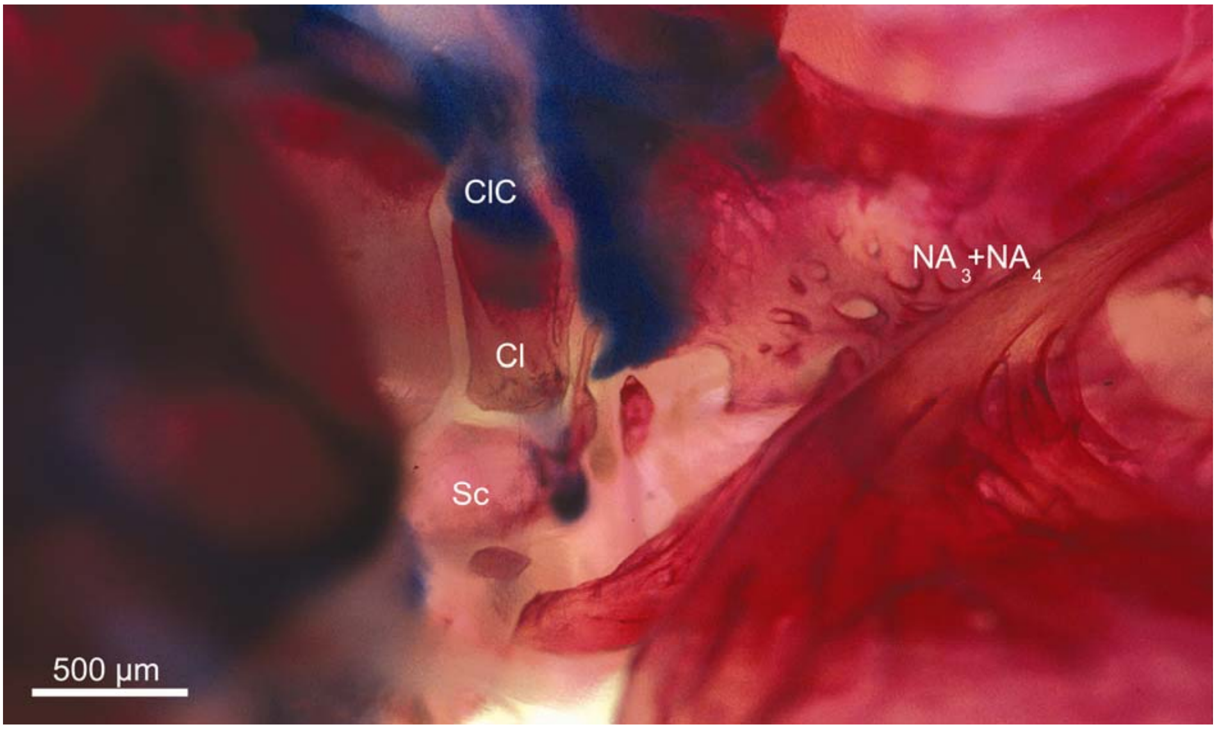

Fig. 108 Developmental stages of the claustrum in Siluriformes. *Diplomystes chilensis*, 60.0 mm, close up and lateral view.

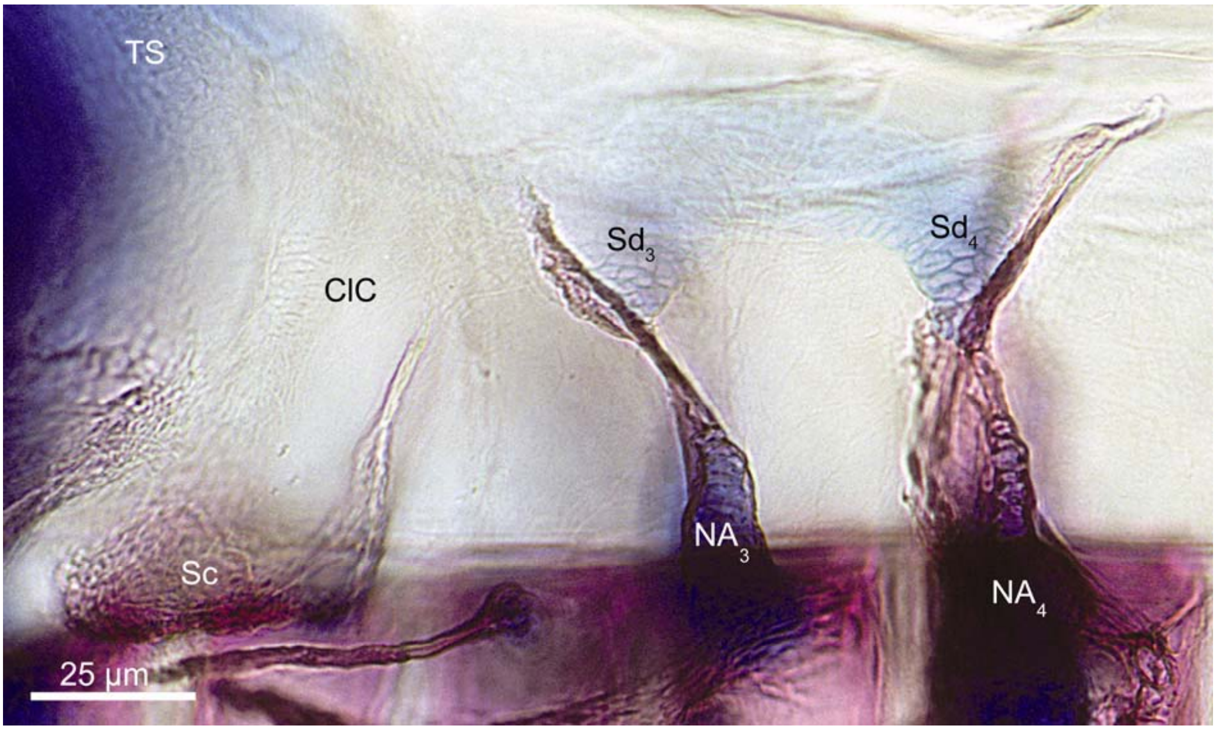

Fig. 109 Developmental stages of the claustrum in Siluriformes. *Silurus glanis*, 13.4 mm, lateral view.

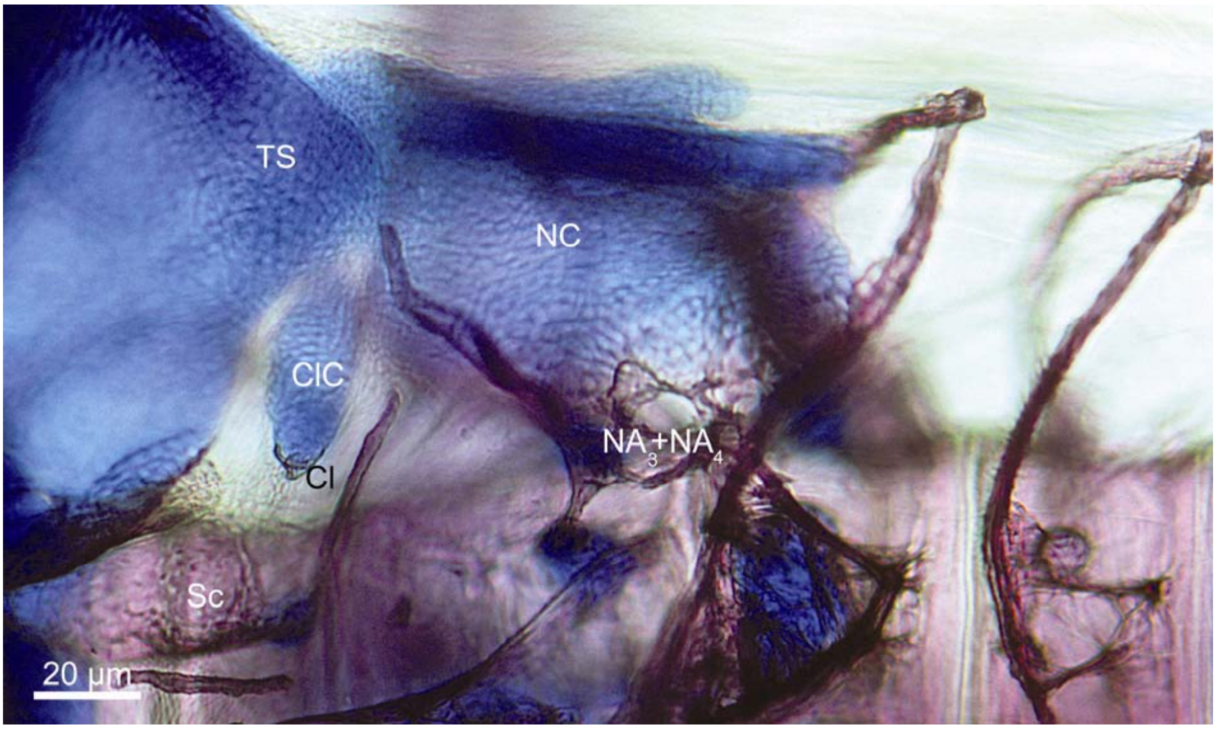

Fig. 110 Developmental stages of the claustrum in Siluriformes. *Silurus glanis*, 16.6 mm, lateral view.

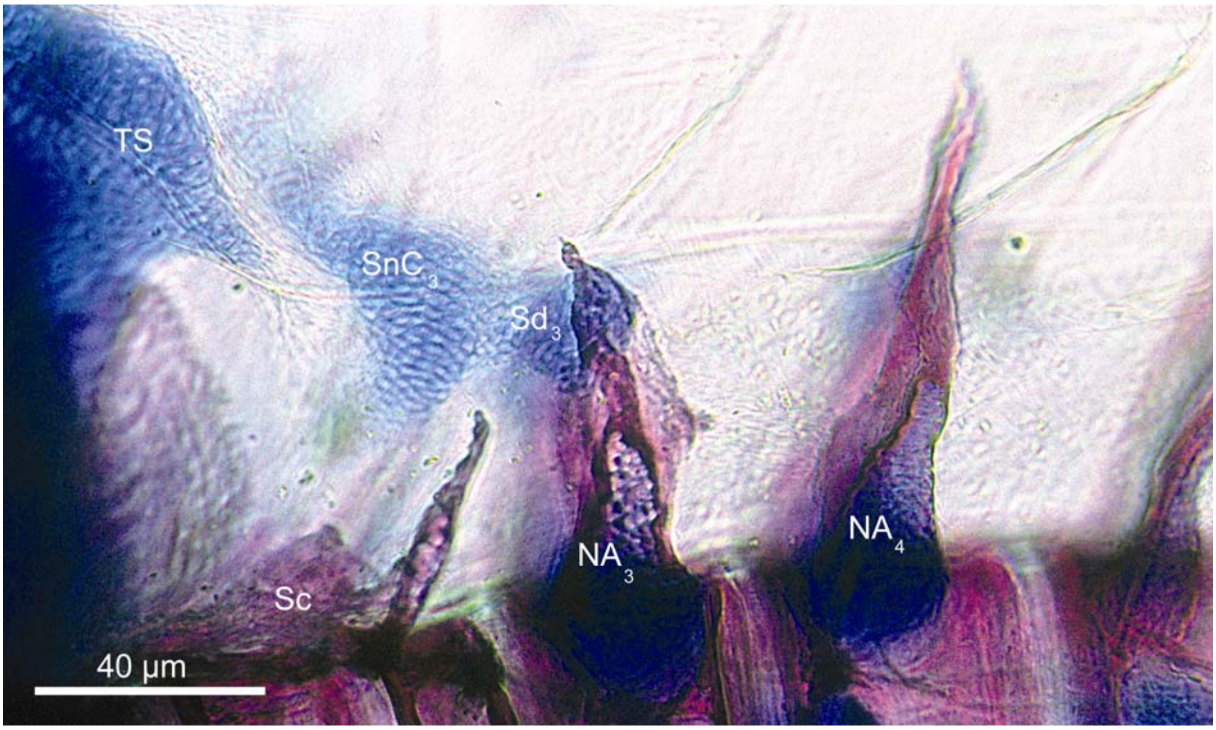

Fig. 111 Developmental stages of the claustrum in Gymnotiformes. *Apteronotus leptorhynchus*, 10.4 mm, lateral view.

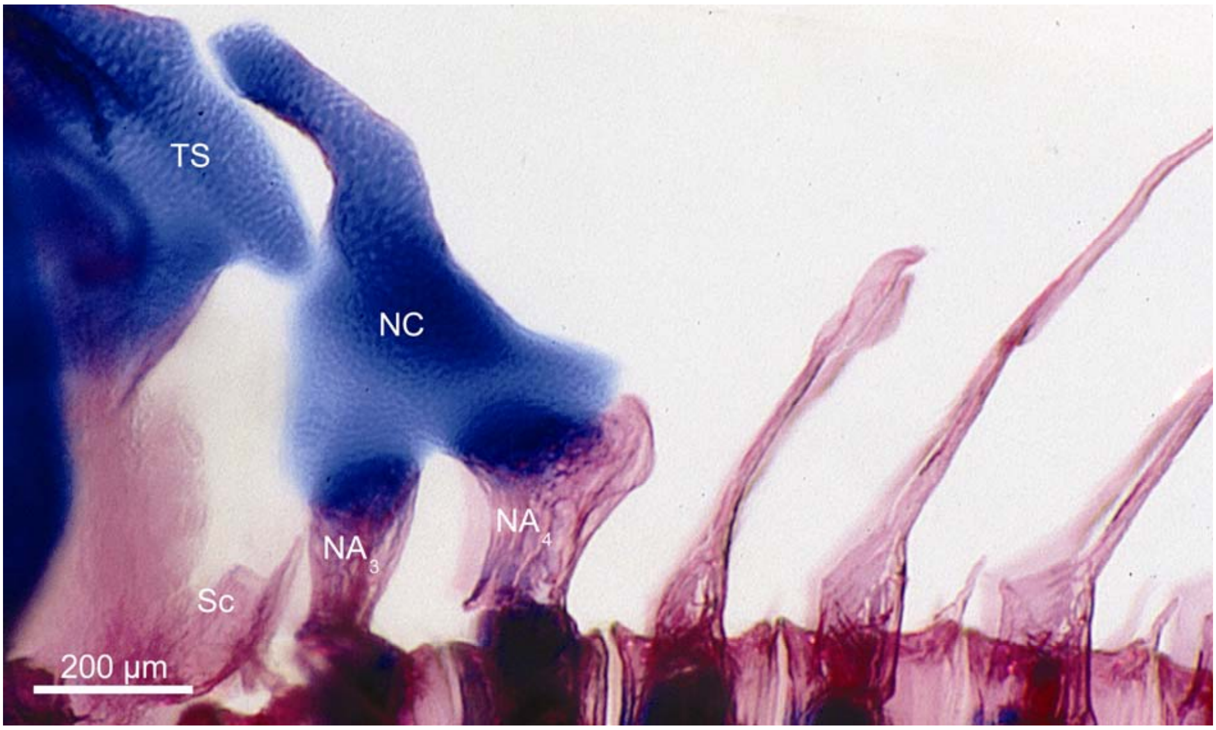

Fig. 112 Developmental stages of the claustrum in Gymnotiformes. *Apteronotus leptorhynchus*, 19.8 mm, lateral view.

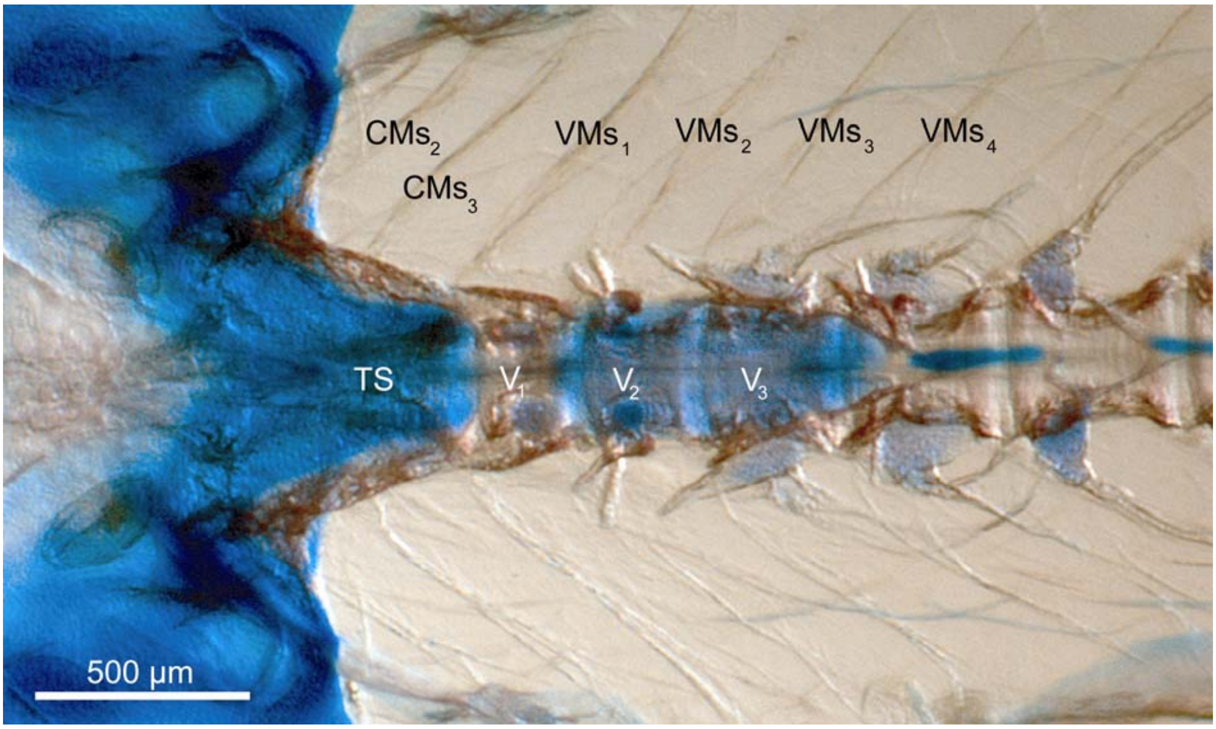

Fig. 113 Occiput, anterior vertebrae and associated myosepta in dorsal view. *Ctenolucius hujeta*, 20.0 mm.

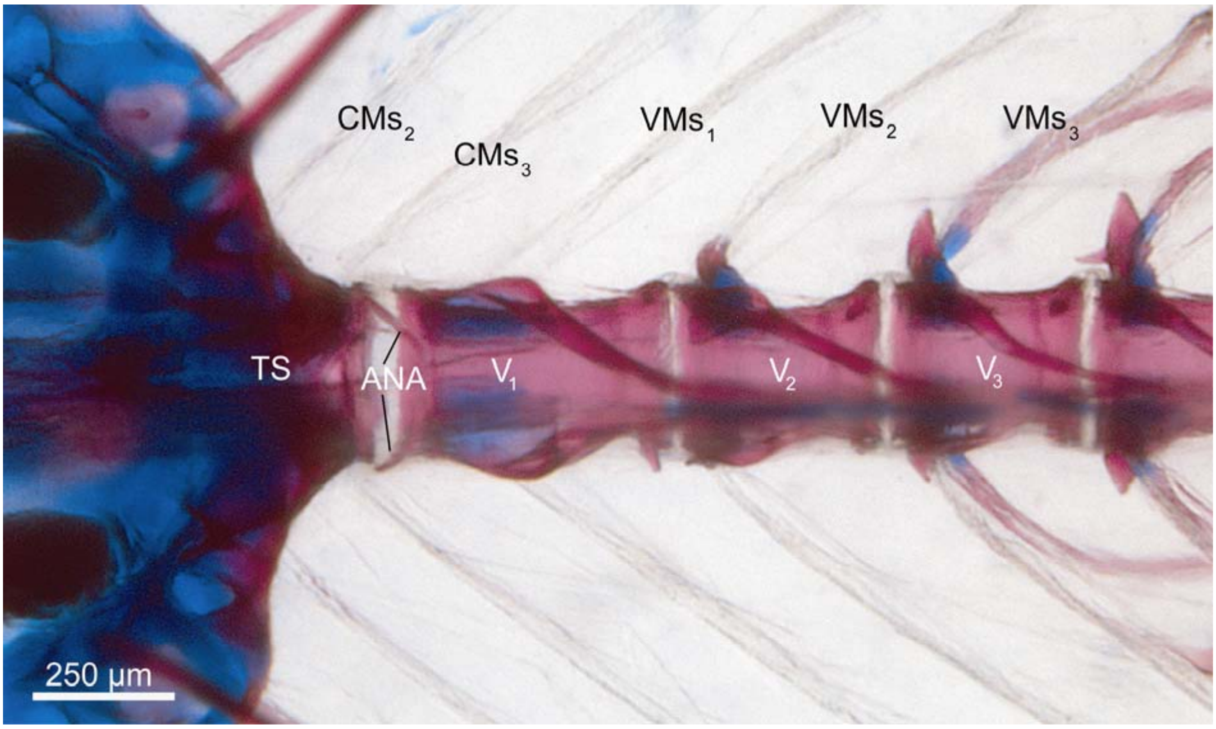

Fig. 114 Occiput, anterior vertebrae and associated myosepta in dorsal view. *Anchoa mitchilli*, 23.0 mm.

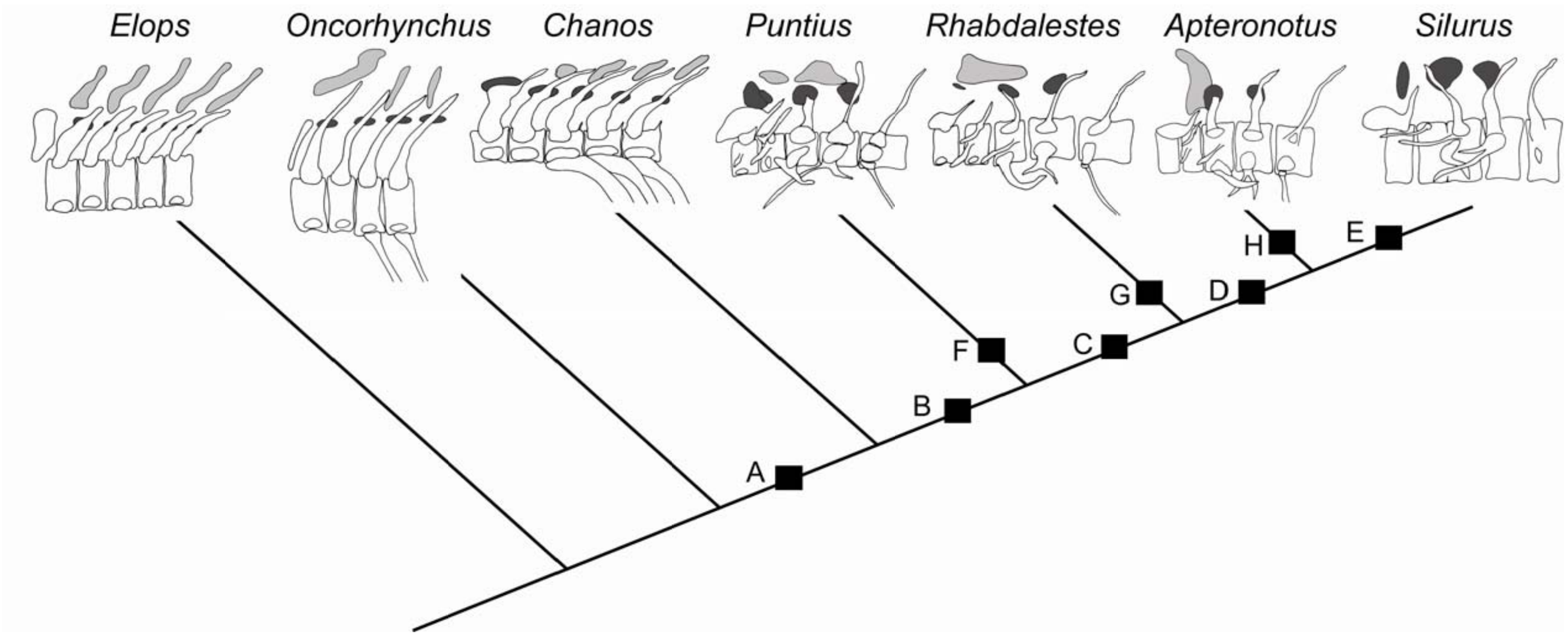

Fig. 115

Schematic representation summarizing my hypotheses of the differences in the composition of the neural complex in otophysan subgroups and the homology of the claustrum, based on the more generalized state of supradorsal and supraneural elements in non-otophysan, basal teleosts. The evolutionary steps are shown as rectangles, with the associated letters refering to the following syn- and autapomorphies. Supraneurals marked in light grey, supradorsals and claustrum in darker grey:

A) loss of supraneural 1.

B) loss of supradorsal 2 and all supradorsals posterior to vertebra 4, neural complex formed by fusion of supradorsals 3 and 4 with supraneurals 2 and 3. Claustrum preformed in cartilage.

C) loss of supraneural 2, neural complex formed by fusion of anteriorly shifted supraneural 3 with supradorsals 3 and 4.

D) supradorsals 3 and 4 develop a cartilaginous bridge with each other that fuses with supraneural 3 to form the neural complex.

E) loss of supraneural 3; note that this element is still present in *Diplomystes*, some ictalurids, pimelodids, and schilbids.

F) claustrum with membrane bone lamina and associated with the medial wall of the sinus impar.

G) loss of cartilaginous prcursor of the claustrum.

H) loss of claustrum

Curriculum vitae

Persönliche Daten

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Schulbildung

09/78 - 05/88	Albert-Einstein-Gymnasium Reutlingen, Abschluss Abitur.

Ersatzdienst

11/88 - 06/90	KBF, Mobile soziale Hilfsdienste der Region Neckar Alb, Mössingen.

Studium und Berufsausbildung

03/90 - 01/98	Lehramtsstudium an der Eberhard-Karls-Universität Tübingen mit den Fachrichtungen Biologie und Sportwissenschaften. Anfertigung der Wissenschaftlichen Arbeit für das Lehramt an Gymnasien mit dem Titel: „Funktionsmorphologische Untersuchung am Ingestionsapparat von Flösselhechten (*Cladistia*; *Polypteridae*), unter besonderer Berücksichtigung der Labialstrukturen.“ Abschluss des Studiums am 07.01. 98 mit der 1. Staatsprüfung für die Laufbahn des höheren Schuldienstes an Gymnasien (Gesamtnote 2,0).
08/94 – 06/95 08/98 – 08/00	Erziehungsurlaub
09/00 – 07/02	Vorbereitungsdienst für die Laufbahn des höheren Schuldienstes an Gymnasien am Staatlichen Seminar für Schulpädagogik Tübingen. Abschluss des Vorbereitungsdienstes am 24.07. 2002 mit der 2. Staatsprüfung für die Laufbahn des höheren Schuldienstes an Gymnasium. Gesamtnote, *mit Auszeichnung bestanden* (1,1).
09/03	Ernennung zum Studienrat
02/04	Verleihung der Eigenschaft eines Beamten auf Lebenszeit.

Promotion

1998 - 2006	Externe Promotionsarbeit am Lehrstuhl für Spezielle Zoologie, Tübingen, betreut durch Prof. Dr. W. Maier, mit dem Titel „Ontogeny and homology of the neural complex and the claustrum of otophysan Ostariophysi (Actinopterygii: Teleostei)

Berufliche Tätigkeit

09/02	Lehrer für Biologie und Sport am Gymnasium im Schulzentrum Längenfeld, Balingen.