



The accessory neural arch: development, morphology, and systematic distribution

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Abstract

The accessory neural arch is an oddly distributed character present in several non-acanthomorph teleostean taxa. Its homology was often implied but never satisfyingly tested. In this study, we attended this pending problem. We analyzed the morphology, development, and systematic distribution of the accessory neural arch in teleosts. Using a comprehensive taxon sampling of cleared and stained specimens, we evaluated if the accessory neural arch fulfils existing homology criteria. We then combined these data with recent genetic phylogenies and ancestral character state estimation to reconstruct the evolutionary history of the accessory neural arch. While its gross morphology and development fit homology criteria, results from ancestral character state estimations suggest multiple independent evolutions within teleosts. Although the accessory neural arch cannot be homologous between several teleostean taxa, the concept of parallelism may explain the presence of such a similar character in a variety of non-acanthomorph teleostean taxa.

Keywords Parallelism · Taxic atavism · Vertebral column · Ancestral character state estimation · Neurocranial vertebrae fusion

Introduction

The accessory neural arch (ANA) is a paired, endochondral ossified structure between the occiput and the neural arch of the first vertebra positioned in the third myoseptum (Brühl 1956; Forey 1973; Fink and Weitzman 1982; Bemis and Forey 2001; Britz and Johnson 2010; Johnson and Britz 2010). Principally it is very much like a regular neural arch in its shape but has no affiliation with a vertebral centrum. Furthermore, it develops much similar as neural arches from a paired cartilaginous precursor (de Pinna and Grande 2003). This has provoked various ideas of vertebrae being ontogenetically fused into the occiput, leaving a ‘free’ neural arch (e.g., Forey 1973; Bemis and Forey 2001). Subsequent

ontogenetic studies, however, could not confirm these hypotheses as neurocranial-vertebrae-fusions do not appear in taxa with ANA (Johnson et al. 2009; Britz and Johnson 2010; Johnson and Britz 2010). In several studies, the ANA was mentioned and described for non-acanthomorph teleosts (Fink and Fink 1981; Rosen 1985). The presence of an ANA in Otophysi was especially critically discussed, because of their modified anterior vertebral column, i.e., the presence of the Weberian apparatus (de Pinna and Grande 2003; Grande and de Pinna 2004; Britz and Hoffmann 2006). Patterson and Johnson (1995) and Johnson and Patterson (1996) summarized the distribution of the ANA in euteleosts (sensu Johnson and Patterson 1996). The remarkable distribution of the ANA puzzled many systematists, who investigated the homology of this structure. In phylogenetic hypotheses, frequent reductions (if homologues) or numerous independent origins (if convergent) had to be assumed (Patterson and Johnson 1995; Johnson and Patterson 1996). A call for a more robust cladogram of teleosts and a more extensive survey of the ANA has, therefore, been formulated more than 25 years ago (Patterson and Johnson 1995).

In recent years, more and more robust cladograms for teleosts have become available based on extensive phylogenomic studies (e.g., Betancur et al. 2013, 2017; Near et al.

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2013; Hughes et al. 2018; Straube et al. 2018). Therefore, analyzing the homology of the ANA becomes a task again. To determine if a character such as the ANA is homologous, the ANA must first be re-evaluated in light of homology criteria as formulated by Remane (1952), i.e., sameness in position, development, and composition. These criteria are needed to ascertain that characters that are compared are actually the ‘same’. Afterwards the homology can be tested based on the continuous presence from extant taxa back to a common ancestor (e.g., Patterson 1982, 1988; Wagner 1989; de Pinna 1991; Rieppel 1992; Brower and Schawaroch 1996; Brigandt 2003; DiFrisco 2021).

While de Pinna (1991) suggested to test the continuous presence of a character by constructing phylogenies using the observed character and letting the most parsimonious phylogeny indicate if the criterion of continuity is fulfilled, mapping character distributions on already present phylogenies and performing ancestral character state estimations (ACE) were applied in recent years (e.g., Davis et al. 2016; Herrel et al. 2016; Zattara and Bely 2016; Sauquet et al. 2017). This procedure was partly met with criticism as the examined character has no influence on the respective phylogenies (e.g., Smith et al. 2005; Assis and Rieppel 2011; Assis and Santos 2014; Assis 2015). However, the independence of phylogeny and character is also a strength of this method.

In this study, we now combine recent phylogenies with a comprehensive survey on the distribution, development and morphology of ANAs in teleosts as well as an ancestral character state estimation to investigate the homology of this puzzling structure.

Material and methods

For examination of accessory neural arches, specimens from the ichthyological collection of the Deutsches Meeresmuseum have been used. The specimens were cleared and double-stained (cartilage in blue and bone in red) following the protocols of Dingerkus and Uhler (1977) and Taylor and Van Dyke (1985). In total 418 specimens of 117 species and 59 families were studied (listed in Supplement 1), including ontogenetic material from six species [*Clupea harengus* Linnaeus 1758, *Coregonus maraena* (Bloch 1779), *Esox lucius* Linnaeus 1758, *Kneria stappersii* Boulenger 1915, *Osmerus eperlanus* Linnaeus 1758, and *Thymallus thymallus* (Linnaeus 1758)]. Pictures were taken with a Canon EOS 80D camera system with a Canon MP-E 65 mm objective.

Character mapping as well as ancestral character state estimations were carried out in R using the packages APE (package version: 5.4-1) (Paradis et al. 2004), Phytools (package version: 0.7-70) (Revell 2012), and Parallel (package version: 4.0.4) (R Core Team 2021). The discrete

character states were obtained from the material mentioned above as well as from literature (Weitzman 1974; Rosen 1985; Patterson and Johnson 1995; Baldwin and Johnson 1996; Fink and Fink 1996; Forey et al. 1996; Johnson and Patterson 1996; Grande and Bemis 1998; Sanford 2000; Harold 2002; Hilton 2002, 2003; Sato and Nakabo 2002; de Pinna and Grande 2003; Grande and de Pinna 2004; Britz and Johnson 2010; Grande 2010; Schnell et al. 2010; McDowall and BurrIDGE 2011; Kanehira et al. 2012; listed in Supplement 2) and afterwards were mapped on the phylogenetic tree provided by Betancur et al. (2017). Non-teleost actinopterygian taxa were chosen as outgroups and reduced to their last common ancestor, i.e., Polypteriformes, Acipenseriformes, *Amia*, and Lepisosteiformes, respectively. Similarly, Myctophiformes and Acanthomorpha in which no accessory neural arch is present were reduced to their last common ancestor. Also, otophysan taxa were reduced to their last common ancestor respectively, i.e., Cypriniformes, Characiformes, Gymnotiformes, and Siluriformes, because the presence or absence of an ANA in these taxa is heavily disputed and it is not possible to document an ANA in adult specimen. However, due to the undisclosed state of the presence of an ANA in Otophysi, we tested two hypotheses: (1) the presence of the ANA in Otophysi based on the assumption that the claustrum of the Weberian apparatus is homologues to the ANA (Grande and de Pinna 2004), and (2) the absence of an ANA in Otophysi (Britz and Hoffmann 2006). For the ancestral character state estimation, different models (character state change on either equal rates or different rates and calculated model parameters, i.e., root probabilities [pi] and transition matrix [Q]) were first calculated for the underlying data using the *fitMK*-function provided by phytools (Revell 2012). Then the Akaike information criterion of all models were compared by calculating the Akaike weights (using the function *aic.w* in phytools), which represent the relative likelihood of a model, to find the most-fitting model. Afterwards ancestral character states were calculated based on 2000 simulated stochastic character maps using the *make.simap*- and *describe.simap*-functions in phytools.

Results

Systematic distribution of the ANA

The accessory neural arch is present in many species of several non-acanthomorph teleost taxa, i.e., Elopidae, Clupeoidei, Alepocephaliformes, some Galaxiidae, Esocidae, Salmoniformes, most Osmeriformes, Gonostomatidae, and some Aulopiformes (Fig. 1). Of the Elopomorpha, the earliest branching taxon within the Teleostei, only in a single genus, *Elops*, an ANA is present (Figs. 1, 2a). Its sister taxon, *Megalops*, does not show any traces of an ANA,

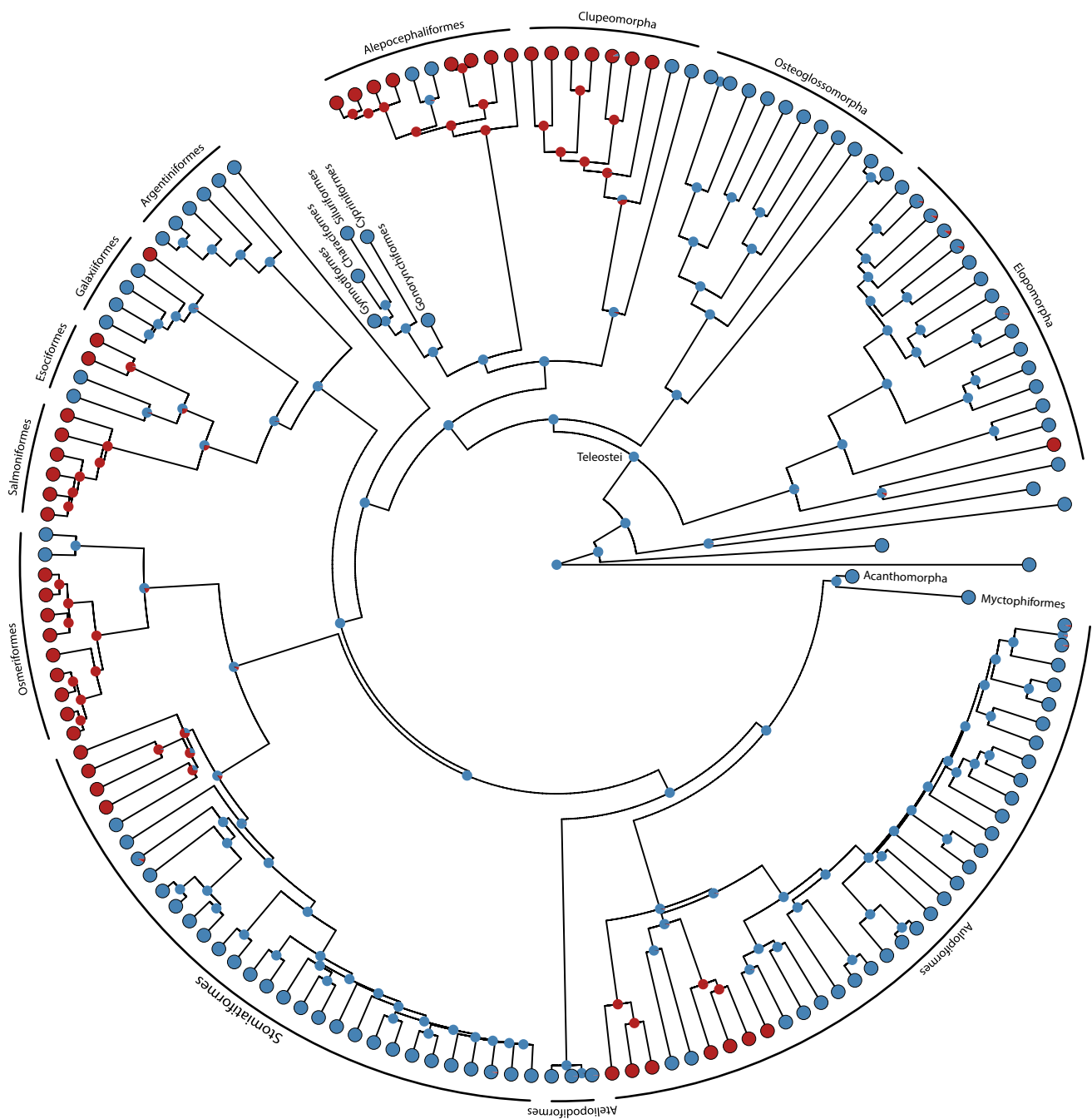


Fig. 1 Phylogenetic relationships of non-acanthomorph actinopterygian fishes based on Betancur et al. (2017) with the mapped absence (blue) and presence (red) of the accessory neural arch. The absence of

the ANA in Otophysi is hypothesized (Britz and Hoffmann 2006) and the estimated likelihoods of absence and presence are plotted for each node, which are based on Model 1 (Table 2)

which is the same for all other investigated elopomorphs. None of the examined Osteoglossomorpha have an accessory neural arch either. Within the Otophysi, which comprise Clupeiformes, Alepocephaliformes, Gonorynchiformes, and the Otophysi, a distinct ANA was observed in two taxa, i.e., Clupeoidei (Fig. 2b, c) and Alepocephaliformes (Fig. 2d, e). While the earliest branching clupeiform,

Denticeps clupeoides, does not have an ANA, it is present in all examined families within its sister taxon, Clupeoidei. Only in few examined clupeid species, i.e., *Hyperlophus vittatus*, *Laeviscutella dekimpei*, and *Pellonula leonensis*, no ANA was observed. In *Clupeichthys aesarnensis*, we observed an unpaired, ossified structure anterior to the first neural arch that could be the remnants of an accessory neural

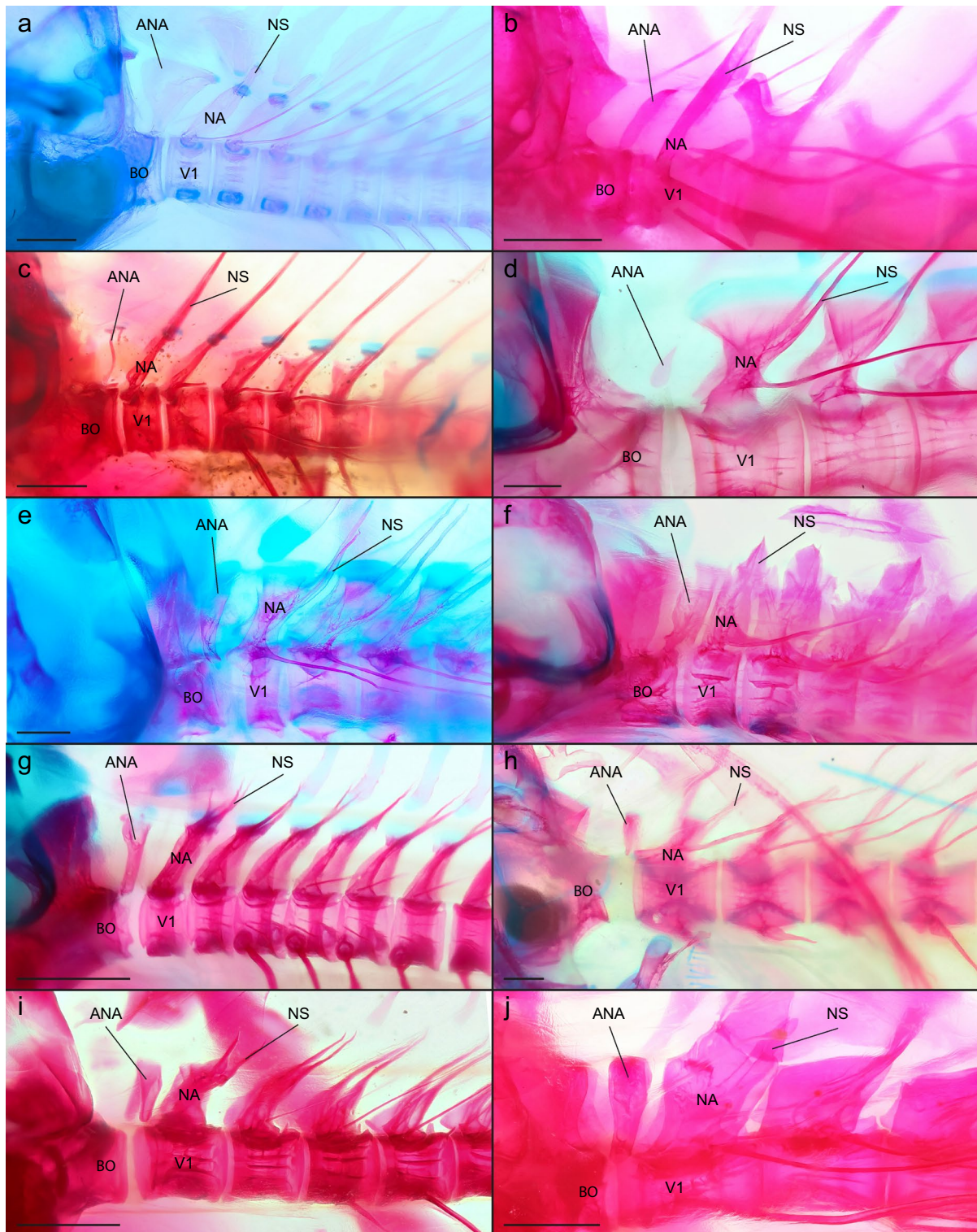


Fig. 2 Lateral view of occipital–vertebral region of cleared and stained specimen of **a** *Elops senegalensis* (DMM IE/11008, SL=59.1 mm); **b** *Anchoviella cayennensis* (DMM IE/14935, SL=64.5 mm); **c** *Clupea harengus* (DMM IE/12064, SL=62.2); **d** *Alepocephalus bicolor* (DMM IE/13719, SL=110.0 mm); **e** *Normichthys operosus* (DMM IE/13808, SL=67.0 mm);

f *Esox lucius* (DMM IE/14327, SL=46.0 mm); **g** *Coregonus maraena* (DMM IE/13723, SL=37.0 mm); **h** *Triplophos hemingi* (DMM IE/12621, SL=165.0 mm); **i** *Osmerus eperlanus* (DMM IE/11742, SL=48.8 mm); **j** *Saurida gracilis* (DMM IE/14949, SL=67.5 mm). ANA accessory neural arch, BO basioccipital, NA neural arch, NS neural spine, V1 first vertebral centrum. Scale bar = 1 mm

arch. Within the Alepocephaliformes, we observed an ANA in Alepocephalidae and Platytroctidae, and only few genera do not exhibit an accessory neural arch, i.e., *Maulisia*, and *Xenodermichthys*. In some specimens of *Alepocephalus bicolor*, we only found one half of the ANA, either the right or the left one (e.g., *A. bicolor* DMM IE/13719, SL = 106.1 mm; Fig. 2d). Within the Gonorynchiformes, no ANA was detected. However, some larvae of *Kneria stappersii* showed a structure similar to an ANA (see below).

Within the Euteleostei, no accessory neural arch is found in the earliest branching taxon, i.e., *Lepidogalaxias*. In the Protacanthopterygii (sensu Betancur et al. 2017), we found no ANA in the galaxiiform genus *Galaxias*, while an ANA is present in the family Esocidae (Fig. 2f) within the Esociformes, and all examined Salmoniformes (Fig. 2g). Within the Stomiati, only the earliest branching taxon of the Stomiatiiformes, i.e., Gonostomatidae (Fig. 2h), and the Osmeriformes (Fig. 2i), except their earliest branching taxon, i.e., Retropinnidae, exhibit an accessory neural arch. None of the examined Ateleopodiformes have an ANA. Within the Aulopiformes, we found an ANA only in three of the examined families, i.e., Aulopidae, Scopelarchidae, and Synodontidae (Fig. 2j). In none of the investigated Myctophiformes and Acanthomorpha an accessory neural arch was observed.

Morphology of the ANA

In general, the accessory neural arch has a similar morphology like the first neural arch. It consists of two ossified halves which together form an arch and that are positioned dorsal to the occipital condyle of the basioccipital or dorsal to the unossified gap between basioccipital and the first vertebra. While only in few taxa the shape of the ANA differs significantly from the respective first neural arch, the shapes of the ANA can significantly vary between taxa.

In *Elops senegalensis*, the accessory neural arch is larger than the neural arches, because its dorsal portion is extended antero-posteriorly (Fig. 2a). We did not witness a similar ANA in any other taxon. In clupeoids the shape of the ANA is much like the shape of the first neural arch. In general, the ANA in clupeoids can be described as rectangular or trapezoid with a smaller proximal and a broader distal portion (Fig. 2b). Depending on the size of the first neural arch, the ANA may be larger or smaller. In Clupeidae, the accessory neural arch is rather narrow and more elongated, which can be summarized as rod-like, than in other clupeoid families (Fig. 2c). In alepocephaliforms two shapes of the ANA can be distinguished: In *Searsia* and *Alepocephalus* the accessory neural arch is drop-shaped and much smaller than the first neural arch (Fig. 2d), while in *Normichthys* and *Holtbyrnia* the ANA is much like the first neural arch in shape (trapezoid) and size (Fig. 2e).

The ANA of *Esox* principally equals the first neural arch (Fig. 2f). Like in *Esox*, the accessory neural arch in salmoniforms does resemble the first neural arch, although it is generally broader dorsally. The ANA of *Coregonus* is narrower than the first neural arch (Fig. 2g). Within the Stomiatiiformes, the accessory neural arch of the Gonostomatidae is narrow and trapezoid (Fig. 2h). In osmeriforms, the shape of the ANA varies between the two families Osmeridae and Salangidae. In osmerids the ANA is rectangular, which is very similar to their first neural arch (Fig. 2i), while in salangids it is short and stout, which, again, is very similar to their first neural arch. The shape of the ANA in aulopiforms in general is almost rectangular, but much narrower than the first neural arch (Fig. 2j).

Development of the ANA

There is a high resemblance in the development of the accessory neural arch in the different taxa. In the studied species of clupeoids (*Clupea harengus*), esocids (*Esox lucius*), salmoniforms (*Coregonus maraena*, *Thymallus thymallus*), and osmerids (*Osmerus eperlanus*) the ANA has a cartilaginous precursor that develops later than the anterior neural arches (Fig. 3a–i). Both, the left and right half, are of the same size when they first emerge. While they are very narrow in *Clupea* (Fig. 3a–c), they are stouter in *Osmerus*. In *Coregonus* and *Thymallus* both halves are very small and of a more plate-like shape. In some of the larval specimens of *Coregonus* we observed only one half of the ANA. While in clupeoids the development timing of the ANA is postponed compared to the neural arches, the ANA develops at the same time as the following neural arches in *Esox* and *Thymallus* (Fig. 3d–i).

In few larval specimens of *Kneria stappersii*, we witnessed an ossified neural arch above the posterior protrusion of the basioccipital (Fig. 3j). It resembles much the first neural arch in its shape and in terms of the developmental progress, however, does not attach to a vertebral centrum and, therefore, meets the criteria of an ANA. In other examined specimens of *Kneria stappersii*, the two anterior-most neural arches differ in shape from the following neural arches (Fig. 3k). In specimen with the presumable ANA, only one of these two neural arches is present, though, the presumable ANA resembles the ‘missing’ neural arch (Fig. 3k, l). Furthermore, the first vertebral centrum in *Kneria stappersii* has a heterocoelous articulation with the occipital condyle, while all vertebral centra articulate amphicoelously. In the specimens with a presumable ANA, the first vertebral centrum and the occipital condyle share an amphicoelous articulation. It seems like in these specimens the true first vertebral centrum is fused to the basioccipital. As a result of this malformation the first neural arch may be perceived as ANA.

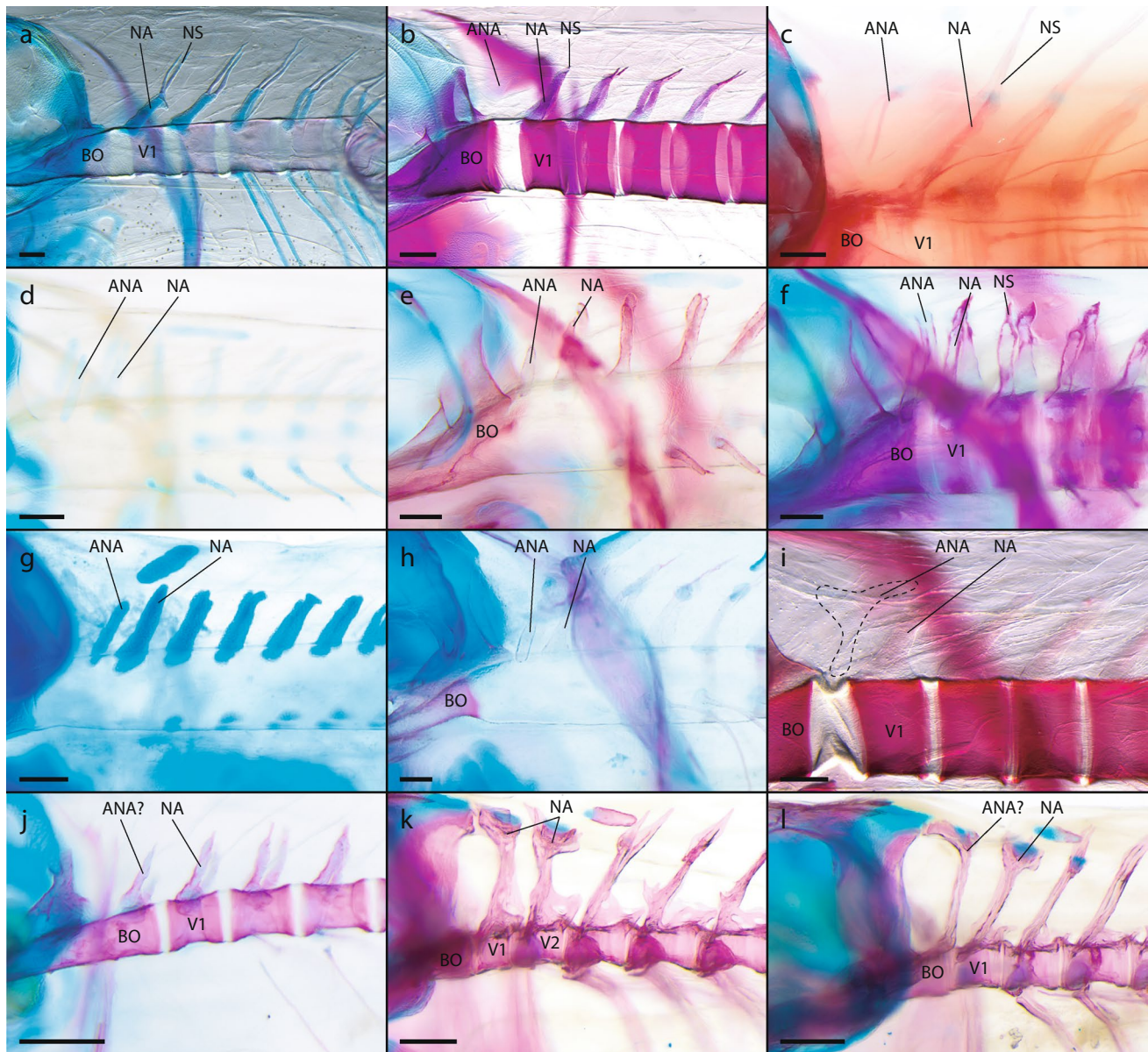


Fig. 3 Cleared and stained ontogenetic stages showing the development of the accessory neural arch in (a–c) the clupeid *Clupea harengus* (a DMM IE/11793, SL=28.5 mm; b DMM IE/13447, SL=22.5; c DMM IE/12076, SL=28.2 mm), d–f the esocid *Esox lucius* (d DMM IE/11789; SL=17.7 mm, e DMM IE/11789, SL=20.8 mm; f DMM IE/15718, SL=24.5 mm), g–h the salmonid *Thymallus thymallus* (DMM IE/11786, g SL=15.5 mm; h SL=26.4 mm), and i

the osmerids *Osmerus eperlanus* (DMM IE/13826, SL=23.2 mm). Ontogenetic stages of *Kneria stappersii* (DMM IE/16879, j SL=8.5 mm; k SL=13.2 mm; l SL=15.7 mm) show individuals with vertebrae 1 fused to the basioccipital (j–k) and without such a fusion (l). ANA accessory neural arch, BO basioccipital, NA neural arch, NS neural spine, V1 first vertebral centrum, V2 second vertebral centrum. Scale bar=200 μ m

Ancestral character state estimation

The evolution of the ANA was analyzed based on two different hypotheses: (1) presence of an ANA in otophysan taxa, and (2) absence of the ANA in otophysan taxa. In the following, we describe the three models with the highest AIC-weights in comparison to each other for both hypotheses in descending order (Tables 1, 2). For hypothesis (1)

the following models were retrieved: Model 1 (Table 1), the most-preferable model (AIC weight = 0.292), suggested the evolution of the ANA in a common ancestor to all actinopterygians and subsequent reductions in non-teleost actinopterygians as well as multiple reductions within teleosts (Fig. 4a). Results from model 2 (Table 1, AIC weight = 0.204) are ambiguous as estimated node probabilities for presence and absence are often equal.

Table 1 Calculated parameters of the three models used for the estimation of the ancestral character states under the assumption of the presence of the ANA in Otophysi

	Pi-Values		Transition matrix			Log-lik	AIC-value	AIC-weight
Model 1	0	1		0	1	-58.996	121.99	0.292
	0.5	0.5	0	-0.0004	0.0004			
			1	0.0056	-0.0056			
Model 2	0	1		0	1	-60.355	122.71	0.204
	0.96	0.04	0	-0.0016	0.0016			
			1	0.0016	-0.0016			
Model 3	0	1		0	1	-59.629	123.26	0.155
	0.93	0.07	0	-0.0008	0.0008			
			1	0.0052	-0.0052			

PI-values describe prior distribution of state 0 (absent) and 1 (present) on the root of the tree; Transition matrix describes under which rates a transition from state 0 to 1 and vice versa occur; Log-lik, the log-likelihood of the transition matrix; AIC-value, Akaike information criterion value calculated for each model; AIC weight, calculated Akaike information criterion weights as proportion of the total amount of predictive power of the compared models (only selection of models shown)

Table 2 Calculated parameters of the three models used for the estimation of the ancestral character states under the assumption of the absence of the ANA in Otophysi

	Pi-Values		Transition matrix			Log-lik	AIC-value	AIC-weight
Model 1	0	1		0	1	-57.389	116.78	0.284
	0.97	0.03	0	-0.0014	0.0014			
			1	0.0014	-0.0014			
Model 2	0	1		0	1	-56.891	117.78	0.172
	0.91	0.09	0	-0.0013	0.0013			
			1	0.0028	-0.0028			
Model 3	0	1		0	1	-58.026	118.05	0.150
	0.5	0.5	0	-0.0013	0.0013			
			1	0.0030	-0.0030			

PI-values describe prior distribution of state 0 (absent) and 1 (present) on the root of the tree; Transition matrix describes under which rates a transition from state 0 to 1 and vice versa occur; Log-lik, the log-likelihood of the transition matrix; AIC-value, Akaike information criterion value calculated for each model; AIC weight, calculated Akaike information criterion weights as proportion of the total amount of predictive power of the compared models (only selection of models shown)

However, the ANA under this model evolved multiple (at least nine) times anew (Fig. 4b). Model 3 (Table 1), the least preferred of the herein described models (AIC weight = 0.155) suggested the evolution of the ANA once in *Elops* and in a common ancestor to all Clupeocephala and with subsequent reductions in multiple taxa and a reversal in Aulopiforms (Fig. 4c).

Under the assumption that the ANA is absent in Otophysi, all three models shown in Table 2 resulted in very similar estimated ancestral character states (Fig. 1) The accessory neural arch evolved at least eleven times independently within the Teleostei independent of model properties (Fig. 1, Table 2): (1) within the Elopomorpha in the genus *Elops*; (2) in the Clupeoidei, where it was reduced

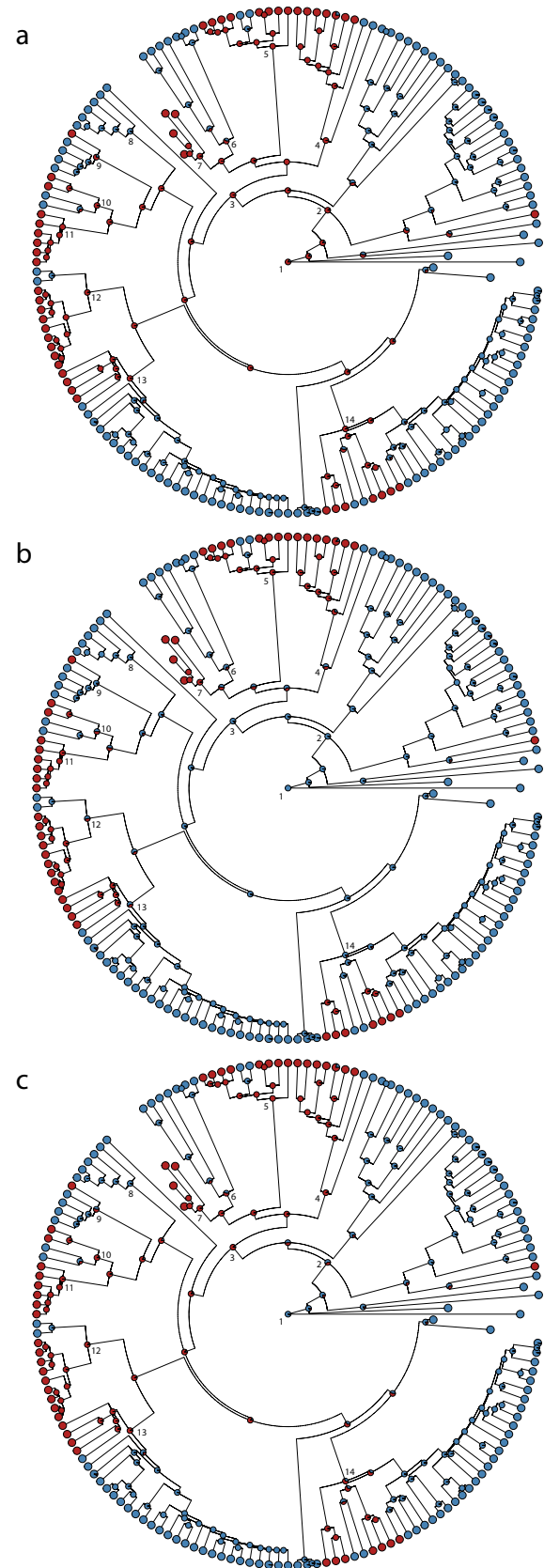
Fig. 4 Phylogenetic relationships of non-acanthomorph actinopterygian fishes based on Betancur et al. (2017) with the mapped absence (blue) and presence (red) of the accessory neural arch. The presence of the ANA in Otophysi is hypothesized (Grande and de Pinna 2004) and the estimated likelihoods of absence and presence are plotted for each node for three different models (a–c) described in Table 1. Numbers indicate taxa: 1, Actinopterygii; 2, Teleostei; 3, Clupeocephala; 4, Clupeiformes; 5, Alepocephaliformes; 6, Gonorynchiformes; 7, Otophysi; 8, Argentiniiformes; 9, Galaxiiformes; 10, Esociformes; 11, Salmoniformes; 12, Osmeriformes; 13, Stomiatiiformes; 14, Aulopiformes

few times afterwards; (3) at the base of the Alepocephaliformes, where it seemingly was reduced once within the family Alepocephalidae; (4) within the Galaxiiformes in the genus *Aplochiton*; (5) within the Esociformes in the genus *Esox*; (6) at the base of the Salmoniformes; (7) in the Osmeriformes at the base of the Osmeroidei, comprising Osmeridae, Plecoglossidae and Salangidae; (8) within the Stomiatiiformes at the base of the Gonostomatidae; (9–11) three times within the Aulopiformes including twice in the paraphyletic Synodontidae (sensu Betancur et al. 2017) and once in the Aulopidae.

Discussion

Systematic distribution

In non-teleost actinopterygians, i.e., Polypteriformes, Acipenseriformes, and Holostei, no accessory neural arch is present (Grande and Bemis 1998; Britz and Johnson 2010; Grande 2010), however, it is widely distributed within non-acanthomorph teleosts (Fig. 1, Suppl. 1–2). Within the two earliest branching teleostean taxa, Elopomorpha and Osteoglossomorpha, the ANA can only be found in one genus, i.e., *Elops* (Patterson and Johnson 1995; Forey et al. 1996; Johnson and Patterson 1996; Hilton 2002, 2003; Kanehira et al. 2012). Bemis and Forey (2001) hypothesized that the ANA in *Elops* is the remnant of a vertebra which is fused into the occiput. However, subsequent studies showed the neurocranial-vertebrae-fusion does not occur in taxa with an ANA (Britz and Johnson 2010). In Otomorpha, the ANA is more common and is present in Clupeiformes and Alepocephaliformes. Within the Clupeiformes, the earliest branching taxon, *Denticeps clupeoides*, has no ANA. Otherwise the ANA is present in all clupeoid family (Patterson and Johnson 1995; Johnson and Patterson 1996), and only absent in few genera, i.e., *Jenkinsia*, *Hyperlophus*, *Laeviscutella*, and *Pellonula* (Patterson and Johnson 1995; de Pinna and Grande 2003). While we found a possible remnant of an ANA in *Clupeichthys*, Patterson and Johnson (1995) reported no ANA for this genus. In Alepocephaliformes, the ANA is present in species of all three families (Johnson



and Patterson 1996). However, several species and genera miss the ANA in the families Alepocephalidae, i.e., *Bajacalifornia burragei*, *Leptochilichthys agassizi*, *Leptoderma macrops*, *Photostylus*, *Rinoctes*, *Rouleina*, and *Xenodermichthys*, and Platytroctidae, i.e., *Maulisia* (Johnson and Patterson 1996). No ANA was found or reported for any gonorynchiform species (Patterson and Johnson 1995). De Pinna and Grande (2003), Grande and Young (2004), and Grande and de Pinna (2004) hypothesized that in Otophysi, the claustrum of the Weberian apparatus is homologous to the ANA, based on developmental data, i.e., their arch-like structure, topographical relationships, derivation from paired cartilages, and delayed formation relative to neural arches. Other extensive studies on the morphology and development of the Weberian apparatus in Otophysi, however, led to different hypotheses about the homology of the claustrum (e.g., Fink and Fink 1981, 1996; Coburn and Futey 1996; Bird and Mabee 2003; Grande and Young 2004; Britz and Hoffmann 2006; Hoffmann and Britz 2006; Bird and Hernandez 2007). This topic is still highly disputed, and no consensus has been reached yet (see Britz and Hoffmann 2006 for discussion). In Euteleostei, an ANA can only be found in Galaxiiformes, Salmoniformes, Esociformes, Stomiatiiformes, Osmeriformes, and Aulopiformes (Weitzman 1974; Patterson and Johnson 1995; Baldwin and Johnson 1996; Johnson and Patterson 1996; Sanford 2000; Harold 2002; Sato and Nakabo 2002; Schnell et al. 2010; McDowall and Burrige 2011). For Galaxiiformes, the ANA is only reported for the genus *Aplochiton* (Johnson and Patterson 1996; McDowall and Burrige 2011), just like the ANA is only present in one genus of the Esociformes, i.e., *Esox* (Patterson and Johnson 1995; Johnson and Patterson 1996). In contrast, an ANA is present in all Salmoniformes (Johnson and Patterson 1996; Sanford 2000). A drawing from Johnson and Patterson (1996) of *Oncorhynchus clarkii* does not depict an ANA, however, Sanford (2000), who also examined *O. clarkii*, did not mention the absence of the ANA in this species. In Osmeriformes, only the Retropinnidae are lacking an ANA (Patterson and Johnson 1995; Johnson and Patterson 1996). While in the Stomiatiiformes an accessory neural arch is only present in one family, the Gonostomatiidae (Weitzman 1974; Patterson and Johnson 1995; Harold 2002; Schnell et al. 2010). Within the Aulopiformes an ANA is present in Aulopidae, Scopelarchidae, and Synodontidae (Patterson and Johnson 1995; Baldwin and Johnson 1996; Sato and Nakabo 2002). However, *Rosenblattichthys* seemingly is the only scopelarchid genus in which an accessory neural arch is found (Baldwin and Johnson 1996).

Morphology and development

The shape of the accessory neural arch varies greatly between some taxa. Yet, within each species, the ANA is

usually very similar to the anterior-most neural arch. It seems likely that the ANA is a serial-homologue to neural arches, therefore, it is to be expected that its shape changes similar to the neural arches. Only few taxa show differences in shape between these two structures. For example, in *Elops* the ANA is dorsally broadened, however, a resemblance to the first neural arch is visible and the ANA could also be described as an anteriorly extended neural arch. The biggest difference may be found in some Alepocephaliformes. While the first neural arch in alepocephaliforms is generally trapezoid, the ANA of *Alepocephalus* and *Searsia* are drop-shaped and much smaller. In the salmoniform *Coregonus* the ANA is much narrower than the first neural arch. Johnson and Patterson (1996: pp 278) reported that the accessory neural arch of the osmerid *Spirinchus* is reduced to a “minute nubbin”. In gonostomatids the ANA is trapezoid and smaller than the first neural arch which is rather rectangular and angled posteriorly (Harold 2002). Also, in aulopiforms the shape of the ANA differs from that of the first neural arch as it is narrower.

The development of the accessory neural arch in the herein examined species *Clupea harengus*, *Coregonus maraena*, *Osmerus eperlanus*, and *Thymallus thymallus* matches previous reports for ANA formation in *Pellona harroweri* and *Alosa sapidissima* (de Pinna and Grande 2003). In these species, the ANA forms as paired cartilages anterior to the neural arch of vertebra 1 and later ossifies. Both, cartilage formation and ossification, are delayed in relation to the anterior neural arches. Only in *Esox* we observed a more or less simultaneous formation of the ANA and anterior neural arches. De Pinna and Grande (2003) reported that the delay is less pronounced in *Esox* and *Coregonus*. We on the other hand found the timing of formation to be very different between these two genera. Coburn and Chai (2003) reported the presence of rudiments of an ANA during a brief period in ontogeny in the gonorynchiform *Chanos chanos*. In the gonorynchiform *Kneria stappersii* we found a similar structure like the ANA in few larval specimens. However, this seems to be the result of a malformation during which the first vertebral centrum fuses to the occiput in some specimen and the ‘true’ first neural arch develops dorsally to the occipital condyle.

Evolution and homology

In previous studies, it was assumed that the accessory neural arch is the same structure in the examined species, although no clear homology assumptions were given (Fink and Fink 1981; Rosen 1985; Patterson and Johnson 1995). Johnson and Patterson (1996: pp 278) were “convinced that ANA was primitively present in that group [Euteleostei] and has been repeatedly lost”. The similar composition, development, and position of the accessory neural arch, fulfil all

criteria formulated by Remane (1952) to determine homologous structures. Analyzing the presence and absence of the accessory neural arch based on the phylogeny in Betancur et al. (2017), resulted in different outcomes depending on the presence of the ANA or a homologous structure in Otophysi. Even considering the claustrum in Otophysi is homologous to the ANA, only one tested model (model 3), which of the herein described models is the least preferable, provided a reasonable estimation in which the accessory neural arch is homologous within the Clupeocephala (Fig. 4c). Model 1, which is the most preferable and that suggests the evolution of the ANA in a common ancestor to all actinopterygians, can be neglected as no extant non-teleost actinopterygian taxon has an ANA (Grande and Bemis 1998; Britz and Johnson 2010; Grande 2010) and fossil data give no indication of an ANA in stem actinopterygians (Bemis and Forey 2001). Model 2 provides concluding estimations only for some nodes while others are ambiguous between absence and presence of the ANA. However, it needs to be assumed that under this model the ANA is not homologous for a larger set of taxa. Accepting the absence of the accessory neural arch or a homologous structure in Otophysi, the ancestral character state estimation showed multiple independent origins of the ANA within non-acanthomorph teleosts rather than a single evolutionary event and the continuous presence in teleosts independent of the applied model (Fig. 1). Because of the dubiousness of homology between the ANA and the claustrum in Otophysi as well as the dependence of a possible continuous presence of the ANA in Clupeocephala on a specific and not preferable model, we proceed on the assumption that the accessory neural arch is not generally homologous in Teleostei.

Other phylogenomic studies resulted in slightly different phylogenetic relationships for non-acanthomorph teleosts (e.g., Hughes et al. 2018; Straube et al. 2018) than retrieved in Betancur et al. (2017). Mainly the position of the Galaxiiformes varies and they were positioned as sister taxon to the Stomiati (Hughes et al. 2018) or as sister taxon to the Neoteleostei (Straube et al. 2018). Although we did not calculate ancestral character state estimations with these phylogenies, no different result due to the altered position of galaxiiforms is expected. Hence, several convergent evolutions of the ANA need to be assumed for all these phylogenies. However, such a scenario seems hard to comprehend because of the very similar morphology of the ANA as well as the matching development in these distantly related species. Especially, as no clear functional effect can be attributed to the ANA and an evolutionary advantage is questionable.

Homology itself as well as homology theories are still under lively discussion (e.g., Assis 2015; Hejnol and Lowe 2015; Richter 2017; Vogt 2017; DiFrisco 2021; DiFrisco and Jaeger 2021). Following a classical approach that

structures are homologous if the ancestor of recent taxa exhibiting this structure already possessed it too (Mayr 1982; Roth 1984; Wagner 1989; Brigandt 2003), the ANA cannot be considered homologous between all taxa exhibiting it (Fig. 2). However, different concepts discussed in the context of homologies and convergences may provide an explanation for the oddly distribution of the accessory neural arch within non-acanthomorph teleosts. Such a concept is “Atavism, or the re-expression of ancestral morphologies” (Stiassny 1992: pp 260). Like homology theories, the principles of atavism were discussed for decades (e.g., Raikow et al. 1979; Hall 1984, 2012; Stiassny 1992; Meyer 1999; Witten and Hall 2015). Atavisms can occur in different forms, such as individual or induced anomalies, or permanent characters manifested in the phenotype of a taxon, which Stiassny (1992) termed taxic atavism. Different examples for taxic atavisms were subsequently found in a variety of taxa (e.g., Gatesy et al. 2003; Huysseune et al. 2009; Grünbaum and Cloutier 2010; Zander 2010). Hall (1984) hypothesized that there is a genetic basis of atavistic characters because they can be selected for. Somewhat following this hypothesis of genetical based atavisms, Meyer (1999) proposed an evolutionary retention of genetic potentiality, which could lead to convergent morphologies due to re-awakening of retained genetical networks or pathways. Hall (2003) later distinguished between atavisms, which only occur infrequently or sporadically on an individual basis, and *parallelism*, which describes the appearance of homoplastic characters in more closely related taxa that, in contrast to convergencies, are using a similar (homologous) developmental pathway. The concept of parallelism, therefore, combines Meyers (1999) hypothesis of retained genetical pathways and Stiassnys (1992) taxic atavism. Hall (2003) referred to Gould (2002), who stated that parallelism is a “gray zone between homology and convergence” (Gould 2002: pp 1088), because parallel characters are not fully independent in their evolution (DiFrisco 2021).

The accessory neural arch may be an example of a parallel character. Its gross morphology is very similar in the taxa that exhibit this character and at least the phenotypic development is the same in the examined species. However, its discontinuous presence suggests multiple independent evolutions. Therefore, the accessory neural arch fits the concept of parallelism. Going forward, the underlying developmental pathways of ANA formation need to be studied and compared to confirm this hypothesis.

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Availability of data and material Supplement 1: List of all examined specimen with indication if an ANA is present or absent. Supplement 2: Data matrix used for the ancestral character state estimation with data sources.

Code availability Not applicable.

Declarations

Conflict of interest Not applicable.

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