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REVIEW

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Development of the dorsal and anal fin in *Kneria stappersii* (Otomorpha: Gonorynchiformes)

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Abstract

The order Gonorynchiformes was repeatedly studied to gain new insights into the evolution of its sister-taxon, the Otophysi, the most successful freshwater fish taxon worldwide. Previous ontogenetic studies of gonorynchiforms mainly focused on the anterior vertebral column to investigate the evolutionary origin of the Weberian apparatus. Herein, we highlight the ontogeny of a different skeletal complex, the dorsal and anal fins. We studied the development of the skeletal elements of both fins in the gonorynchiform *Kneria stappersii*. We gained new insights into the developmental and formation patterns of *K. stappersii*. We discuss these patterns as well as the development of certain elements like the fin stay in comparison to other gonorynchiforms and available otomorph data. In general, the fin development in *K. stappersii* is very similar to that of other gonorynchiforms and even otomorphs. Specific differences, however, reveal that much remains unknown about the evolution of median fin elements such as the fin stay.

KEYWORDS

fin stay, Kneriidae, ontogeny, Ostariophysi, Otophysi, pterygiophore

1 | INTRODUCTION

The Gonorynchiformes are a small order of fish comprising only 38 species (Fricke et al., 2022). However, within the last two decades, gonorynchiforms were studied extensively because of their phylogenetic position within otomorphs (e.g., Britz & Moritz, 2007; Coburn & Chai, 2003; Grande & Arratia, 2010). The Gonorynchiformes represents the sister taxon of the Otophysi, which are a very diverse group comprising two-thirds of the worldwide freshwater species (Betancur-R et al., 2017; Nakatani et al., 2011; Nelson et al., 2016; Rosen et al., 1970). While both taxa share multiple synapomorphies, for example, the absence of the supramaxilla as a separate ossification, the absence of supraneural 1, and the presence of the Schreckstoff system (Fink & Fink, 1981; Nelson et al., 2016; Rosen et al., 1970; Wiley & Johnson, 2010), some characterizing features evolved within the Otophysi, for example the Weberian apparatus, that are not present in the Gonorynchiformes. Therefore, a few developmental and comparative studies focused on the anterior vertebral column in gonorynchiforms to gain new insights into the origins of the Weberian apparatus of the Otophysi (Coburn & Chai, 2003; Rosen et al., 1970). Our understanding of the evolution of the Weberian apparatus profited from these studies, yet the evolution of other characters need the same amount of attention to learn more about the successful evolution of these taxa within Otomorpha in general as well as Gonorynchiformes and Otophysi. Studying the evolution of the median fins, that is, the dorsal and anal fins, will provide further data on the radiation of the Otophysi.

Most non-acanthomorph actinopterygians are characterised by the presence of one dorsal and one anal fin (Nelson et al., 2016). Exceptions are the Polypteriformes, which have a series of finlets, and some teleost taxa, such as Characiformes, Siluriformes, or Salmoniformes, that additionally have an adipose fin (Bender & Moritz, 2013; Stewart et al., 2014, 2019). While in Acipenseriformes each pterygiophore supports multiple fin rays, there is a one-to-one relation of pterygiophores and fin rays within Neopterygii (Grande, 2010; Grande & Bemis, 1998). Pterygiophores in Neopterygii principally consist of a proximal, a middle, and a distal radial (Grande, 2010; Grande & Bemis, 1998; Mabee et al., 2002). The proximal radial is usually the longest element while the distal radial is the smallest element being located at the base of the fin ray (Hilton, 2011). However, within Teleostei the number of radials per pterygiophore has been reduced many times, presumably either due to fusion of the proximal and middle radial or due to loss of either one of them. This issue has only gotten little attention and it remains unclear what led to the differences in the pterygiophore morphology in different teleostean taxa. Furthermore, posterior to the pterygiophores of the dorsal and anal fin there is another element present in many teleosts, the fin stay (see, e.g., Conway, 2011; Mattox & Conway, 2021). Bridge (1896) first described this element, which was later named "stay" or "end piece" by Weitzman (1962). Studies on the evolution and distribution of this structure are lacking for otomorphs and non-euteleosts. There is nothing known about its function and only few ontogenetic studies provide data on its development (e.g., Balart, 1995; Fischbach et al., 2022; Taki et al., 1986). In this study, we describe in detail the dorsal and anal fin development of the gonorynchiform species *Kneria stappersii*. We focus on the formation of the pterygiophores and fin rays as well as their formation patterns within the dorsal and anal fins. Further, we analyse the development of the fin stay. This data is discussed in comparison with the dorsal and anal fin development of other gonorynchiforms and available otomorphs in order to understand the general developmental patterns in otomorphs.

2 | MATERIAL AND METHODS

Specimens examined in this study were taken from the ichthyological collection of the Deutsches Meeresmuseum (Table 1). The individuals of *K. stappersii* used for the ontogenetic description are F2-descendants from wild-caught specimens, collected in the Kampatete River close to Kassapa in the Democratic Republic of the Congo (Table 1). The larvae were cleared and double stained using Alcian blue for cartilage and Alizarin red for bones principally following the protocols of Dingerkus and Uhler (1977) and Thieme et al. (2021). Larvae and adult specimens were photographed using a Canon EOS 80D with a Sigma DG Macro 105 mm (1:2.8) objective and a Leica M165 C stereomicroscope equipped with a dedicated Leica DFC425 lens using the software Leica Application Suite (Leica Microsystems, version: 4.9.0). The photographs were first processed in Adobe Photoshop CC (version: 22.0.5) in terms of tonal corrections, contrast and saturation, without altering any morphological structures within the image. Drawings are based on the photographs and were done in Adobe Illustrator CC (version: 25.2.3), which was also used to compile the plates. The standard length (SL) was measured with a sliding calliper in millimetres rounded to one decimal.

TABLE 1 Material of Gonorynchiformes used in the study; all deposited at the Deutsches Meeresmuseum, Stralsund, Germany

Species	Collection ID	Standard length (mm)
Kneria stappersii	DMM IE/16880 A–D	7.6–15.1
K. stappersii	DMM IE/16882 A–C	13.4–18.1
K. stappersii	DMM IE/16883 A–I	6.0–10.6
K. stappersii	DMM IE/16884 A–D	5.0–8.9
K. stappersii	DMM IE/12025	16.5–25.1
Kneria sp.	DMM IE/11079	41.5
Chanos chanos	DMM IE/14318	47.2
C. chanos	DMM IE/14319	63.4
C. chanos	DMM IE/11010	66.0
Gonorynchus abbreviatus	DMM IE/14345	81.5
G. abbreviatus	DMM IE/16935	78.2
Cromeria occidentalis	DMM IE/13442 L1–L10	18.8–23.5
Phractolaemus ansorgii	DMM IE/11045	49.0
P. ansorgii	DMM IE/14313	47.8
P. ansorgii	DMM IE/11062	72.1

3 | RESULTS

3.1 | 7.3 mm SL

A larval fin fold surrounds the trunk dorsally, caudally, and ventrally (Figure 1a). Dorsally it stretches along the posterior two thirds of the body and ventrally it is split

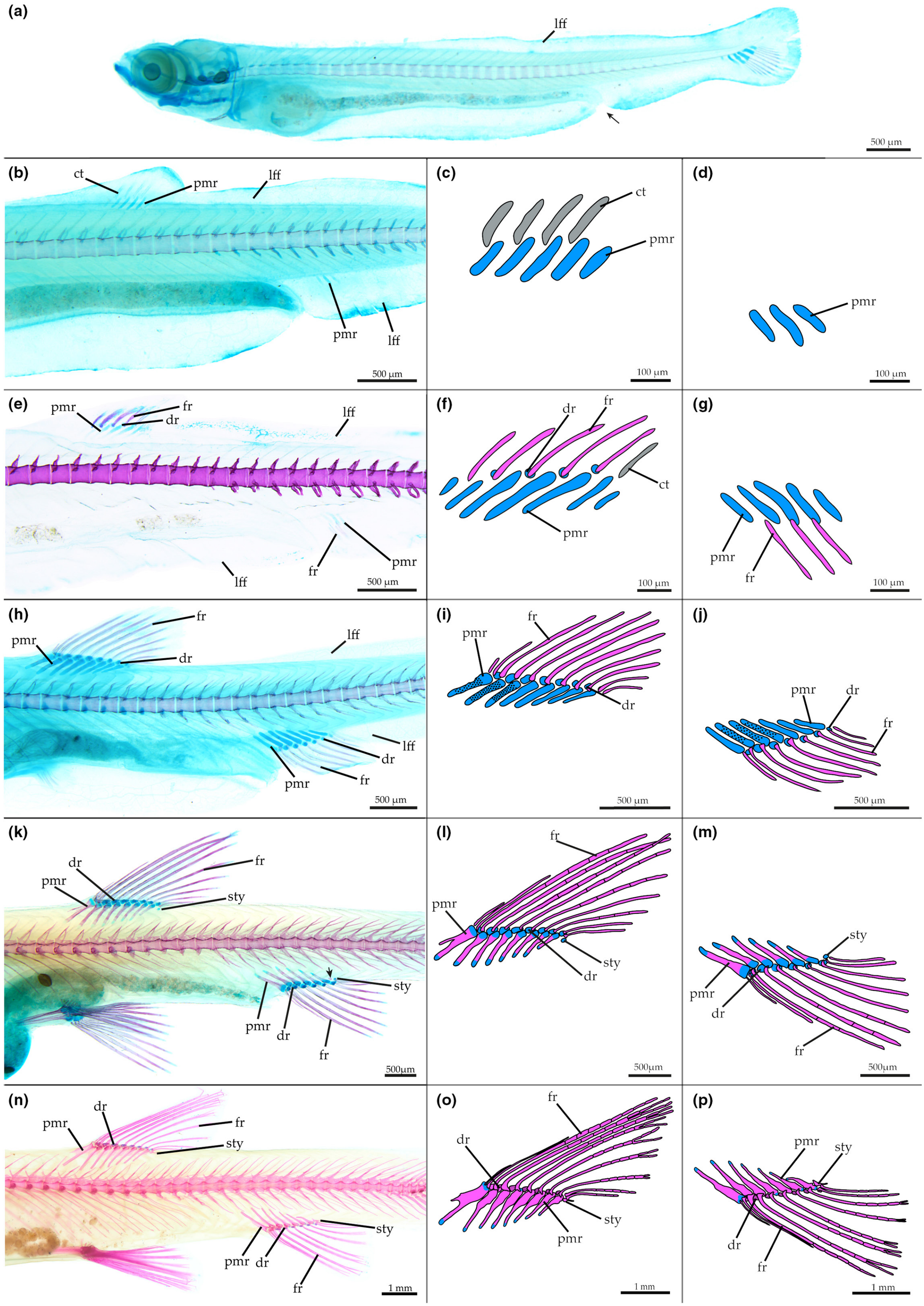

FIGURE 1 Ontogeny of the dorsal and anal fins in *Kneria stappersii* in photographs (a, b, e, h, k, n); and illustrations (c, d, f, g, i, j, l, m, o, p). (a) Whole specimen (7.3 mm SL). (b–d) SL 8.4 mm. (e–g) SL 9.3 mm. (h–j) SL 10.8 mm. (k–m) SL 15.0 mm. (n–p) SL 20.6 mm. ct, condensated tissue; dr, distal radial; fr, fin ray; lff, larval fin fold; pmr, proximal-middle radial; sty, stay [Colour figure can be viewed at wileyonlinelibrary.com]

in two portions, one posterior to the anus and the other between yolk-sac and anus. No skeletal elements of the dorsal or anal fin are visible yet.

3.2 | 8.4 mm SL

A well pronounced elevation of the larval fin fold is visible dorsally and clearly indicates the position of the future dorsal fin (Figure 1b). Five cartilaginous, rod-shaped proximal-middle radials of the dorsal fin are present of which the anterior-most and posterior-most ones are smaller than the middle ones (Figure 1b). Within the elevated dorsal fin fold four lepidotrichia precursors are visible (Figure 1b,c).

The ventral larval fin fold is still intact and there are three cartilaginous, rod-shaped proximal-middle radials present of which the middle one seems, by far, the most developed (Figure 1b,d).

3.3 | 9.3 mm SL

The dorsal portion of the larval fin fold is reduced anteriorly and the future dorsal fin becomes even more pronounced than before. There are seven cartilaginous proximal-middle radials present in the dorsal fin of which the three middle ones are the largest. Dorsal to the proximal-middle radials, four distal radials on the second to fifth anterior proximal-middle radial are present as well as five fin rays ossified via intermembranous ossification (Figure 1e,f).

The ventral portion of the larval fin fold is still intact. In the future anal fin, five cartilaginous proximal-middle radials and three fin rays are visible (Figure 1e,g).

3.4 | 10.8 mm SL

The dorsal fin is clearly visible and separate from the caudal larval fin fold. The latter is further reduced and dorsally begins at the level of the end of the anal fin (Figure 1h). The final number of proximal-middle radials in the dorsal fin (eight) are present. The distal portion of the first proximal-middle radial is enlarged. Furthermore, ossification of the proximal-middle radials begins in most pterygiophores except for the posterior two. A layer of bony tissue encompasses most of these proximal-middle radials, but their core is still cartilaginous. Cartilaginous distal radials are present dorsally to all proximal-middle radials. The 11 ossified fin rays articulate with these distal radials, mostly one fin ray per distal radial. At the anterior-most distal radial one fin ray and two supernumerary rays are present. Directly at the posterior-most distal radial there is only one fin ray, but there is a second, supernumerary fin ray which is slightly displaced posteriorly (Figure 1h,i).

The ventral larval fin fold posterior to the anus is still complete. Reduction of the larval fin fold posterior to the anal fin begins. In the anal fin seven cartilaginous proximal-middle radials as well as seven cartilaginous distal radials are visible. There are some thin patches of ossifications visible on the second, third, and fourth proximal-middle radial. Nine anal fin rays are ossified. One supernumerary fin ray is present anterior to the first distal radial and a second one posterior to the last distal radial, which as well as in the dorsal fin is slightly displaced posteriorly (Figure 1h,j).

3.5 | 15.0 mm SL

The dorsal and ventral portions of the larval fin fold are completely reduced. The proximal-middle radials of both fins are ossified except for the proximal and distal tips, which are still cartilaginous. The dorsal anterior-most proximal-middle radial becomes broader and develops an outgrowth through membrane ossification. Its overall shape resembles an inverted “Y” (Figure 1k,l). The distal radials are still cartilaginous, but their shape is more elongated instead of rounded. Posterior to the last complete pterygiophore in both fins another cartilaginous, roundish shaped structure, the fin stay, is present (Figure 1l,m). The dorsal and anal fin rays have grown in length resulting in higher dorsal and anal fins (Figure 1k). In the dorsal fin the length of the first supernumerary fin ray is half the length of the second supernumerary fin ray which, in turn, is half the length of the third fin ray associated with the anterior-most distal radial. This also holds true for the first three fin rays associated with the anterior-most distal radial in the anal fin (Figure 1m). The fin rays are well segmented in the dorsal and anal fin, except for the two anterior-most fin rays of both fins and the two posterior-most anal fin rays. In both fins the most posterior fin ray moved closer towards the posterior-most distal radial.

3.6 | 20.6 mm SL

Most parts of the pterygiophores in both fins are ossified, except for the proximal and few distal tips of the proximal-middle radials and the core of most distal radials. The outgrowth of the anterior-most proximal-middle radial of the dorsal fin has gotten broader and now looks less like an inverted “Y” (Figure 1n,o). In both fins all proximal-middle radials have developed thin membrane ossifications anteriorly and posteriorly along their distal half. The anterior-most proximal-middle radial of the anal fin is broadened (Figure 1n,p).

The fin stay is already ossified and has developed a proximal as well as a posterior outgrowth. Its shape is now similar to a triangle. The tips of the fin rays start to bifurcate, only the two anterior-most and posterior-most fin rays remain unbranched.

3.7 | 45.1 mm SL

In adult *K. stappersii* the proximal-middle radials of both fins are completely ossified and the anterior and posterior membrane ossifications even more extended (Figure 2a–d). Of the distal radials in the dorsal fin only the last one has a small cartilaginous core left, and in the anal fin this is the case for the last two distal radials. The shape of the fin stay has not changed; however, it grew in size. The fin stay of the anal fin of one examined specimen is missing the proximal outgrowth but in other individuals it is present (Figure 1n,p).

The fin rays in both fins grew in length, are segmented, and are deeply branched. In the dorsal fin the supernumerary fin rays as well as the fin ray at the anterior-most distal radial are unbranched. The anterior supernumerary fin rays are unsegmented. In the anal fin the two supernumerary fin rays at the anterior-most distal radial are unsegmented and unbranched. The corresponding fin ray on the same distal radial is segmented but unbranched as well. The supernumerary fin ray at the posterior-most distal radial is unbranched but segmented.

4 | DISCUSSION

In order to understand the general pattern of fin development of Otomorpha and Otophysi we discuss the median-fin development of *K. stappersii* mainly in comparison to its close relative *Chanos chanos* (Taki et al., 1986) as well as three other otomorph taxa the clupeiforms *Clupea harengus* (Fischbach et al., 2022) and *Engraulis japonicus* (Balart, 1995), and the cypriniform *Danio rerio* (Bird & Mabee, 2003; Parichy et al., 2009) (Table 2). The adult state of the dorsal fin of *K. stappersii* was also compared

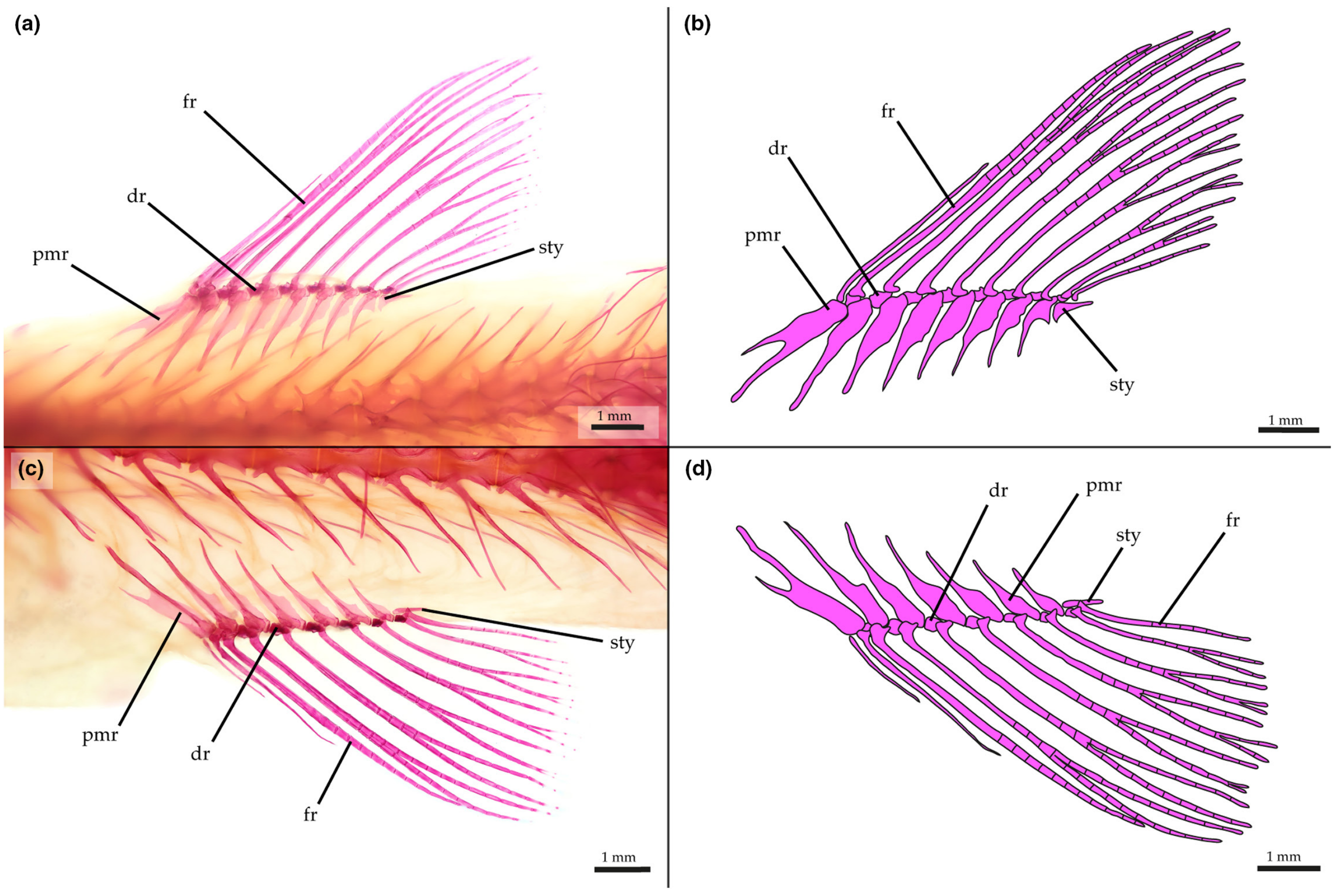

FIGURE 2 Cleared and double-stained adult *Kneria stappersii* with 45.1 mm (SL). (a) Photograph of the dorsal fin and (b) a detailed illustration. (c) Photograph of the anal fin and (d) a detailed illustration. dr, distal radial; fr, fin ray; pmr, proximal-middle radial; sty, stay [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Differences in dorsal (D) and anal (A) fin formation in *Kneria stappersii* (this study), *Chanos chanos* (Taki et al., 1986), *Danio rerio* (Bird & Mabee, 2003; Parichy et al., 2009), *Engraulis japonicus* (Balart, 1995), and *Clupea harengus* (Fischbach et al., 2022)

	Pterygioph. formation D versus A	Pterygioph. formation in D	Pterygioph. ossification in D	Pterygioph. ossification in A	Fin ray ossification D versus A	Fin ray ossification in D	Fin ray ossification in A	Stay in D and A
Kneria	D before A	←●→	●→	●→	D before A	←●→	←●→	Separate
Chanos	A before D	←●→	?	?	?	?	?	Separate
Danio	A before D	←●→	←●→	←●→	D before A[a]	?	?	Separate
Engraulis	D before A	←●	←●	●→	D before A	←●	●→	Early fused
Clupea	D before A	←●→	●→	●→	D before A	←●→	←●→	Early fused

Note: ←●→: Bilateral, ●→: Anterior to posterior, ←●: Posterior to anterior.

[a]Uncertainty in study (for details see text).

with a fossil relative †*Mahengichthys singidaensis* (Davis et al., 2013). In general, the development of the median fins of teleosts resembles much each other: a continuous, uniformly high larval fin fold surrounds the trunk of the early larvae. During growth, the larval fin fold is reduced in large areas, but remains and even increases its height in the areas where the dorsal, anal, and caudal fins will be formed (e.g., Bender & Moritz, 2013; Mabee et al., 2002). In the areas where the dorsal and anal fins will develop pterygiophores emerge close to the margin but still inside the body, and fin rays emerge within the fin fold.

In the three species *K. stappersii*, *C. harengus*, and *E. japonicus* the pterygiophores in the dorsal fin develop prior to the pterygiophore in the anal fin (Balart, 1995; Fischbach et al., 2022). In the two other species, *C. chanos* and *D. rerio*, first the pterygiophores in the anal fin and then slightly delayed the pterygiophores in the dorsal fin develop (Bird & Mabee, 2003; Parichy et al., 2009; Taki et al., 1986). In all species, the first elements of the pterygiophores to form are the cartilaginous, rod-shaped proximal-middle radials which later broaden dorsally (Bird & Mabee, 2003; Fischbach et al., 2022; Parichy et al., 2009; Taki et al., 1986). Balart (1995) observed "pre-cartilaginous dorsal anlagen" which are located dorsally in the body on the margin towards the larval fin fold, which then condense and form the cartilaginous, rod-shaped proximal-middle radials. The pterygiophores later start to ossify after all fin rays are formed. In *K. stappersii* the ossification of each pterygiophore starts in the centre of the proximal portion of the proximal-middle radial. By the time most parts of the proximal portion of the pterygiophore are ossified, the ossification process starts in the middle portion. The proximal tips of the pterygiophores remain in cartilage during further growth and ossify late in development. The ossification of distal radials first starts when all other elements in the fins have at least started to ossify. Taki et al. (1986) reported that proximal radials first started to ossify in their centre and later the middle radials of the posterior pterygiophores ossified from a separate ossification centre. Similarly, Bird and Mabee (2003) also observed two ossification centres within the proximal-middle radials in *D. rerio*.

Regarding the formation and ossification of pterygiophores within a fin, Mabee et al. (2002) reported that in many teleosts pterygiophores and fin rays develop in a bidirectional pattern, with later emerging radials or rays developing anterior and posterior to the first ones. Dorsal and anal fin development in *K. stappersii* correspond with these observations (Mabee, 1988; Mabee et al., 2002) (Table 2). The bidirectional development of fin elements is also found for *C. harengus* (Fischbach et al., 2022), *C. chanos* (Taki et al., 1986), *D. rerio* (Bird & Mabee, 2003; Parichy et al., 2009), and *Rutilus caspicus* (Hasanpour et al., 2015).

The anal fin of *E. japonicus* displays the same bidirectional development as described for the other species but in the dorsal fin the development of the first elements is shifted posterior and only few elements develop more posterior while most elements later emerge anterior (Balart, 1995). The ossification sequences not necessarily follow the same pattern (Table 2). In *K. stappersii* and *C. harengus*, the ossification of the pterygiophores starts at the anterior-most part of the fin and continues posteriorly (Fischbach et al., 2022). In contrast, in *E. japonicus*, the ossification of the pterygiophores in the dorsal fin proceeds from posterior to anterior, and in the anal fin from anterior to posterior (Balart, 1995). Bird and Mabee (2003) described a bidirectional ossification of the pterygiophores in *D. rerio*.

The fin rays in *K. stappersii*, *C. harengus*, and *E. japonicus* form slightly delayed to the proximal-middle radials. The fin rays in all three species are first visible in the dorsal fin and slightly delayed in the anal fin (Balart, 1995; Fischbach et al., 2022). There is no description about the time sequence for the fin development of the *D. rerio*, but due to the given length it seems like the anal-fin rays (5.5 mm) start to develop first and shortly after the dorsal-fin rays (5.6 mm) follow (Bird & Mabee, 2003). As there is only such a small difference in the size of the specimens of that study, it is however possible, that the fin rays of both fins developed at the same time as described for *C. chanos* (Taki et al., 1986). In both fins of *K. stappersii* and *C. harengus* (Fischbach et al., 2022), the ossification of the first fin rays begins in the middle of the future fin, before precursors to all future fin rays are visible (Table 2). There is no information on the formation pattern of the fin rays of *C. chanos* (Taki et al., 1986) and *D. rerio* (Bird & Mabee, 2003). However, Mabee et al. (2002: figure 4) suggested that the fin ray formation follows the same pattern as the pterygiophore formation, which develop bidirectionally, in both taxa. In *E. japonicus*, the fin formation follows the same pattern as the pterygiophore formation: dorsal fin rays develop from posterior to anterior, while anal fin rays develop bidirectionally (Balart, 1995).

In Neopterygii, the pterygiophores in the dorsal and anal fins consist of three elements: a proximal, a middle, and a dorsal radial (Hilton, 2011). As shown above, in *K. stappersii* there are only two elements present, which generally are termed proximal-middle and distal-radial (Britz & Moritz, 2007; Hilton, 2011). Grande and Arratia (2010) reported that in another *Kneria* species, *K. wittei*, three elements are present. In other Kneriidae, such as *Cromeria occidentalis* and *Phractolemus ansorgii*, pterygiophores with only two elements can be found, similar to *K. stappersii*. Based on the reconstructions of the fossil records of †*M. singidaensis*, Davis et al. (2013) reported that at least in the dorsal fin, proximal and middle radials are present with distal radials not observable due to conditions of preservation of the fossils. However, as distal radials are generally located between the bases of the fin rays and function as articulations sites for them (Hilton, 2011), their presence in †*M. singidaensis* can be supposed. All pterygiophores of the gonorynchid *Gonorynchus abbreviatus* consist of three elements. In the chanid *C. chanos*, an interesting combination can be found as the anterior pterygiophores of both the dorsal and anal fins consist of two elements while the posterior pterygiophores consist of three elements (Taki et al., 1986). Due to the inconclusive distribution of the pterygiophore composition within Kneriidae and Gonorynchiformes, the evolution of the pterygiophores in these taxa still is doubtful. Ontogenetic data of *K. stappersii* shows that proximal-middle radials forms from one cartilage that has two distinct ossification centres, while the posterior proximal and middle radials in *C. chanos* develop from two cartilages that each has its own ossification centre (Taki et al., 1986). It remains unknown if the anterior proximal-middle radials in *C. chanos* also have a second ossification centre. However it seems likely that the proximal-middle radials in gonorynchiforms represent a fusion of the proximal and middle radial. In other otomorphs there seems to be no clear pattern on the presence of proximal-middle or proximal and middle radials. In cypriniforms, there are species that have pterygiophores with two, for instance *D. rerio* (Bird & Mabee, 2003), or three elements, found in *Rutilus caspicus* (Hasanpour et al., 2015). In another cypriniform, *Barboides gracilis*, there are proximal-middle as well as proximal and middle radials present in both the dorsal and anal fins, very similar to *C. chanos* (Conway et al., 2017; Taki et al., 1986). However, there are no summarising studies evaluating the distribution of the diverse morphologies of this character among otomorphs or teleosts in general.

Another feature in many adult teleostean specimens is an enlarged anterior-most proximal-middle radial in the dorsal and anal fins. At least for otomorphs, previous studies reported that its shape and size is the result of a fusion of two cartilaginous proximal-middle radials (Balart, 1995; Fischbach et al., 2022; Taki et al., 1986). The anterior one of these two proximal-middle radials does not develop a distal radial so that the fused product, the pterygiophore present in adults, only bears a single distal radial. Our study, however, showed that the anterior enlargement of the first proximal-middle radial in *K. stappersii* forms solely by an outgrowth of membrane bone. The fossil records of †*M. singidaensis* show that the first pterygiophore looks similar in shape and relative size to *K. stappersii* (Davis et al., 2013). Both species share the anterior enlargement (Davis et al., 2013). A more detailed analysis of the development of this structure in a variety of otomorphs will provide further insight in its evolution.

The fin stay in *K. stappersii* and *C. chanos* (Taki et al., 1986) develops posterior to the last pterygiophore as a separate cartilaginous structure and stays separate in adult specimens. A rectangular shaped dorsal fin-stay, as in *K. stappersii*, can also be found in the dorsal fin of †*M. singidaensis*, called 8th dorsal pterygiophore by Davis et al. (2013: figure 11). Fin-stay development in the two clupeiforms *C. harengus* and *E. japonicus* differs from the described gonorynchiform pattern (Balart, 1995; Fischbach et al., 2022): The fin-stay develops as a separate element but quickly becomes connected to the last proximal-middle radial by a cartilaginous band. Furthermore, Balart (1995) described that the fin-stay development in the dorsal fin of *E. japonicus* slightly differs from the anal fin-stay development as the anal fin-stay starts as a rod-shaped outgrowth of the middle part of the posterior-most proximal-middle radial and later stays connected to it through a cartilaginous band. In *E. japonicus*, both fin-stays elongate posteriorly by membrane ossification (Balart, 1995). Even though Fischbach et al. (2022) only described the larval to juvenile development of *C. harengus*, there are indications that the fin-stays of *C. harengus* elongate posteriorly as described for *E. japonicus*. Although a fin-stay is reportedly present in some species of a majority of teleostean taxa (for example Conway et al., 2017; Hilton, 2002; Johnson & Patterson, 1996; Konstantinidis & Johnson, 2016), not much is known about their actual distribution and evolution within actinopterygians, its function, or differences in its development.

The median fin development of *K. stappersii* shows many similarities to other gonorynchiforms and more broadly to otomorphs. Especially, the developmental pattern of the dorsal and anal fins fit well with previously reported data for other otomorphs and teleosts. In detail these are: (1) proximal-middle radials form before distal radials; (2) fin ray ossification starts before pterygiophore ossification; (3) within the proximal-middle radials the proximal part ossifies first; (4) the distal radials are the latest elements starting to ossify; (5) the proximal tips of the proximal-middle radials remain cartilaginous for a long time in development. These character states are likely to have been present in the last common ancestor of otophysi and also otomorphs. On the other hand, several differences can be found even in a small sub-set of well-studied species (Table 2). Remarkable differences are the development of the fin-stay and the enlarged anterior pterygiophore. These details revealed that not much is known about the development, evolution, and function of the respective characters.

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REFERENCES

Balart, E. F. (1995). Development of the vertebral column, fins and fin supports in the Japanese anchovy, *Engraulis japonicus* (Clupeiformes: Engraulididae). *Bulletin of Marine Science*, *56*(2), 495–522.

Bender, A., & Moritz, T. (2013). Developmental residue and developmental novelty – Different modes of adipose-fin formation during ontogeny. *Zoosystematics and Evolution*, *89*(2), 209–214. https://doi.org/10.1002/zoos.201300007

Betancur-R, R., Wiley, E. O., Arratia, G., Acero, A., Bailly, N., Miya, M., Lecointre, G., & Ortí, G. (2017). Phylogenetic classification of bony fishes. *BMC Evolutionary Biology*, *17*(1), 162. https://doi.org/10.1186/s12862-017-0958-3

Bird, N. C., & Mabee, P. M. (2003). Developmental morphology of the axial skeleton of the zebrafish, *Danio rerio* (Ostariophysi: Cyprinidae). *Developmental Dynamics*, *228*(3), 337–357. https://doi.org/10.1002/dvdy.10387

Bridge, T. W. (1896). The mesial fins of ganoids and teleosts. *Zoological Journal of the Linnean Society*, *25*(165), 530–602.

Britz, R., & Moritz, T. (2007). Reinvestigation of the osteology of the miniature African freshwater fishes *Cromeria* and *Grasseichthys* (Teleostei, Gonorynchiformes, Kneriidae), with comments on kneriid relationships. *Zoosystematics and Evolution*, *83*(1), 3–42. https://doi.org/10.1002/mmnz.200600016

Coburn, M. M., & Chai, P. (2003). Development of the anterior vertebrae of *Chanos chanos* (Ostariophysi: Gonorynchiformes). *Copeia*, *2003*(1), 175–180. https://doi.org/10.1643/0045-8511(2003)003[0175:DOTAVO]2.0.CO;2

Conway, K. W. (2011). Osteology of the south Asian genus *Psilorhynchus* McClelland, 1839 (Teleostei: Ostariophysi: Psilorhynchidae), with investigation of its phylogenetic relationships within the order Cypriniformes. *Zoological Journal of the Linnean Society*, *163*(1), 50–154. https://doi.org/10.1111/j.1096-3642.2011.00698.x

Conway, K. W., Kubicek, K. M., & Britz, R. (2017). Morphological novelty and modest developmental truncation in *Barboides*, Africa's smallest vertebrates (Teleostei: Cyprinidae). *Journal of Morphology*, *278*(6), 750–767. https://doi.org/10.1002/jmor.20670

Davis, M. P., Arratia, G., & Kaiser, T. M. (2013). The first fossil shellear and its implications for the evolution and divergence of the Kneriidae (Teleostei: Gonorynchiformes). In G. Arratia, H.-P. Schultze, & M. V. H. Wilson (Eds.), *Mesozoic fishes 5* (pp. 325–362). Verlag Dr. Friedrich Pfeil.

Dingerkus, G., & Uhler, L. D. (1977). Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technology*, *52*(4), 229–232. https://doi.org/10.3109/10520297709116780

Fink, S. V., & Fink, W. L. (1981). Interrelationships of the ostariophysan fishes (Teleostei). *Zoological Journal of the Linnean Society*, *72*(4), 297–353.

Fischbach, V., Moritz, T., & Thieme, P. (2022). Postcranial skeletal development of the Atlantic herring (Clupeomorpha: Clupeidae: *Clupea harengus*). *Zoologischer Anzeiger*, *299*, 189–199. https://doi.org/10.1016/j.jcz.2022.06.002

Fricke, R., Eschmeyer, W. N., & Van der Laan, R. (Eds.) (2022). *Eschmeyer's catalog of fishes: Genera, species, references*. Retrieved April 21, 2022, from http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp

Grande, L. (2010). An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of Holostei. *Copeia*, *10*(2A), 1–871.

Grande, L., & Bemis, W. E. (1998). A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. *Journal of Vertebrate Paleontology*, *18*(S1), 1–696. https://doi.org/10.1080/02724634.1998.10011114

Grande, T., & Arratia, G. (2010). Morphological analysis of the gonorynchiform postcranial skeleton. In T. Grande, F. J. Poyato-Ariza, & R. Diogo (Eds.), *Gonorynchiformes and ostariophysan relationships: A comprehensive review* (pp. 39–71). Science Publishers.

Hasanpour, S., Eagderi, S., & Mojazi Amiri, B. (2015). Osteological development of the vertebral column, paired, dorsal and anal fins in *Rutilus caspicus*, Pravdin (1927) (Teleostei: Cyprinidae). *Caspian Journal of Environmental Sciences*, *13*(3), 207–219.

Hilton, E. J. (2002). Osteology of the extant north American fishes of the genus *Hiodon* Lesueur, 1818 (Teleostei: Osteoglossomorpha: Hiodontiformes). *Fieldiana Zoology*, *100*, 1–142.

Hilton, E. J. (2011). Bony fish skeleton. In A. P. Farrell (Ed.), *Encyclopedia of fish physiology: From genome to environmentvol* (1st ed., pp. 434–448). Academic Press.

Johnson, G. D., & Patterson, C. (1996). Relationships of lower euteleostean fishes. In M. L. J. Stiassny, L. R. Parenti, & D. G. Johnson (Eds.), *Interrelationships of fishes* (pp. 251–332). Academic Press, Inc..

Konstantinidis, P., & Johnson, G. (2016). Osteology of the telescopefishes of the genus *Gigantura* (Brauer, 1901), Teleostei: Aulopiformes. *Zoological Journal of the Linnean Society*, *179*, 338–353. https://doi.org/10.1111/zoj.12469

Mabee, P. M. (1988). Supraneural and predorsal bones in fishes: Development and homologies. *Copeia*, *4*(4), 827–838.

Mabee, P. M., Crotwell, P. L., Bird, N. C., & Burke, A. C. (2002). Evolution of median fin modules in the axial skeleton of fishes. *Journal of Experimental Zoology*, *294*(2), 77–90. https://doi.org/10.1002/jez.10076

Mattox, G. M., & Conway, K. W. (2021). Osteology of *Tucanoichthys tucano* Géry and Römer, an enigmatic miniature fish from the Amazon basin, Brazil (Teleostei: Characiformes: Characidae). *Vertebrate Zoology*, *71*, 645–667. https://doi.org/10.3897/vz.71.e71886

Nakatani, M., Miya, M., Mabuchi, K., Saitoh, K., & Nishida, M. (2011). Evolutionary history of Otophysi (Teleostei), a major clade of the modern freshwater fishes: Pangaean origin and Mesozoic radiation. *BMC Evolutionary Biology*, *11*(1), 1–25. https://doi.org/10.1186/1471-2148-11-177

Nelson, J. S., Grande, T. C., & Wilson, M. V. H. (2016). *Fishes of the world* (5th ed.). John Wiley & Sons.

Parichy, D. M., Elizondo, M. R., Mills, M. G., Gordon, T. N., & Engeszer, R. E. (2009). Normal table of postembryonic zebrafish development: Staging by externally visible anatomy of the living fish. *Developmental Dynamics*, *238*(12), 2975–3015. https://doi.org/10.1089/zeb.2006.9997

Rosen, D. E., Anderson, S., Weitzman, S. H., & Greenwood, P. H. (1970). Origin of the Weberian apparatus and the relationships of the ostariophysan and gonorynchiform fishes. *American Museum Novitates*, *2428*, 1–25.

Stewart, T. A., Bonilla, M. M., Ho, R. K., & Hale, M. E. (2019). Adipose fin development and its relation to the evolutionary origins of median fins. *Scientific Reports*, *9*(512), 1–12. https://doi.org/10.1038/s41598-018-37040-5

Stewart, T. A., Smith, W. L., & Coates, M. I. (2014). The origins of adipose fins: An analysis of homoplasy and the serial homology of vertebrate appendages. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 1–9. https://doi.org/10.1098/rspb.2013.3120

Taki, Y., Kohno, H., & Hara, S. (1986). Early development of fin-supports and fin-rays in the milkfish *Chanos chanos*. *Japanese Journal of Ichthyology*, *32*(4), 413–420.

Thieme, P., Warth, P., & Moritz, T. (2021). Development of the caudal-fin skeleton reveals multiple convergent fusions within Atherinomorpha. *Frontiers in Zoology*, *18*(1), 20. https://doi.org/10.1186/s12983-021-00408-x

Weitzman, S. H. (1962). The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. *Stanford Ichthyological Bulletin*, *8*, 1–77.

Wiley, E. O., & Johnson, G. D. (2010). A teleost classification based on monophyletic groups. In J. S. Nelson, H.-P. Schultze, & M. V. H. Wilson (Eds.), *Origin and phylogenetic interrelationships of teleosts* (pp. 123–182). Verlag Dr. Friedrich Pfeil.

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