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A true caudal fin or not? New insights in the evolution of the gadiform caudal fin

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ABSTRACT

The distinctive caudal-fin skeleton of gadiforms has puzzled scientists for a long time, because of its many differences in comparison to other teleosts. Contradicting hypotheses interpreted this structure as (i) a highly derived teleostean caudal fin, (ii) a new formation with parts from the caudal, dorsal and anal fins, a so called pseudocaudal, or (iii) a complete evolutionary novelty, a so called neocaudal. To shed light on to this issue, the caudal-fin ontogeny of *Lota lota* was studied in detail. It differs from the development in non-gadiform teleostean taxa, e.g. by absence of a distinct and early notochord flexion. However, there are also many similarities with other teleosts, e.g. the caudal fin develops before the dorsal and anal fins. Furthermore, the morphology of adult caudal fins of all major gadiform families were studied and reviewed. Our results, in combination with the latest molecular phylogenies, allowed us to discuss the evolution of the gadiform caudal fin and resolve the origin of this highly debated character complex. Although their caudal-fin skeleton shows several derived apomorphies, the gadiform caudal fin is homologous to the caudal fins of other teleosts, without principal inclusion of dorsal- or anal-fin elements.

Keywords: Homology; morphology; ontogeny; osteology; Paracanthopterygii

The tail of Phycis and of Gadus […] do not in reality differ from the tails of other bony fishes; […].
(*Agassiz 1877: 122*)

I regard the isocercal condition of the Gadidae as the result of the formation of a new caudal fin, the homocercal extremity of the vertebral column having been lost by the direct ancestors of these fishes.
(*Boulenger 1902: 298*)

The caudal skeleton of the cods […] seems to be far more aberrant than even that of the eels, and its parts cannot easily be homologized with those of any of the fishes dealt with here.
(*Gosline 1961: 11*)

INTRODUCTION

The caudal fin in fishes usually provides the major source of propulsion (Lauder 1989). Teleostei, or Teleocephala (*sensu* de Pinna 1996), possess a unique caudal fin providing several apomorphies substantiating their monophyly: their caudal fin (i) is externally homocercal, (ii) is diural, i.e. at least in adults there are two ural vertebrae (but these may originate from slightly different ontogenetic components; Schultze and Arratia 1989, Arratia and Schultze 1992), (iii) possesses a maximum of three epurals (de Pinna 1996), (iv) has up to seven hypurals, which are (v) divided by a gap, the diastema, in an upper and lower group (Monod 1968), (vi) has the first two hypurals connected to ural centrum 1 (Patterson and Rosen 1977), and (vii) has their ural neural arches modified to pairs of uroneurals (Arratia 1999). The caudal fin in teleosts has undergone many modifications during evolution, such as loss or fusion of various elements (Monod 1968, Fujita 990) and, therefore is often used in phylogenetic and systematic investigations (e.g. Johnson and Patterson 1996, de Pinna 1996, Arratia 1999, Thieme *et al.* 2022).

The Gadiformes, commonly known as cods and hakes, consist of 13 families comprising about 84 genera (Nelson *et al.* 2016) with, presently, 622 species (Fricke *et al.* 2022). Many commercially important fishes are included in this order that collectively account for about a quarter of the world's marine fish catch (Nelson *et al.* 2016). There are many interesting aspects about the morphology of gadiforms (e.g. their pince-nez shaped

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saccular otolith), but especially the caudal fin of gadiforms has puzzled scientists for a long time because their caudal fin differs in several aspects from the generalized form of teleosts (Agassiz 1877, Boulenger 1902, Dietz 1921, Barrington 1937, Monod 1968). In gadiforms, there are some typical elements missing, such as the uroneurals (Borden *et al.* 2013). Sometimes accessory bones, i.e. X- and Y-bones, are present (Fahay and Markle 1984). Furthermore, major differences in their general morphology can be found, especially the absence of the dorsal flexion of the posteriormost end of the vertebral column in the caudal fin of adults (e.g. Fujita 1990, Borden *et al.* 2013). Therefore, some authors have suspected that the caudal fin of gadiforms represents a new formation (Boulenger 1902), thus not homologous to the caudal fin of other teleosts. In contrast, other authors have regarded the gadiform caudal fin simply as a specialized teleost caudal fin (e.g. Agassiz 1877, Dietz 1921, Borden *et al.* 2013). Goodrich (1958: 111) proposed two possible identities of the gadiform caudal fin: first, it is a true teleost caudal fin that extends anteriorly or, second, it is formed from true caudal-fin elements plus derivatives from the anal and dorsal fins. The second hypothesis was later seized by Fahay and Markle (1984) and Markle (1989), who termed it the 'continuous caudal' hypothesis. Available data do not unambiguously support any of these three hypotheses: (i) a caudal fin derived from a typical teleost caudal fin, i.e. a true caudal fin (e.g. Agassiz 1877, Dietz 1921, Borden *et al.* 2013), (ii) a combination of teleost caudal fin plus elements from the dorsal and anal fin, i.e. a 'pseudocaudal' (*sensu* Goodrich 1909, 1958) or 'continuous caudal' (*sensu* Fahay and Markle 1984, Markle 1989), or (iii) a new formation not homologous to the caudal fin of other teleosts, i.e. a 'neocaudal' (*sensu* Boulenger 1902).

The present study aims to shed light on the evolutionary origin of the gadiform caudal fin by studying its ontogeny and its skeletal diversity. The burbot, *Lota lota* (Linnaeus, 1758) represents the only completely freshwater species of the order Gadiformes, and thus can be reared more easily under aquaria conditions to obtain an ontogenetic series. The results from the ontogeny of the caudal-fin development in *Lota* are then compared with other gadiforms and outgroups to discuss the interpretation of the gadiform caudal fin. An in-depth comparison and evaluation of adult gadiform caudal skeletons based on the latest phylogenetic hypotheses (Han *et al.* 2021, Roa-Varón *et al.* 2021) gives insight into the evolution of the caudal skeleton of gadiforms.

MATERIAL AND METHODS

Lota lota belongs to the lings or rocklings (Lotidae) and is the only gadiform member spending its whole life-history in freshwater. Eggs and larvae were obtained from three different suppliers: Werner Loch (Fischerei Hohen Sprenz), the Landesfischereiverband Westfalen-Lippe and Hendrik Wocher (LOTAqua Satzfischzucht, Überlingen). Eggs and larvae were kept in an 80-L aquarium (12–14°C, well aerated, 30% of the water was exchanged every 3-4 days) and fed with microartemia, artemia and live chironomid larvae, depending on size. Specimens of different sizes were anaesthetized and killed with an overdose of benzocaine prior to fixation in 4% formalin. For permanent storage, specimens were transferred into 70% ethanol. Despite uniform temperature regime and food supply, growth of individuals was variable and, therefore, development in this study is only discussed in relation to size and developmental stage, not to days or degree days.

Some of the specimens of this ontogenetic series, as well as comparative material of other gadiforms and outgroups (Table 1), i.e. Zeiformes and *Polymixia*, were cleared and double-stained for bone and cartilage following a modified protocol of Dingerkus and Uhler (1977) and Taylor and Van Dyke (1985), as described in detail in Thieme *et al.* (2021). Specimens were photographed using either a Leica M165C binocular with a dedicated camera (Leica DFC425) and software (LAS 4.9.0, Leica), or a Canon EOS 80D supplemented with macro-objectives (Canon MP-E 65 mm and Sigma EX 105 mm). Images were optimized (without ay alteration of anatomical content) using the freeware GIMP 2.10.14 (www.gimp.org) and plates were compiled with the freeware Open Office Draw (www.openoffice.org) or Adobe Illustrator CC (v.26.2). A µ-CT-scan of the caudal fin of *Muraenolepis microps* Lönnberg, 1905 (ZMH 115205) was obtained from a Xradia 410 (Carl Zeiss) at the Institute for Bioscience at the University Rostock. The scan at 40 kV resulted in a voxel size of 19.4 µm. Processing of µ-CT-data was performed with the software AMIRA 6.0 and MAYA 2019.

To allow unbiased comparisons of anatomical structures, we use a neutral nomenclature for caudal skeleton elements (Fig. 1). Terminal dorsal elements are abbreviated by 'x' and terminal ventral elements by 'y', respectively, based on the term X- and Y-bones for elements in the caudal fin with unclear homology (Monod 1968). Herein, the abbreviation is supplemented by a number indicating the affiliation to a terminal vertebral centrum 't' based on the idea that they might belong to the same somite. In cases where more than one element can be assigned to one vertebral centrum, the number is additionally supplemented by a letter, e.g. y2a (Fig. 1). This nomenclature allows comparison of homologous structures among gadiform taxa and with typical teleostean caudal fins free of priori homologies.

RESULTS

Development of the caudal fin in *Lota Lota*

Caudal-fin skeleton of Lota lota (Fig. 2A)

The caudal-fin skeleton of adult *L. lota* comprises a terminal centrum t1 in the shape of a half centrum anteriorly and a slightly posterodorsal directed cone, to which the triangular and plate-like y1 is fused posteriorly. Furthermore, a paired dorsal outgrowth is present on t1. Terminal centrum t2 is lacking a haemal arch, instead y2a is connected to it via cartilage ventrally (Fig. 2A). Dorsally, t2 also has a paired outgrowth that resembles the neural arch of more anterior vertebral centra (Fig. 2A: asterisks). Dorsally to t2, two separate elements x1 and x2 are present, which in some *L. lota* specimens are fused proximally. Anterior to y2a another separate element, y2b, is present. Terminal centrum t3 has a neural arch to which a broadened element with a cartilaginous distal tip, x3a, is fused. It is more similar to x1 and x2 than to other neural spines, which are spine-like without a cartilaginous distal tip. Ventrally, t3 has a haemal arch and in some specimens, there is also a broadened element with a cartilaginous distal tip, y3a, fused to it. Three fin rays are associated with y1, two with y2a, and one each with every other terminal

Table 1. Studied specimens; all cleared and double stained except for *Muraenolepis microps* (ZMH 115205), which are ethanol specimens and were μ-CT-scanned. Length is given either as standard length (SL) or total length (TL) depending on species or developmental stage; values below 110 mm are given to 0.1 mm accuracy and above this value to the next millimetre. Specimens are deposited at the Deutsches Meeresmuseum (DMM), Stralsund, Germany and the Zoological Museum Hamburg (ZMH), Germany. Classification follows (Nelson *et al.* 2016).

Taxon	Number	Length (mm)	Registration
Polymixiidae			
Polymixia berndti (Gilbert, 1905)	2	73.1–99.5 (SL)	DMM IE/13296
Parazenidae			
Cyttopsis rosea Lowe, 1843	2	41.8–44.5 (SL)	DMM IE/12017
Zeidae			
Zenopsis nebulosa (Temminck and Schlegel, 1845)	1	82.7 (SL)	DMM IE/13214
Macrouridae			
Coelorinchus coelorhincus (Risso, 1910)	1	111.0 (TL)	DMM IE/11146
Coryphaenoides rupestris Günther, 1878	1	449.0 (SL)	DMM IE/16851
Nezumia sclerorhynchus (Valenciennes, 1838)	1	117.0 (TL)	DMM IE/11139
Ventrifossa nigrodorsalis Gilbert and Hubbs, 1920	2	95.1–127.0 (TL)	DMM IE/15799
V. nigrodorsalis	1	155.0 (TL)	DMM IE/15800
Trachyrincidae			
Trachyrincus scabrus (Rafinesque, 1810)	3	140.0–170.0 (TL)	DMM IE/15809
Moridae			
Gadella jordani (Böhlke and Mead, 1951)	1	83.9.0 (SL)	DMM IE/9881
G. jordani	1	108.9 (SL)	DMM IE/15881
G. jordani	1	143.0 (SL)	DMM IE/15882
Mora moro (Risso, 1810)	2	92.5–98.6 (SL)	DMM IE/12188
M. moro	2	100.8–104.4 (SL)	DMM IE/12187
Merlucciidae			
Merluccius merluccius (Linnaeus, 1758)	1	99.4 (SL)	DMM IE/15794
M. merluccius	1	110.0 (SL)	DMM IE/13270
Bregmacerotidae			
Bregmaceros sp.	2	37.1–52.4 (SL)	DMM IE/13820
Bregmaceros sp.	4	49.3–69.8 (SL)	DMM IE/12218
Muraenolepididae			
Muraenolepis microps Lönnberg, 1905	2	145.0–149.0 (TL)	ZMH 115205
M. microps	1	151.0 (TL)	ZMH 115067
Gadidae			
Phycinae			
Phycis blennoides (Brünnich, 1768)	1	99.0 (SL)	DMM IE/12177
P. blennoides	2	122.0–130.0 (SL)	DMM IE/15810
Gadinae			
Boreogadus saida (Lepechin, 1774)	1	121.0 (SL)	DMM IE/15936
Gadiculus argenteus Guichenot, 1850	4	72.4–84.2 (SL)	DMM IE/11811
G. argenteus	1	84.3 (SL)	DMM IE/15807
G. argenteus	1	117.0 (SL)	DMM IE/15883
Gadus morhua Linnaeus, 1758	3	82.6–106.2 (SL)	DMM IE/12022
G. morhua	1	137.0 (SL)	DMM IE/11140
Merlangius merlangus (Linnaeus, 1758)	1	129.0 (SL)	DMM IE/15872
Pollachius virens (Linnaeus, 1758)	2	26.8–29.9 (SL)	DMM IE/10233
P. virens	2	46.0–49.4 (SL)	DMM IE/12222
Trisopterus esmarkii (Nilsson, 1855)	1	108.0 (SL)	DMM IE/15797
T. esmarkii	1	111.0 (SL)	DMM IE/12185
T. esmarkii	1	113.0 (SL)	DMM IE/12186
T. luscus (Linnaeus, 1758)	1	90.8 (SL)	DMM IE/11145

Table 1. Continued

Taxon	Number	Length (mm)	Registration
Gaidropsarinae			
Ciliata mustela (Linnaeus, 1758)	1	106.1 (SL)	DMM IE/11784
Enchelyopus cimbrius (Linnaeus, 1766)	2	106.4–108.1 (SL)	DMM IE/6080
Gaidropsarus mediterraneus (Linnaeus, 1758)	1	81.9 (SL)	DMM IE/11789
Lotinae			
Lota lota (Linnaeus, 1758)	23	6.0–22.1 (TL)	DMM IE/16100
L. lota	30	8.2–35.1 (TL)	DMM IE/16101
L. lota	13	8.3–19.4 (TL)	DMM IE/16099
L. lota	1	41.5 (SL)/46.4 (TL)	DMM IE/16098
L. lota	1	75.8 (SL)/83.5 (TL)	DMM IE/15805
L. lota	1	86.9 (SL)	DMM IE/15804
L. lota	1	99.3 (SL)	DMM IE/15806

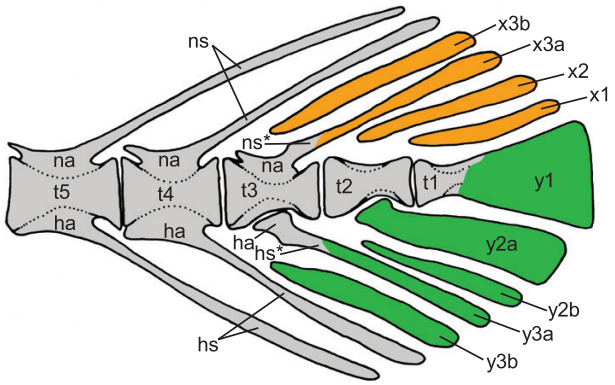

Figure 1. Neutral nomenclature for skeletal elements of the caudal fin in Gadiformes used in this study; here on a schematized *Phycis blennoides*. Dorsal terminal elements are coloured in orange, ventral terminal elements in green, and other elements of the vertebral column in grey. Abbreviations: ha, haemal arch; hs, haemal spine; na, neural arch; ns, neural spine; t, terminal centrum; x, terminal dorsal element; y, terminal ventral element; *indicates haemal and neural spines associated with terminal centrum 3.

element (Fig. 2A). Further caudal-fin rays are supported by the appendages of t4 to about t12 or t13.

6.5 mm total length (Fig. 2B)

Along the vertebral column, the first five to six neural arches form directly behind the neurocranium. There are no further ossifications visible in the postcranial area: any trace of fin rays and notches in the larval fin fold, which would delimit dorsal, anal and caudal fins, are absent. However, there are mesenchymal accumulations both dorsally and ventrally in the posterior portion of the larval fin fold (Fig. 2B).

7.2 mm total length (Fig. 2C)

Vertebrae appear from anterior to posterior in the following sequence: neural arches and, directly thereafter, haemal arches develop; then the centra form, originating from the bases of the neural and haemal arches. There are no traces of vertebrae visible in the caudal area at this stage (Fig. 2C). First caudal-fin rays become visible as condensed connective tissue in a bidirectional pattern, not at the end of the notochord, but more anterior in the dorsal and ventral portion of the larval fin fold (Fig. 2C: lt). Directly anterior to them, notches in the larval fin fold appear dorsally and ventrally. Except for these fin rays, there are no skeletal elements visible in the caudal fin. Any traces of fin rays or fin ray supports from the anal and dorsal fins are absent at this stage.

10.2 mm total length (Fig. 2D)

Formation of the vertebral column has proceeded posteriorly. About three-quarters of the specimen's vertebral centra are present. Towards the caudal end of the fish no centra have formed. Neural and haemal arches have directly ossified without precursors, except for the last five to seven arches present at this stage: paired cartilaginous anlagen are present dorsally (basidorsals) and ventrally (basiventrals) to the caudal notochord (Fig. 2D) from which the arches ossify. The posteriormost paired cartilages represent the future neural and haemal arches of terminal centrum t3. Two unpaired cartilages become visible dorsally at this stage: one dorsally to the basidorsals of t3 (Fig. 2D: x3a) and one more posterior to the latter (Fig. 2D: x2). Additionally, three unpaired cartilages are present ventrally: the terminal ventral elements y2a and y2b, as well as y1, of which y2a is the largest (Fig. 2D). Of the ventral elements, y2a develops first, then y2b, and lastly y1. Both dorsal elements develop after y2a. In one specimen of a similar size, we observed two darkly stained areas within y2a, which are connected by a less stained area. This may indicate the presence of two formation sites. The terminal elements x2 and y2b originate distant from the notochord, close to the lepidotrichia. The latter are already starting to ossify in this stage, although the number of fin rays preformed by connective tissue, i.e. about five dorsally and seven ventrally, is far from complete. Still, neither pterygiophores nor preformed lepidotrichia from the anal and dorsal fins are visible at this stage.

11.4 mm total length (Fig. 2E)

In this stage, vertebral centra up to t4 have formed. Terminal centrum t3 develops starting from the neural and haemal arches peripherally around the notochord. No trace of t2 and t1 are visible (Fig. 2E). In specimens of this stage, x3a is closely associated with the neural arch of t3, but in some specimens it is separated

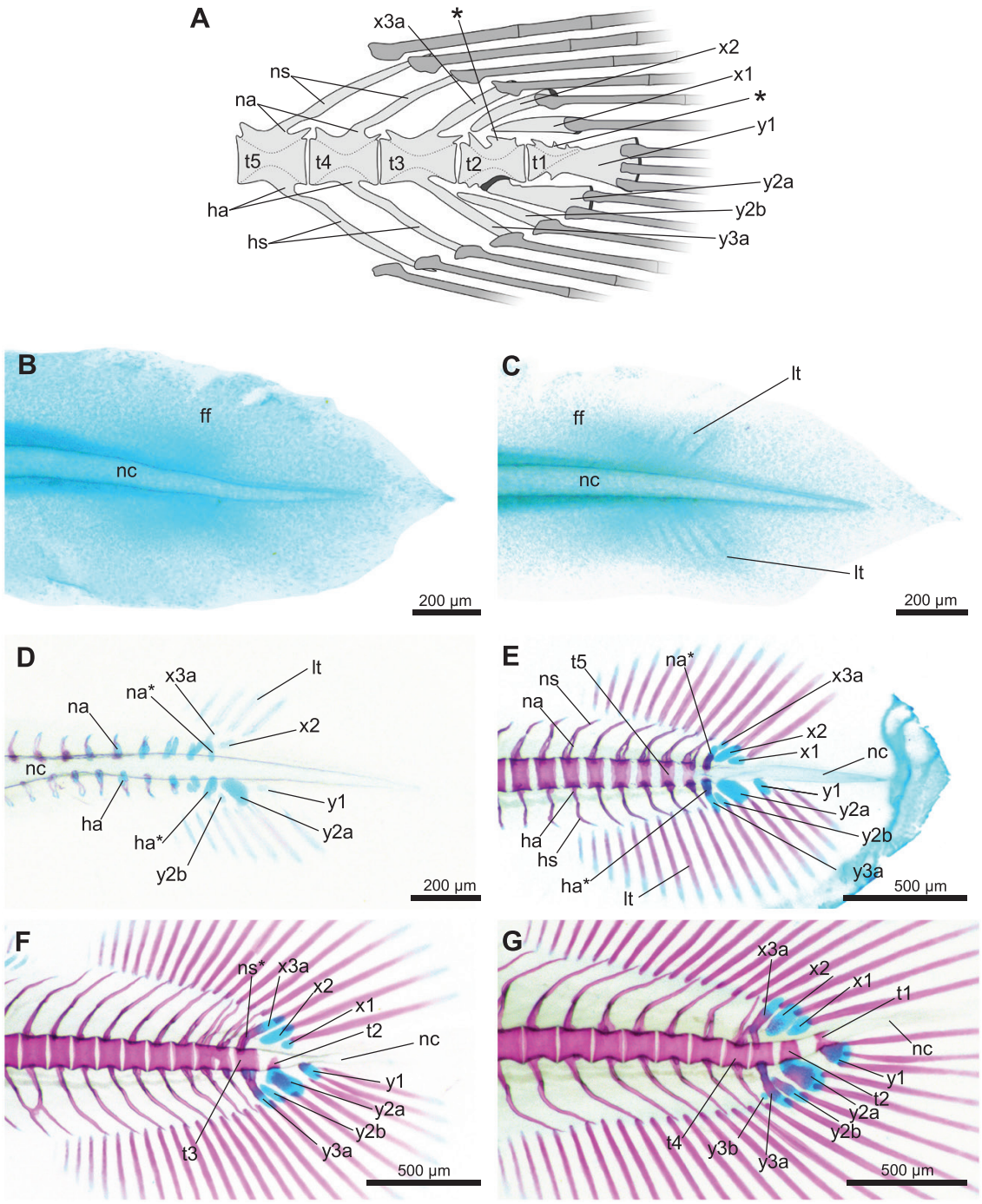

Figure 2. Caudal fin in *Lota lota*, adult and early development from cleared and stained specimens. A, schematized drawing of adult condition, light grey:bones, grey:fin rays, dark grey:cartilage; B, 6.5 mm total length (TL); C, 7.2 mm TL; D, 10.2 mm TL; E, 11.4 mm TL; F, 14.2 mm TL; G, 15.3 mm TL. Abbreviations: asterisk, neural arch-like outgrowth; ff, larval fin fold; ha, haemal arch; hs, haemal spine; lt, lepidotrichia; na, neural arch; nc, notochord; ns, neural spine; t, terminal centrum; x, terminal dorsal element; y, terminal ventral element; * indicates haemal and neural spines associated with terminal centrum 3. There are two sets of asterisks used in this figure - is this referring to the asterisk in (A), or to those associated with the letters na*/ns*/ha*.

in two portions (Fig. 2E). Additionally, x2 has grown larger and x1 formed in cartilage. Ventral to the notochord, y3a developed and is positioned between the distal tips of the haemal arch of t3. The cartilages posterior to y3a, i.e. y2b, y2a, and y1, have grown. The notochord still extends to the caudal end of the median fin fold without any sign of flexion. Ossification of lepidotrichia has proceeded and 13 dorsal and 17 ventral caudal rays are present in the depicted specimen (Fig. 2E).

At this stage, proximal radials of the anal and first and second dorsal fins are present in cartilage. Furthermore, lepidotrichia of the anal and dorsal fins start to appear.

14.2 mm total length (Fig. 2F)

In contrast to the previous stage, formation of terminal centrum t2 has begun. t2 has a ventral ossification site at the proximal tip of y2a from where it ossifies in a dorsal direction (Fig. 2F). There

is still no sign of the last terminal centrum (t1). Also, ossification of dorsal and ventral terminal elements, i.e. x3a, y3a, y2b, y2a, and y1, begins. x3a is firmly fused to the neural spine of t3 as is y3a to the respective haemal arch. Just posterior to y1, the notochord is constricted (Fig. 2F). More lepidotrichia are present compared to the previous stage and the most-posterior ones exceed the end of the notochord. Some specimens in this size class also have a y3b element.

15.3 mm total length (Fig. 2G)

All vertebral centra are present (Fig. 2G). Terminal centrum t1 is forming from two ossification centres within the notochord: one ventrally, where y1 contacts the notochord, and one opposite to it on the dorsal side of the notochord. The notochord is slightly bent upwards starting anterior to t2. Both y2a and y1 are directed dorsally. Ossification of ventral terminal elements has proceeded and dorsal terminal elements, i.e. x2 and x1, start to ossify. A cartilaginous y3b is only present in a few specimens (Fig. 2G). More lepidotrichia appear and while y3a and y2b each support one fin ray, y2a supports two and y1 supports three fin rays.

20.3–22.1 mm total length (Fig. 3A–D)

At this stage, all caudal elements that are usually present are ossified, except for y3b, if present (Fig. 3A–D). In smaller specimens, proximal and distal tips of terminal elements may still be cartilaginous. The most-posterior terminal element, y1, has grown dorsally and has undergone a transformation from elliptical (Fig. 2E) to triangular (Fig. 3A–D) or even to a reversed axe-shaped structure (Fig. 3B). y1 is firmly fused to t1, whereas y2a is connected to t2 via cartilage. y2b remains isolated but in close proximity to y3a. Flexion of the notochord can be more (Fig. 3A, B) or less (Fig. 3C, D) pronounced. The remaining notochord surpassing t1 has shortened.

30.8 mm total length (Fig. 3E)

In comparison to the previous stages, most caudal elements are relatively slimmer in this and subsequent stages. y1 has grown posteriorly and exceeds t1. The notochord has shortened even more and ends on the level of the posterior margin of y1. t2 takes the typical hourglass shape of the more anterior vertebral centra (Fig. 3E). In the illustrated specimen, y2b was not formed and is missing.

83.5 mm total length (Fig. 3F)

This stage represents the adult condition of the caudal fin. All caudal elements are completely ossified with only distal cartilaginous margins. Furthermore, there remains a cartilaginous connection between y2a and t2 (Fig. 3F). The caudalmost tip of the notochord is completely enclosed by t1, which now has the shape of a half centrum with a slightly upward bend in the posterior tip. y1 has extended even more posteriorly and has reached its final shape in line with the vertebral column (Fig. 3F).

The caudal fin extends anteriorly to the dorsal and anal fins. From t12 or t13 backward, neural and haemal spines support caudal fin lepidotrichia. The spinous appendages of the vertebrae are evenly spaced, which holds also true for the lepidotrichia. However, there is no clear numerical relation between both structures: from t3 in anterior direction there are 17 to 18 lepidotrichia supported by 10 to 11 neural and haemal spines, respectively. The neural and haemal spine of t3, as well as x2, x1, and y2b, each support a single lepidotrichia; y2a supports two and y1 three lepidotrichia, respectively.

General remarks

The individuals did not grow and develop uniformly, and the development of the skeletal elements was not necessarily more advanced in larger specimens. X- and Y-bones, corresponding to x3b and y3b elements, are principally absent, but in some individuals small, roundish, or irregular elements in the respective positions may be present. The variability in caudal anatomy between individuals is high. There are often more specimens showing different aberrant conditions, i.e. various types of fusions between elements or accessory elements, than specimens showing the 'typical' condition (Fig. 2A). These variations happen in most cases at or in the periphery of t3. For example, additional elements like y3b may be present (Fig. 2G); y2b may fuse to t3 (Fig. 3A) or be completely absent (Fig. 3D, E). Well-visible neural or haemal spines may be present on t3 (like haemal spines in Fig. 3D, F), or t3 fuses with t4 (Fig. 3C, E). More variations include fusions of terminal dorsal elements (Fig. 3E), more than one lepidotrichia per dorsal caudal element, or fusions between other terminal vertebrae (Fig. 2F, where t4 and t5 fuse). Furthermore, paired elements, i.e. neural or haemal arches, are sometimes expressed on one side only.

Systematic comparison

Gadidae–Gadinae

The caudal-fin skeleton of the Gadinae is similar among the herein examined species, i.e. *Boreogadus saida* (Lepechin, 1774), *Gadus morhua* Linnaeus, 1758, *Gadiculus argenteus* Guichenot, 1850, *Merlangius merlangus* (Linnaeus, 1758), *Pollachius virens* (Linnaeus, 1758), *Trisopterus esmarkii* (Nilsson, 1855) (Fig. 4A), and (Linnaeus, 1758). Much like *L. lota*, the end of the vertebral column is formed by t1 to which an enlarged, plate-like y1 is fused. t1 has the shape of a half centrum with a dorso-caudally directed posterior tip. Additionally, a large, paired extension that is directed postero-dorsally is connected to t1 (Fig. 4A: arrow). t2 does not bear a neural or haemal arch, although there is a bilateral extension visible dorsally to the centrum, which can be more (e.g. *Bo. saida*, *Merlangius merlangus*) or less (e.g. *Gadiculus argenteus*) pronounced. Starting in the middle of t2, the proximal end of the vertebral column is slightly bent upwards. x1, x2, y2a, and y2b are present as separate elements, whereas x3a and y3a are fused to the neural and haemal arches of t3, respectively. x3b and y3b are absent. y2a shows an extensive cartilaginous articulation with t2. The distal tips/margins of x1, x2, x3a, y1, y2a, y2b, and y3a are cartilaginous, while neural and haemal spines of other centra do not have such cartilaginous tips, but few are split in an anterior and a posterior tip. In a few specimens (e.g. *Gadiculus argenteus* DMM IE/15883) we observed that the caudal artery splits after passing through the haemal arch of t3 and in front of y2a. There are five fin rays articulating with y1 in *Gadiculus*, *Pollachius*, and *Trisopterus* (Fig. 4A) and only four in *Boerogadus*, *Gadus*, and *Merlangius*. In all studied Gadinae,

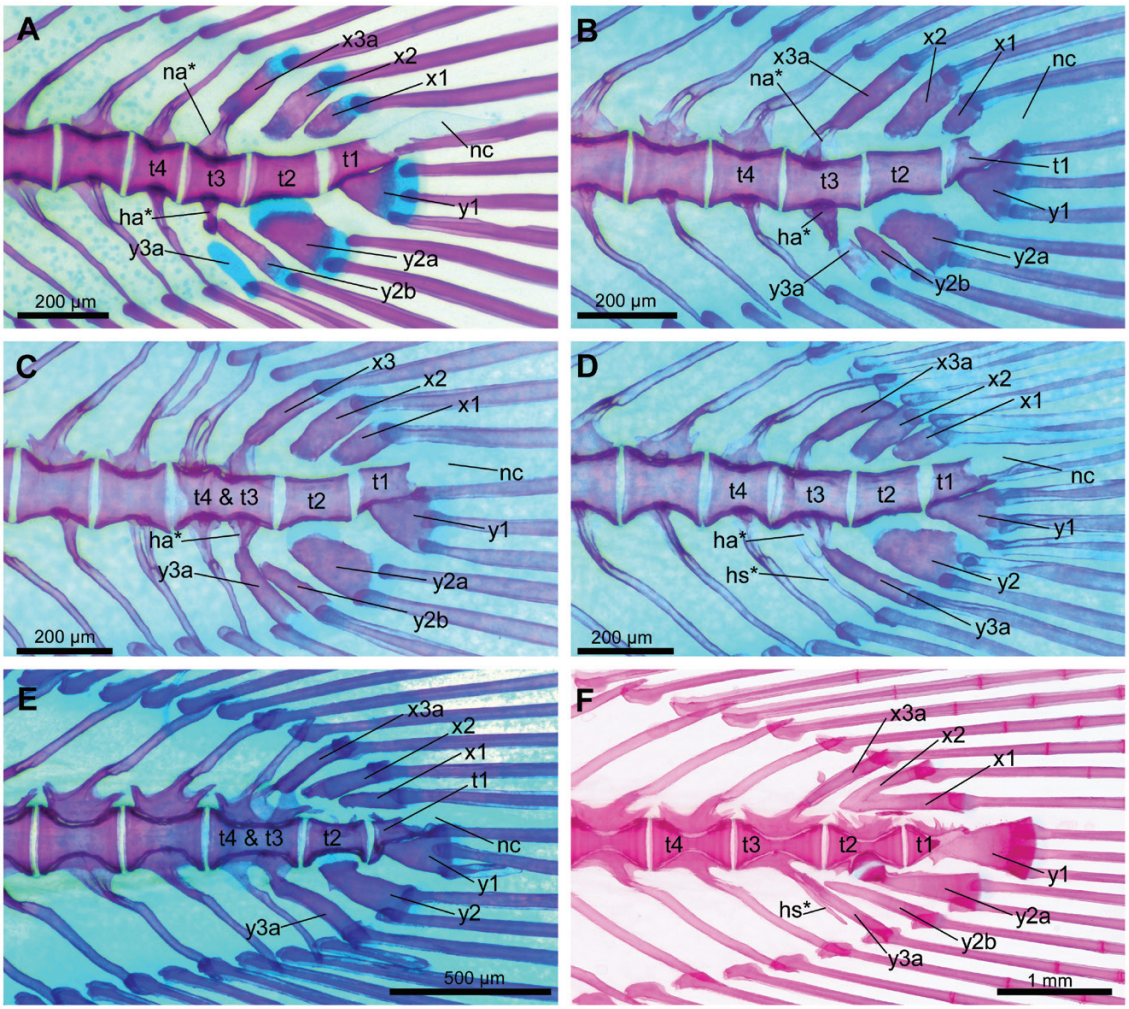

Figure 3. Caudal fin development and variability in *Lota lota*, cleared and stained specimens. A, 20.3 mm total length (TL); B, 20.8 mm TL; C; 21.0 mm TL; D, 22.1 mm TL; E, 30.8 mm TL; F, 83.5 mm TL. Abbreviations: ha, haemal arch; hs, haemal spine; na, neural arch; nc, notochord; ns, neural spine; t, terminal centrum; x, terminal dorsal element; y, terminal ventral element; * indicates haemal and neural spines associated with terminal centrum 3.

two fin rays articulate with y2a, whereas one fin ray articulates with the other terminal elements. The number of terminal centra that support caudal-fin rays with their respective appendages varies more between, but also within, some species: *Bo. saida* up to t13, *Gadus morhua* up to t14, *Gadiculus argenteus* up to t11, *Merlangius merlangus* up to t14, *Po. virens* up to t17, *Trisopterus esmarkii* varying between t13 and t15 (most t14), and *Trisopterus luscus* up to t12. The size of the vertebrae is reduced in the posterior direction.

Gadidae–Phycinae

The caudal-fin skeleton of *Phycis blennoides* (Brünnich, 1768) (Fig. 4B) closely resembles that of the Gadinae (Fig. 4A) with three major differences: first, x3b and y3b are present as separate elements; second, the haemal arch of t3 is not fused to the centrum but connected by cartilage much like y2a is connected to t2; and, third, the paired dorsal process on t1 is absent. Furthermore, there is no paired dorsal extension on t2. All terminal elements have cartilaginous distal tips/margins, but the proximal tips, except for y2a and y3a, are without cartilage. Six fin rays articulate with y1, whereas two fin rays articulate with y2a. All other terminal elements support one fin ray each. Further caudal-fin rays are supported by the appendages of t4 to t7/t8. The size of the vertebrae is reduced in the posterior direction.

Gadidae–Gaidropsarinae

The caudal-fin skeleton of the examined Gaidropsarinae, i.e. *Ciliata mustela* (Linnaeus, 1758), *Enchelyopus cimbrius* (Linnaeus, 1766), and *Gaidropsaurus mediterraneus* (Linnaeus, 1758), again resembles that of the Gadinae and Phycinae. A large, paired posterodorsal extension on t1 is present in *Gaidropsaurus mediterraneus* and in one specimen of *En. cimbrius* but is absent in *Ci. mustela* and the other specimen of *En. cimbrius*. Further, paired dorsal extensions on t2 are pronounced in *Gaidropsarus mediterraneus*, almost absent in *Ci. mustela*, and absent in *En. cimbrius*. x3b and y3b are present as separate elements. All terminal elements have cartilaginous distal tips/margins. In *Gaidropsarus mediterraneus* and *Ci. mustela*, the split of the caudal artery between the haemal arch of t3 anteriorly and the proximal portion of y2a posteriorly is clearly visible. In all three

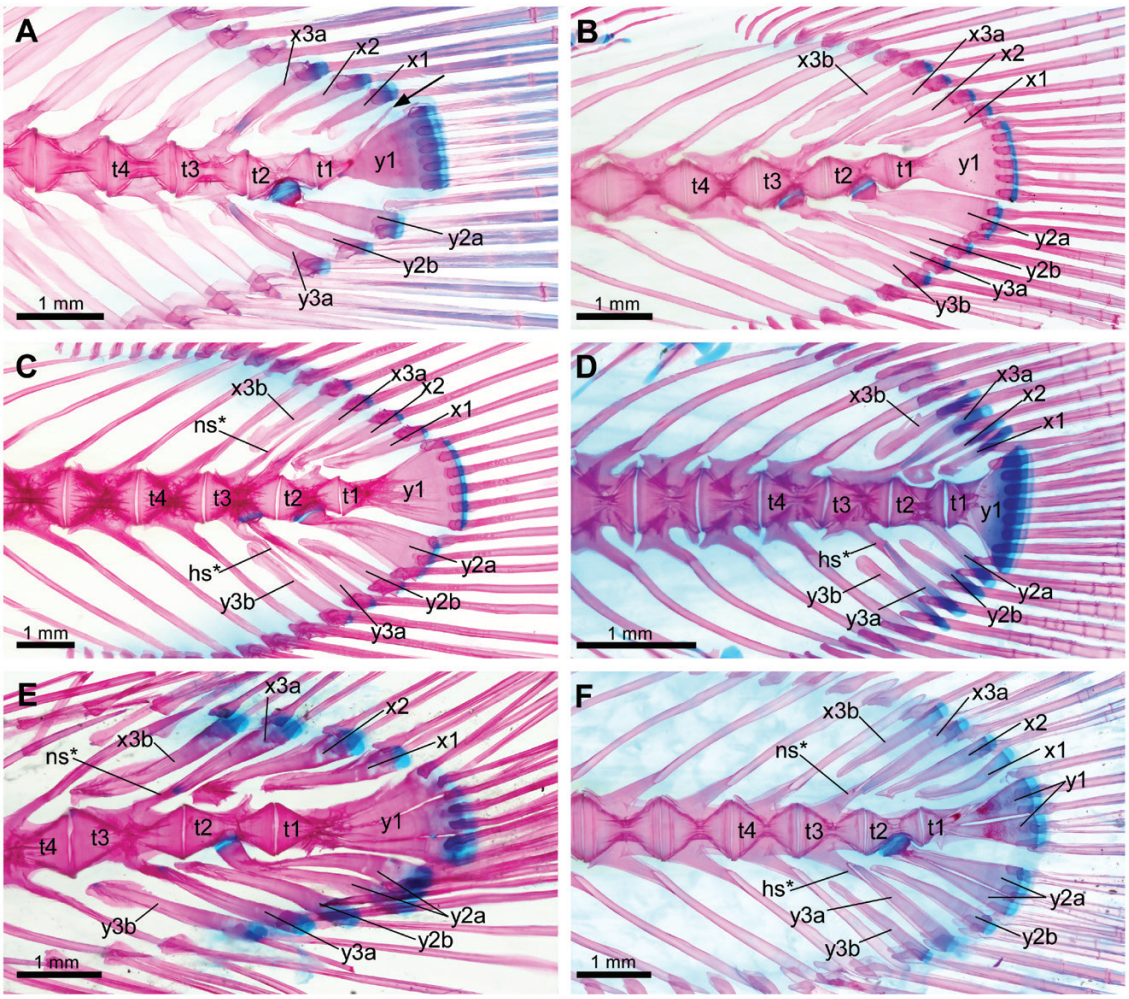

Figure 4. Caudal fins of Gadiformes, cleared and stained specimens. A, *Trisopterus esmarkii*, Gadidae, DMM IE/12185, 111.0 mm standard length (SL); B, *Phycis blennoides*, Phycidae, DMM IE/12177, 99.0 mm SL; C, *Merluccius merluccius*, Merlucciidae, DMM IE/13270, 110.3 mm SL; D, *Bregmaceros* species, Bregmacerotidae, 71.2 mm SL; E, *Gadella jordani*, Moridae, DMM IE/15882, 143 mm SL; F, *Mora moro*, Moridae, DMM IE/12187, 99.6 mm SL. Abbreviations: ha, haemal arch; hs, haemal spine; na, neural arch; ns, neural spine; t, terminal centrum; x, terminal dorsal element; y, terminal ventral element; * indicates haemal and neural spines associated with terminal centrum 3; arrow indicates dorso-caudal prolongation of terminal centrum 1.

species, y1 supports five fin rays, y2a two fin rays, and all other terminal elements bear one fin ray each. Further caudal-fin rays are supported by the neural and haemal spines of t4 to t9. Size of vertebrae is reduced in posterior direction.

Merlucciidae

The caudal-fin skeleton of *Merluccius merluccius* (Linnaeus, 1758) (Fig. 4C) is similar to that of gadids. Terminal element y1 is enlarged and plate-like and fused to t1, to which a paired, postero-dorsally elongated process extends in one examined specimen. The shape of t1 is much like that of other gadiforms. Dorsally to t2, a paired extension is present that is open dorsally and surrounds the spinal cord. Terminal elements x1, x2, x3b, y2a, y2b, and x3b are present as separate structures. The proximal tip of x2 is broadened bilaterally, much like x2 in *Bregmaceros* sp. but less extensive. y2a is connected to t2 via a cartilaginous bridge and is distally broadened. x3a and y3a are fused to the neural and haemal arches of t3, respectively. Furthermore, both herein studied specimens show additional and well-formed neural and haemal arches with a neural and haemal spine, respectively, on t3 anterior to the neural and haemal arches to which x3a and y3a are fused (Fig. 4C). The two neural arches share a joint base, while the anterior haemal arch is directly fused to the centrum. The haemal arch, to which y3a is connected, articulates with t3 via cartilage, similar to the connection of t2 and y2a. Again, all terminal caudal elements have cartilaginous distal tips. Six fin rays are connected to y1, two fin rays to y2a, and one fin ray is supported by each of the other terminal elements. Further caudal-fin rays are supported by the appendages of t4 to t9. The size of the vertebrae is reduced posteriorly.

Bregmacerotidae

The caudal-fin skeleton of *Bregmaceros* species is characterized by an extremely enlarged y1 that is fused to t1, which dorsally has small, paired extensions (Fig. 4D). t1 has the shape of a half centrum with a dorso-caudally directed posterior tip. Terminal elements x1, x2, x3b, y2b, and y3b are present as separate elements, while y2a is fused directly to t2, and x3a and y3a are fused

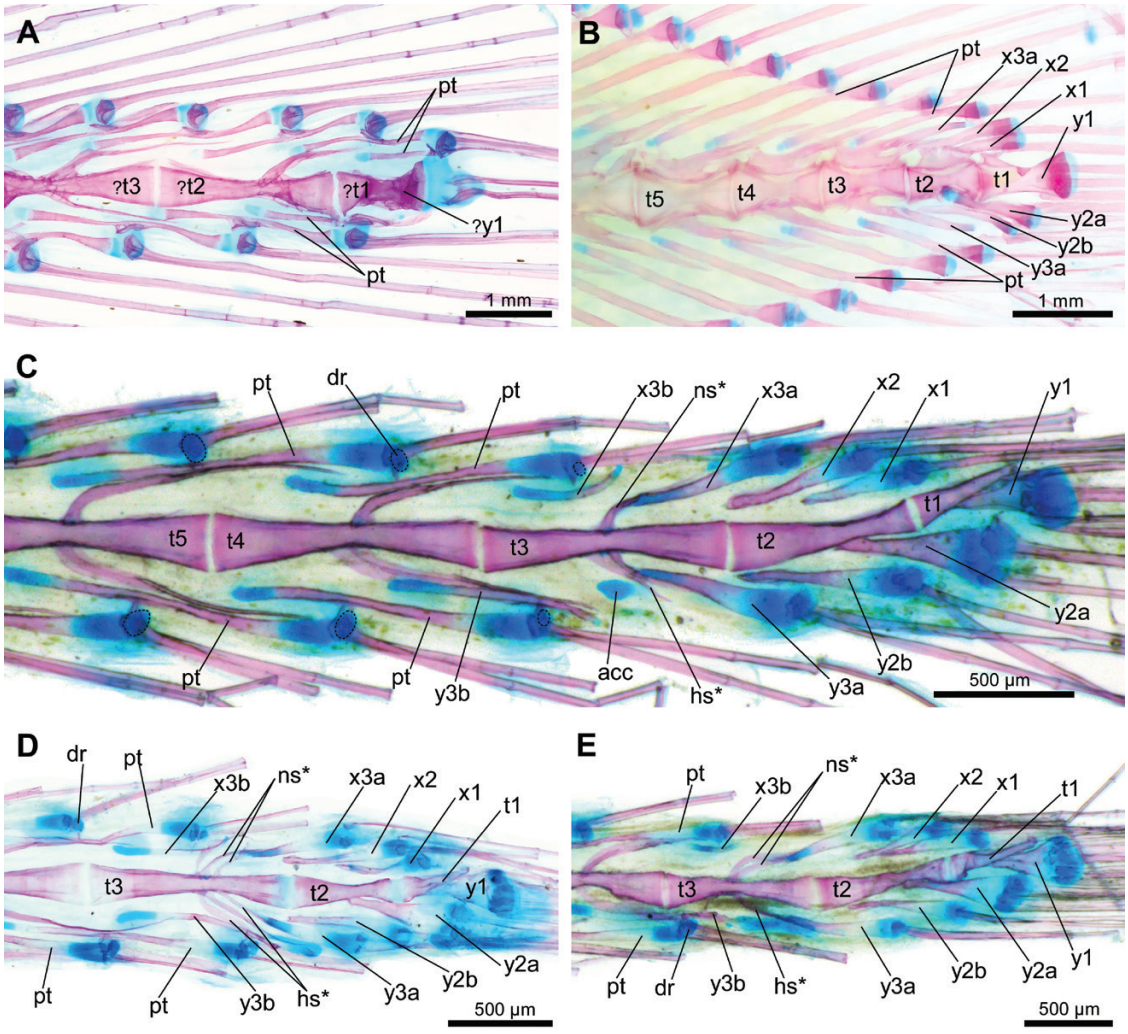

Figure 5. Caudal fins of Gadiformes, cleared and stained specimens. A, *Coryphaenoides rupestris*, Macrouridae, DMM IE/16887, 449 mm TL; B, *Muraenolepis microps*, Muraenolepididae, ZMH 115205, 145 mm total length (TL); C–E, *Trachyrincus scabrus*, Trachyrincidae, DMM IE/15809, 140 mm TL (C), 148 mm TL (D), 170 mm TL (E). Abbreviations: ha, haemal arch; hs, haemal spine; na, neural arch; ns, neural spine; pt, pterygiophore; t, terminal centrum; x, terminal dorsal element; y, terminal ventral element; * indicates haemal and neural spines associated with terminal centrum 3.

with the neural and haemal arches of t3, respectively. x2, and in some cases also x1, proximally have bilateral extensions that can encompass the spinal cord. Dorsally to the vertebral centrum t2, short, paired extensions are present. The distal tips/margins of all terminal elements are cartilaginous. Seven fin rays are supported by y1; for the other terminal elements it is not possible to assign an unambiguous number of associated fin rays. Besides t1 to t3, caudal-fin rays are supported by the appendages of t4 to t7/t8. The size of the vertebrae is reduced posteriorly.

Moridae

The two morid species investigated herein differ from the aforementioned gadiforms in two aspects: first, y1 is principally divided in three single elements, each fused to t1; and, second, y2a is deeply split in two portions, which share a proximal base that is connected to t2 via cartilage (Fig. 4E, F). In two specimens of *Mora moro* (Risso, 1810) y1 is only divided into two single elements (Fig. 4F); however, in one specimen the upper element is enlarged. t1 has the shape of a half centrum with a dorso-caudally directed posterior tip. In *Gadella jordani* (Böhlke and Mead, 1951), a paired, postero-dorsally elongated extension is present on t1, whereas in *M. moro* only a paired outgrowth dorsal to t1 is present. In contrast to all other gadiforms, a paired, spiny and ventrally directed outgrowth is present between t1 and the ventral element of y1. As in other gadiforms, x1, x2, x3b, y2b, and y3b are present as separate elements. x3a and y3a are fused to the neural and haemal arches of t3, respectively. Dorsally to vertebral centrum t2, paired extensions are present that are pronounced in *Gadella jordani* (Fig. 4E), but less prominent in *Mo. moro* (Fig. 4F). In *Gadella jordani*, the ventral tip of x2 may be laterally elongated much like in *Merluccius merluccius* and *Bregmaceros* sp. All terminal elements have cartilaginous distal tips. In *Mo. moro*, we observed that the caudal artery splits between the haemal arch of t3 and the proximal portion of y2a. Five or six fin rays articulate with y1, two or three fin rays with y2a, and one fin ray each with the other terminal elements. Besides the terminal elements, the appendages of t4 to t11/t12 (*Mo. moro*) or t4 to t8/t9 (*Gadella jordani*) support additional caudal-fin rays,

whereby dorsal caudal-fin rays are always supported by one less vertebra. The size of the vertebrae is reduced in the posterior direction.

Macrouridae

The caudal fin of macrourids is characterized by a tapering tail and previous studies have suggested that a true caudal fin and its skeleton are completely absent in macrourid species (Howes and Crimmen 1990). In most of the herein examined specimens we were not able to observe a caudal fin or a caudal-fin skeleton. However, clearing and staining revealed that the vertebral columns in these specimens are broken between two vertebrae and that the most-caudal region is missing. But, in a specimen of *Coryphaenoides rupestris* Günther, 1878 we identified a caudal fin or caudal fin-like elements (Fig. 5A). In contrast to all other gadiforms, the vertebrae in the caudal region are dorso-ventrally compressed and elongated. Furthermore, the dorsal and anal fins merge directly into the caudal fin. The most-caudal centrum may be described as an anterior half-centrum transitioning into a posteriorly directed cone similar to what can be seen in gadids. Posterior to this half centrum, a terminal element with a large cartilaginous margin, which postero-ventrally is further extended, is fused. Two fin rays attach to this terminal element. The half centrum is missing a neural and a haemal arch, while the penultimate vertebra has a neural but no haemal arch. No other caudal elements are present, as dorsal and anal-fin pterygiophores extend up to the last vertebra (Fig. 5A). The pterygiophores comprise a distal and a proximal-middle radial, which can be characterized by a cartilaginous proximal and distal tip, as well as a modified middle part that, similar to a socket, is round and concave and encompasses the distal radial of the pterygiophore in front of it. The last dorsal pterygiophore is lacking a distal radial, and both the last dorsal and anal fin pterygiophore do not support a fin ray. It may be assumed that the caudal-fin skeleton of *Coryphaenoides rupestris* is almost completely reduced and only two elements, i.e. a half centrum that is similar to t1 and a plate-like terminal element that may correspond to y1, remain.

Muraenolepididae

Similar to macrourids, no distinct caudal fin is visible in *Muraenolepis microps* Lönnberg, 1905 from an external view. Internally, it is difficult to distinguish between dorsal and anal fins and caudal-fin elements based on μ-CT or X-ray data. However, the cleared and stained specimen helps to distinguish between these structures (Fig. 5B). In general, the caudal vertebrae are dorso-ventrally compressed but not elongated. Terminal centrum t1 anteriorly has the shape of a half centrum, while a posterior portion is not distinguishable due to the fusion with y1, which is narrow but still plate-like. Dorsally on t1 a paired outgrowth much like a neural arch is present. Terminal elements x1, x2, y2a, and y2b are present as separate elements and can be distinguished from pterygiophores by missing cartilaginous proximal tips, and in case of y2a by the cartilaginous articulation with t2 (Fig. 5B). Terminal elements x3a and y3a are fused to the neural and haemal arches of t3, respectively. Terminal centrum t2 has distinct bilateral extensions dorsally that resemble the neural arches of more anterior vertebrae but are not fused dorsally. Three fin rays articulate with y1, two fin rays with y2a, and one each with x1, x2, and y2b.

Trachyrincidae

Similar to macrourids, *Trachyrincus scabrous* (Rafinesque, 1810) is characterized by a tapering tail, where an external distinction between dorsal and anal fins and caudal fin is not possible. Internally, *Trachyrincus scabrus* shows dorso-ventrally compressed and anterior–posterior elongated vertebra of which the two most-posterior ones, terminal centra t1 and t2, are bent upwards (Fig. 5C–E). Furthermore, dorsal and anal pterygiophores extend far posteriorly, making discrimination between them and terminal elements difficult. However, pterygiophores in the examined specimens of *Trachyrincus scabrus* are characterized by cartilaginous proximal and distal tips of the proximal–middle radials and the presence of cartilaginous distal radials (Fig. 5C–E). A few terminal elements can be easily identified: y1 is a triangular bone that is proximally fused to t1, y2a is similar in shape to y1 and proximally fused to t2, and dorsally to t2, two bones with cartilaginous distal tips are present, presumably representing x1 and x2. Anterior to y2a, a bone with a cartilaginous distal tip, which may be identified as y2b, is present. Dorsally and ventrally to t3, one bone each is in close contact with the neural and haemal arches of t3, respectively. These bones have a cartilaginous distal and proximal tip, but no additional, cartilaginous distal element can be observed. Therefore, they might represent x3a and y3a. Anterior to the neural arch of t3 a small, curved bone with cartilaginous distal and proximal tips is present. Its shape differs much from the anterior pterygiophores and, therefore, presumably is x3b. Anterior to the haemal arch of t3 a cartilaginous element that varies in shape between the herein examined specimens (round in Fig. 5C or rod-like in Fig 5D, E) is present. In one of the examined specimens (DMM IE/15809, 140 mm TL; Fig. 5C) there is another, rod-like structure, which is in close contact with the haemal arch of t4, anterior to the round cartilage and similar to the rod-like element in the other examined specimens. Presumably the rod-like element represents y3b in the three specimens (Fig. 5C–E), while the round structure is an accessory cartilage (Fig. 5C). Because of the direct transition from dorsal and anal fin to caudal fin, caudal-fin rays are only present from t3 backwards. There are three fin rays associated with y1 and two fin rays with y2a. One fin ray connects to x1, x2, x3a, and y2b, respectively (Fig. 5C–E).

DISCUSSION

The mystery of the gadiform caudal fin

The caudal fin and its skeleton in gadiforms are seemingly different from those of other teleosts (e.g. Monod 1968, Fujita 1990, Borden *et al.* 2013). This has puzzled scientists for a long time and led to different hypotheses about the nature of the gadiform caudal fin. Boulenger (1902) proposed that it represents a new formation that is not homologous to the caudal fin of other teleosts, terming it 'neocaudal'. This means that skeletal elements of the caudal fin were completely reduced within the gadiform lineage and skeletal elements present in extant

gadiform species evolved anew in a common ancestor. Goodrich (1909, 1958) proposed the term 'pseudocaudal', meaning that a combination of teleost caudal-fin elements plus elements from the dorsal and anal fin, i.e. pterygiophores, were incorporated into the gadiform caudal-fin skeleton. Fahay and Markle (1984) and Markle (1989) later proposed their own hypothesis on how the gadiform caudal skeleton evolved from a combination of anal- and dorsal-fin elements and true caudal-fin elements. Their 'continuous caudal' hypothesis is, therefore, equivalent to Goodrich's (1909, 1958) 'pseudocaudal'. These different views are best illustrated by the preceding citations (Agassiz 1877, Boulenger 1902, Gosline 1971), or exemplarily by the dispute of Whitehouse (1935) and Barrington (1935) carried out in the journal *Nature*: Whitehouse (1935: 70) stated that 'It is scarcely possible to call the fin anything else but homocercal, as in the majority of Teleosts. There is clearly nothing peculiar whatever about the structure', while Barrington (1935: 270) replied that 'the term "pseudocaudal" appears to me to be the most satisfactory designation for the Gadoid fin'.

Several authors transferred the nomenclature of a generalized teleostean caudal fin to the anatomical structures found in gadiforms without further discussing possible problems with homology (e.g. Fujita 1990, Endo 2002, Borden *et al.* 2013, Grande *et al.* 2013, Table 2). Monod (1968: 568–570) proposed three hypotheses on how a gadiform caudal fin could be homologized with a typical teleost caudal fin. The major difference in these hypotheses is the position of the parhypural: (i) fused to the terminal centrum t1, i.e. part of y1, (ii) representing the penultimate terminal ventral element, i.e. y2a, or (iii) being the haemal spine plus arch of terminal centrum 3. But a fourth hypothesis, not mentioned by Monod (1968), that the parhypural corresponds to y2b, became the prevailing one (e.g. Rosen and Patterson 1969, Howes 1991, Meléndez and Markle 1997, Endo 2002, Borden *et al.* 2013, Grande *et al.* 2013), (Table 2).

One major difference between the gadiform caudal fin and the typical teleost caudal fin is the reported absence of the dorsal flexion of the notochord during ontogeny (Barrington 1937) and of the posteriormost end of the vertebral column in adult gadiforms. Further, the formation of caudal-fin rays differs significantly from other teleosts (Agassiz 1877, Barrington 1937, Matarese *et al.* 1981, Markle 1982). Besides the difference during ontogeny, there are additional bones present, i.e. the X- and Y-bones, that are not found in any other closely related taxon (Fujita 1990, Betancur-R *et al.* 2017), while uroneurals are completely absent in gadiforms.

Until now, no study has evaluated the different hypotheses on the nature of the gadiform caudal fin. Herein, we compare the caudal-fin development and anatomy of gadiforms to evaluate the evolution of this puzzling structure in such a diverse taxon and present a conclusion on the terminology of gadiform caudal-fin elements.

The ontogeny of the gadiform caudal fin

Several scientists studied the development of the caudal region in different gadiform species to better understand the gadiform caudal fin. Agassiz (1877: 121–122) was one of the first persons studying gadiform development and depicting stages of the caudal fin formation of *Phycis* and *Gadus*. Barrington (1937) later gave a more detailed description of the caudal-fin development in *Gadus*. Matarese *et al.* (1981) then added further developmental data for *Mircogadus*, while Markle (1982) compared several gadiforms, including *Gaidropsaurus*, *Melanogrammus*, *Gadus*, and *Lota*.

Agassiz (1877) observed a slight upward bending in the notochord of a 15 mm larva of *Phycis* and a 20 mm larva of *Gadus*, which he interpreted as true notochord flexion. Although, he had only four larval stages from two different species available, he concluded that the tails of *Gadus* and *Phycis* 'do not differ from the tails of other bony fishes; having like them a truly heterocercal termination' (Agassiz 1877: 122). Barrington (1937) argued that a normal flexure, such as in other teleosts, does not occur in gadiforms. He reasoned that normal flexure is induced by exaggerated growth of the ventral caudal lobe, which he argues cannot occur in gadiforms because of the equal growth of the ventral and dorsal lobes. Following studies showed notochord flexion in *Mircogadus*, induced by the growth of y1 (Matarese *et al.* 1981: fig. 3, HY4-6), and a distinct flexion in *Gaidropsaurus*, as well as less distinct notochord flexion in *Melanogrammus* and *Gadus* (Markle 1982). In the species depicted in these two studies, flexion occurs late in ontogeny when y2a and y1 are growing and ossifying, and terminal centra t1 and t2 have already emerged. In *Lota lota*, we witnessed the slight upward bend as described for other gadiforms above. Notochord flexion in gadiforms occurs much later and is less extensive than in other teleosts [e.g. Arratia and Schultze 1992 (Salmonidae); Balart 1995 (Engraulidae); Bird and Mabee 2003 (Cyprinidae); Burdi and Grande 2010 (Esocidae); Doosey and Domke 2014 (Osmeridae); Faustino and Power 1998 (Sparidae); Gavaia *et al.* 2002 (Soleidae); Hilton and Britz 2010 (Hiodontidae, Arapaimidae, Mormyridae); Moritz *et al.* 2019 (Salmonidae, Thymallidae, Coregonidae, Osmeridae, Stomiidae, Sternoptychidae); Potthoff 1975 (Scombridae); 1980 (Coryphaenidae); Potthoff and Kelley 1982 (Xiphiidae); Thieme *et al.* 2021 (Melanotaeniidae, Adrianichthyidae, Hemiramphidae, Procatopodidae)], but it follows the same mechanism in which the development of the ventral lobe is exaggerated compared to the dorsal lobe. In other teleosts, this occurs during growth of the cartilaginous lower hypurals (hypural 1 and hypural 2) and before ossification of the ural centra. In gadiforms, flexion only starts when y2a and y1 begin to ossify, as well as during or after formation of terminal centra 1 and 2, but also includes growth of y2a and y1 and shape change of y1, (Fig. 2F, G, 3A, B).

Another difference of caudal-fin formation between gadiforms and other teleosts is the appearance of the caudal-fin rays. Typically, two types of fin rays, i.e. principal and procurrent fin rays, occur in teleost caudal fins. In general, principal fin rays form bidirectionally in the ventral lobe and are connected to the hypurals and the parhypural, but can also extend anteriorly, both ventrally and dorsally, and be associated with epurals and neural and haemal spines (e.g. Potthoff 1975, 1980, Potthoff and Kelley 1982, Arratia and Schultze 1992, Burdi and Grande 2010, Schultze and Arratia 2013, Thieme *et al.* 2021). Procurrent fin rays complement the principal fin rays anteriorly and form from posterior to anterior. In contrast, in gadiforms the caudal-fin rays form in the dorsal and ventral lobes of the larval fin fold simultaneously and bidirectionally (Barrington 1937, Matarese *et al.* 1981, Markle 1982, Fahay and Markle 1984). Furthermore, in

Table 2. Overview on gadiform caudal-fin nomenclature used in previous studies and the neutral and homologized nomenclature used in this study († and * indicate small variations in the nomenclature in the marked references).

Neutral nomenclature	**Whitehouse (1935)**	**Barrington (1937)**	**Okamura (1970)** **Matarese *et al.* (1981) †** **Dunn and Matarese (1984) ***	**Markle (1982)** **Fahay and Markle (1984)†** **Markle (1989)** **Meléndez and Markle (1997)** **Endo (2002)***	**Howes (1991)†** **Howes (1993)**	**Paulin (1983)** **Fujita (1990)** **Borden *et al.* (2013)**	**Present study** **Borden *et al.* (2013)**
Terminal centrum 1 (t1)	Last vertebra	Terminal vertebra	Terminal centurm †Anterior ural centrum *Ural centrum 2	Ural centrum 2	Ural centrum 2	Ural centrum 2	Ural centrum 2
Terminal centrum 2 (t2)		Penultimate vertebra	Postterminal centrum †Postural centrum *Ural centrum 1	Ural centrum 1	Preural centrum 1 + Ural centrum 1	Preural centrum 1 + Ural centrum 1	Ural centrum 1
Terminal centrum 3 (t3)		Ante-penultimate vertebra	- †Terminal Preural centrum *Preural centrum 1	Preural centrum 1	Preural centrum 2	Preural centrum 2	Preural centrum 2
Terminal ventral element 1 (y1)	Hypural	Hypural	Hypural 4–6	Hypural 3–5 *superior hypurals	Hypural 3–5	Hypural 3–5	Upper hypural plate (Hyp 3–5)
Terminal ventral element 2a (y2a)	Hypural	Hypural	Hypural 2–3	Hypural 1–2 *inferior hypurals	Hypural 1–2	Hypural 1–2	Lower hypural plate (Hyp 1–2)
Terminal ventral element 2b (y2b)	Ventral radial	Ventral radial	Hypural 1	Parhypural	Parhypural	Parhypural	Parhypural
Terminal ventral element 3a (y3a)		Hypural	†+* Haemal spine	Haemal spine	Anal fin radial † + Haemal spine	(coalesced) haemal spine of PU2	Autogenous haemal spine of PU2
Terminal ventral element 3b (y3b)			†+* Y-Bone	Y-Bone † accessory bone	Y-Bone	Y-Bone	Y-Bone
Terminal dorsal element 1 (x1)	Dorsal caudal radial	Dorsal radial 1	Epural 2	Epural 2	Epural	Epural 2	Epural 2
Terminal dorsal element 2 (x2)	Dorsal caudal radial	Dorsal radial 2	Epural 1	Epural 1	Epural	Epural 1	Epural 1
Terminal dorsal element 3a (x3a)	Epural	Epural	†+* Neural spine	Neural spine	Dorsal fin radial † + neural spine	Neural spine of PU2	Autogenous neural spine of PU2
Terminal dorsal element 3b (x3b)			†+* X-Bone	X-Bone † accessory bone	X-Bone	X-Bone	X-Bone

comparison to other teleosts these fin rays extend far anteriorly, e.g. in *Pollachius virens* anterior to terminal centrum 17.

Similar to the formation of the fin rays, dorsal and ventral skeletal structures of the caudal fin develop almost simultaneously in gadiforms (Agassiz 1877, Barrington 1937, Markle 1982). In other teleosts, ventral elements, i.e. hypurals and the parhypural, form much earlier than dorsal elements, i.e. epurals (Potthoff 1975, 1980, Houde and Potthoff 1976, Potthoff and Kelley 1982, Arratia and Schultze 1992, Balart 1995, Gavaia *et al.* 2002, Bird and Mabee 2003, Burdi and Grande 2010, Doosey and Domke 2014). In *Lota lota* we observed that y2a develops first followed by y2b, x2, as well as x3, and afterwards by y1. Matarese *et al.* (1981) noted that in *Microgadus proximus* (Girard, 1854) the ventral elements form before dorsal elements emerge. Although the development of ventral and dorsal elements seems to be simultaneous, there are slight nuances and at least some ventral elements, i.e. y2a, develop before dorsal elements first appear. While ventral elements y2a and y1 are later connected to terminal centrum t2 and t1, respectively, y2b remains free, not associated with any particular centrum. While in basal teleosts the parhypural is associated with preural centrum 1, it has no corresponding centrum in almost all euteleosts where it is often connected to ural centrum 1 or the compound centrum (e.g. Fujita 1990, Schultze and Arratia 2013). In many comparative studies it was assumed that preural centrum 1 fuses with ural centrum 1 in various euteleosts. However, ontogenetic studies show that in such taxa, preural centrum 1 is not present as a separate entity during any stage of ontogeny (Doosey and Domke 2014, Thieme *et al.* 2021). In gadiforms, no fusion of two centra in the caudal region can be observed and the presence of y2b resembles the condition of the parhypural in other teleosts.

An interesting variation from the development of other teleosts is the late formation of terminal centra 1 and 2, which in gadiforms emerge only after all other vertebral centra ossified (Barrington 1937, Matarese *et al.* 1981). The formation of vertebral centra in *Lota lota* follows a one-directional pattern from anterior to posterior and matches previous reports. In other teleosts, ural centra typically form before some preural centra develop (Potthoff 1975, 1980, Houde and Potthoff 1976, Potthoff and Kelley 1982, Arratia and Schultze 1992, Balart 1995, Gavaia *et al.* 2002, Bird and Mabee 2003, Burdi and Grande 2010, Doosey and Domke 2014, Thieme *et al.* 2021).

As in many other teleosts (e.g. Potthoff 1980, Potthoff and Tellock 1993, Thieme *et al.* 2020), the caudal fin and its skeletal elements in gadiforms start to form before any skeletal structures or precursors of the dorsal and anal fin emerge. Pterygiophores and fin rays start to develop only after all ventral and dorsal elements of the caudal fin are present in cartilage and several fin rays are present both ventrally and dorsally.

The development of the caudal fin of *Lota lota* and other gadiforms shows intriguing differences compared to other teleosts: formation pattern of caudal-fin rays; almost simultaneous occurrence of dorsal and ventral skeletal elements; and sequential development of terminal centra. Yet, there are details with high resemblance to the caudal-fin ontogeny in non-gadiform teleosts: the caudal fin is the first to develop supporting structures and rays (before dorsal and anal fin); caudal elements are preformed in cartilage, like hypurals, epurals, neural- and haemal spines (of at least some preural centra); there are two terminal centra that only support unpaired ventral elements; and in most euteleost taxa an (independent) first preural centrum was lost, which resulted in a parhypural without a corresponding centrum, similar to y2b.

An early notochord flexion typical of other teleosts is absent in gadiforms. However, a slight notochord flexion was observed in multiple gadiform species that shows some similarities to the notochord flexion observed in other teleostean taxa: upward bending of the notochord by increased ventral lobe growth. The major differences are the timing and extent of this flexion. We suggest that this may be the result of a shift in developmental timing. A postponed and less extensive growth of ventral elements, which in gadiforms occurs only after ossification of y1 and y2a, can lead to a reduced flexion of the notochord, because a larger space ventrally to the notochord is available to be occupied by the growing ventral elements before the notochord is bent dorsally.

Diversity of the gadiform caudal-fin skeleton

Caudal fins of gadiforms have previously been examined, described, and depicted (Agassiz 1877, Barrington 1935, 1937, Whitehouse 1935, Monod 1968, Rosen and Patterson 1969, Okamura 1970, Matarese *et al.* 1981, Paulin 1983, Dunn and Matarese 1984, Fahay and Markle 1984, Howes 1989, Markle 1989, Patterson and Rosen 1989, Fujita 1990, Meléndez and Markle 1997, Endo 2002, Borden *et al.* 2013, Grande *et al.* 2013). A PhD thesis recently treated this issue in detail (Roa-Varon 2018); as the results of this study are not yet published, we refrain from discussing them in detail here. Among teleosts, the caudal fins of gadiforms are unique and, even within this taxon, variation of shape and skeletal composition is present. While there are families in which the caudal fin is forked (Bregmacerotidae), rounded (Ranicipitidae, Gadidae), or truncated (Euclichthyidae, Moridae, Gadidae), and externally resembles that of other teleostean taxa, there are other families with more exceptional caudal fins: In Melanonidae, it is pointed and connected to the anal fin; in Macruronidae and Muraenolepididae, it is pointed but both the dorsal and anal fins are connected to the caudal fin; and in Macrouridae, the dorsal and anal fin taper off caudally and a caudal fin is almost not distinguishable (Okamura 1970, Nelson *et al.* 2016).

Within some gadiform taxa, i.e. bathygadids, the macrourid genera *Coelorinchus*, *Coryphaenoides*, *Malacocephalus*, *Nezumia*, and *Ventrifossa*, as well as the trachyrincid *Squalogadus*, and the steindachneriid *Steindachneria*, a caudal skeleton is supposedly absent (Endo 2002: 93). However, we found that in the macrourid *Coryphaenoides rupestris* a caudal fin, although difficult to distinguish, and a caudal fin-like skeleton are present. Previously, Okamura (1970) described the caudal-fin skeleton of *Coelorinchus hubbsi* Matsubara, 1936 and noted that two conditions may be found (if a caudal fin could be identified): either a series of elongated vertebral centra without neural and haemal spines surrounded by 'interneurals' and 'interhaemals' to which fin rays articulate are present, or a caudal fin-like organ characterized by a modified last centrum as a bony plate that supports a large cartilaginous plate is present. The second condition is similar to our observations in *Coryphaenoides rupestris,* and Okamura (1970) believed this to be the result of a recovery process if the tail in a living specimen was broken or torn off, which

he termed 'pseudocaudal', differing from the original use of the term by Goodrich (1909, 1958). Based on his description of the first condition, this may be true but it makes the examination of the true caudal fin of macrourids more challenging, as specimens with a caudal fin representing the first condition are extremely rare in collections. Okamura (1970) proceeded to interpret some of his 'interhaemals' to be the same as the split y1, y2a, and y2b in morids. However, this hypothesis currently cannot be evaluated due to missing specimens that show this caudal-fin condition. Howes and Crimmen (1990) noted that in bathygadids the caudal-fin skeleton is similar to Okamura's (1970) second condition but pointed out that it is difficult to distinguish between a normal and a regenerated caudal fin. Due to the uncertainty of the true structure of the caudal-fin skeleton of macrourids and bathygadids (Okamura 1970, Howes and Crimmen 1990), the unclear homology of caudal elements of *Steindachneria* to other gadiforms (Fahay 1989, Borden *et al.* 2013), and the scarce availability of data of *Squalogadus* (Okamura 1989), we will not include the aforementioned taxa in the skeletal comparison.

Within gadiforms, different numbers of terminal centra support the caudal fin. In most species there are two terminal centra, t1 and t2, to which two unpaired ventral elements, y1 and y2a, are connected (either by fusion or articulation). Endo (2002) reported that t1 and t2 are fused (based on the respective appendages) in *Macruronus novaezelandiae* (Hector, 1871) of the family Macruronidae. However, Howes (1991) previously showed that t1 and t2 are present in another specimen of *M. novaezelandiae*. There are no reports of any other species in which such a fusion occurs, although we observed some malformations, including terminal centra fusion, in single specimens, e.g. *Pollachius virens* (DMM IE/12222 standard length (SL) = 46.0 mm). In many gadiforms, these two centra are characterized by being slightly bent upwards and three degrees of flexion can be distinguished: (i) no bending (terminal centrum ends straight, e.g. *Bregmaceros* species, *Merluccius merluccius*, *Muraenolepis microps*; Fig 4A–D, 5B), (ii) bending within the last terminal centrum (e.g. *Guttigadus*, *Melanonus*; Howes 1993, Meléndez and Markle 1997), and (iii) terminal centra 1 and 2 are slightly directed dorsally (e.g. *Trachyrincus scabrus*, *Trisopterus esmarkii*; Fig. 4A, 5C). In other teleosts, a more pronounced flexion of the vertebral column in the caudal region is visible either due to the bending of ural centrum I and II or due to the upward-bent posterior portion of the urostyle/compound centrum (e.g. Rosen and Patterson 1969, Fujita 1990). Based on our observations and drawings from previous studies (Whitehouse 1935, Rosen and Patterson 1969, Matarese *et al.* 1981, Dunn and Matarese 1984, Fahay and Markle 1984, Markle 1989, Meléndez and Markle 1997, Endo 2002, Borden *et al.* 2013, Grande *et al.* 2013), we found no clear pattern of flexions within these genera or families, although absence of species in some families restricts the validity of this statement.

Terminal centrum t1 is characterized by its distinct shape: its anterior portion is shaped like a half centrum, whereas the posterior portion is cone-like and can be bent upward. A similar shape of the most posterior vertebral centrum can be found in other teleosts and often is termed compound centrum (Schultze and Arratia 2013, Thieme *et al.* 2022). t1 can bear a paired dorsal outgrowth that is similar to a neural arch in most examined species, but not enclosed dorsally, e.g. Bregmacerotidae, *Mora*, *Physiculus*, *Muraenolepis*, *Macruronus*, Ranicipitidae, and Lotinae (Markle 1989, Fujita 1990, Howes 1991, Endo 2002). In some gadiform taxa this outgrowth extends postero-dorsally, e.g. *Enchelyopus*, *Gaidropsaurus*, *Eretmophorus*, *Euclichthys*, *Urophycis*, and Gadinae (Markle 1989, Patterson and Rosen 1989, Fujita 1990, Howes 1991), while in others it is completely absent, e.g. *Ciliata*, *Guttigadus*, *Laemonema*, *Melanonus*, *Phycis*, *Trachyrincus*, and *Steindachneria* (Meléndez and Markle 1997, Endo 2002, Borden *et al.* 2013). Within some larger taxa, e.g. Gadinae and Lotinae, the outgrowth is generally similar between the respective species. However, there are other species, where the outgrowth varies even between individuals, e.g. *Gadella jordani* (extended or neural arch-like) or *Merluccius merluccius* (extended, neural arch-like, or absent). Rosen and Patterson (1969) depicted the outgrowth in *Eretmophorus* as a separate element dorsally to t1 that they termed uroneural. Similarly, Markle (1982: 3430 and fig. 7) described a separated uroneural dorsally to t1 in *Bregmaceros*. Other studies and data presented herein, show that a separate element dorsally to t1 is not present in gadiforms and that the uroneural-like structure more likely is a neural arch that is fused to t1. Furthermore, developmental data show that this structure develops without a cartilaginous precursor and directly from t1, which is different from a uroneural as shown by Schultze and Arratia (2013).

Terminal centrum t2 is shaped like other caudal vertebrae, but in contrast has a similar paired dorsal outgrowth as t1, which might represent its neural arch. However, there are also differences in its shape. It can be small, not extending above the centrum, e.g. *Phycis blennoides* (Fig. 4B), extending dorsally in shape of a triangle, e.g. *Merluccius merluccius* (Fig. 4C), or completely absent, e.g. *Trachyrincus scabrus* (Fig. 5C–E).

Ventral terminal element y1 is positioned posterior to t1 and is fused to it in all gadiforms (e.g. Patterson and Rosen 1989, Fujita 1990, Howes 1991, Endo 2002, Borden *et al.* 2013). In most gadiforms, y1 is plate-like and more, e.g. *Bregmaceros* (Fig. 4D), or less, e.g. *Muraenolepis* (Fig. 5B), enlarged with a cartilaginous posterior margin. Within three gadiform taxa, i.e. Euclichthyidae, Moridae, and Melanonidae, y1 consists of three separate elements that each are fused to t1 and in *Euclichthys* are fused distally and share a cartilaginous distal margin (Rosen and Patterson 1969, Markle 1989, Patterson and Rosen 1989, Fujita 1990, Howes 1993, Endo 2002, Borden *et al.* 2013). While all herein examined specimens of *Gadella jordani* show three separate elements, which agrees with previous findings (Fujita 1990) and the number of elements reported for *Eretmophorus kleinenbergi* Giglioli, 1889 (Rosen and Patterson 1969), *Gadella edelmanni* (Brauer, 1906) (Okamura 1970), *Guttigadus* and *Laemonema* (Meléndez and Markle 1997), *Physiculus japonicus* Hilgendorf, 1879 (Fujita 1990), and *Melanonus zugmayeri* Norman, 1930 (Endo 2002), we examined two specimens of *Mora moro* that show only two elements, which similarly was reported for *Euclichthys polynemus* McCulloch, 1926 (Markle 1989, Patterson and Rosen 1989). In one specimen of *Mora moro* the upper of the two elements is enlarged, which may indicate the fusion of two formerly separate elements. Dunn and Matarese (1984) reported that in *Raniceps* y1 consists of two elements, of which the upper one is enlarged, which are fused anteriorly and posteriorly, and remarked that they found a third element in one

larva. This is similar to our observations in the previously mentioned specimen of *Mora moro*. In the herein examined morids, a paired and ventrally directed outgrowth is present between t1 and the ventral element of y1, which may be characteristic for this taxon. However, only Fujita (1990) depicted this character for *Physiculus japonicus* and *Gadella jordani* and it was not mentioned nor depicted in any other study.

Antero-ventrally to y1, terminal element y2a is positioned ventrally to t2 with which it either articulates via cartilage or to which it is fused. In most gadiform species, the connection is via cartilage and only few taxa of which the caudal-fin skeleton was studied, i.e. Bregmacerotidae and *Trachyrincus*, have y2a fused to t2 (e.g. Okamura 1970, Paulin 1983, Dunn and Matarese 1984, Markle 1989, Patterson and Rosen 1989, Howes and Crimmen 1990, Howes 1991, 1993, Endo 2002, Jawad *et al.* 2020). The distal tip of y2a is cartilaginous. In Moridae, *Euclichthys*, *Raniceps*, and *Melanonus*, y2a consists of two separate elements that are only fused at their base (Paulin 1983, Dunn and Matarese 1984, Markle 1989, Patterson and Rosen 1989, Howes 1993, Endo 2002, Jawad *et al.* 2020). In other gadiforms, i.e. Merlucciidae and Gadidae, y2a is distally broadened in the anterior–posterior direction, which may indicate that originally two elements fused to form y2a.

A separated and autogenous terminal element y2b is present anterior to y2a and ventral to t2 in all gadiform species, except species with an extremely reduced caudal-fin skeleton, i.e. Bathygadidae, Macrouridae, Steindachneriidae, and Macrouroidinae (Okamura 1970, Fahay 1989, Howes and Crimmen 1990). In some species y2b is elongated, in others it is distally broadened. In specimens studied herein y2b always has a cartilaginous distal tip.

Two separate and autogenous terminal elements, x1 and x2, are present dorsally to t1 and t2 in all gadiform species (Okamura 1970, Fahay 1989, Howes and Crimmen 1990). The shape of x1 and x2 does not vary much between gadiform species. In some species, e.g. *Gadella jordani* and *Merluccius merluccius*, we observed bilateral outgrowths ventrally to x2, or x1 and x2 that appear to cover the spinal cord dorsally. Much like in the ventral terminal elements, the distal tips of x1 and x2 are cartilaginous.

In contrast to t1 and t2, terminal centrum t3 has functional neural and haemal arches in all species with a caudal-fin skeleton. Neural and haemal arches are fused to the centrum, except for Phycinae and *Raniceps*, in which the haemal arch articulates with the centrum via cartilage (Dunn and Matarese 1984, Endo 2002). t3 differs much from the other terminal centra, as the neural and haemal spines of t3 are autogenous with cartilaginous distal tips, much like x1 and x2 or y1, y2a, and y2b. Therefore, they are regarded as terminal elements, i.e. x3a and y3a. In many specimens we found an additional, non-autogenous haemal and/or neural spine at t3, which coincides with previous reports and figures (e.g. Fig 3F, 4C). These may be regarded as malformations, as they do not occur regularly within a species across most gadiform taxa. In some cleared and stained specimens, e.g. *Gadiculus argenteus* and *Gaidropsaurus mediterranus*, we observed the ventral artery running through the haemal arches of terminal centra up to t3. In these specimens, the ventral artery splits after exiting the haemal arch of t3, anterior to y2b, and two branches run posterior bilateral to y2a to y1. In non-gadiform teleosts the ventral artery generally splits behind the haemal arch of preural centrum 2 and in front of the parhypural (Schultze and Arratia 2013).

A supposedly characteristic feature of gadiforms is the X- and Y-bones (Fahay and Markle 1984), which in this study correspond to x3b and y3b. They are positioned anterior to x3a and y3a, respectively, and like other terminal elements are characterized by cartilaginous distal tips. In all species studied herein, as well as all gadiform species previously studied, either both, x3b and y3b, are present or both are absent: x3b and y3b are present in Bregmacerotidae, Euclichthyidae, Gaidropsarinae, Merlucciidae, Moridae, Ranicipitidae, Phycinae, and *Trachyrincus*; and absent in Bathygadidae, Gadinae, Lotinae, Macrouridae, Macruronidae, Melanonidae, Muraenolepididae, and Steindachneriidae. In most species they are slender bones, except for Euclichthyidae, where in *Euclichthys* x3b is small and round and y3b is stout.

A true caudal fin or not? Evolution and identity of the gadiform caudal fin

In recent molecular phylogenetic studies, the Gadiformes were retrieved as part of the Paracanthopterygii, including the Percopsiformes, Zeiformes, and *Stylephorus*, the sister-taxon to the Gadiformes (Betancur-R *et al.* 2013, 2017). The caudal-fin skeleton of Percopsiformes incorporates two ural centra, a lower hypural plate that is connected to ural centrum 1, as well as four upper hypurals that are connected to ural centrum 2, a parhypural that is in close contact with ural centrum 1, but missing a respective centrum, two epurals, two uroneurals and a haemal and neural spine of preural centrum 2 with cartilaginous tips (Fujita 1990). The zeiform caudal skeleton generally differs from that of percopsiforms by the presence of a compound centrum instead of two ural centra, the absence of hypural 6 and a parhypural that is separated from the compound centrum in some species (Fujita 1990). *Stylephorus* has a highly modified caudal-fin skeleton that is also difficult to homologize with that of other teleosts. Borden *et al.* (2013) suggested that two ural centra are present that show no flexion, and that the parhypural and two hypurals are associated with ural centrum 1, while a hypural plate is fused to ural centrum 2. No other caudal elements are present.

In studies of the evolution of the gadiform caudal fin, the assumption was that taxa with continuous dorsal and anal fins and tapering tails reflect the ancestral gadiform caudal fin, whereas taxa with seemingly teleost-like caudal fins were more derived within gadiforms (Fahay and Markle 1984). Recently, two studies updated the phylogenetic relationships within gadiforms based on extensive genomic analyses (Han *et al.* 2021, Roa-Varón *et al.* 2021, Fig. 6). While the phylogeny provided in the preprint from Han *et al.* (2021) does not include some gadiform taxa such as Euclichthyidae, Macruronidae, and Steindachneriidae, Roa-Varón *et al.* (2021) analysed species of all recognized families. Results of both studies show many similarities, such as the Bregmacerotidae presumably being the earliest branching family within the Gadiformes, as well as three larger clades, i.e. Gadidae comprising Phycinae, Lotinae, Gadinae, and Gaidropsarinae, the subclade comprising Trachyrincidae, Euclichthyidae, Melanonidae, and Muraenolepididae (subclade I after Roa-Varón *et al.* 2021), and the subclade comprising Moridae, Macrouridae, Bathygadidae, Macruronidae, and Steindachneriidae

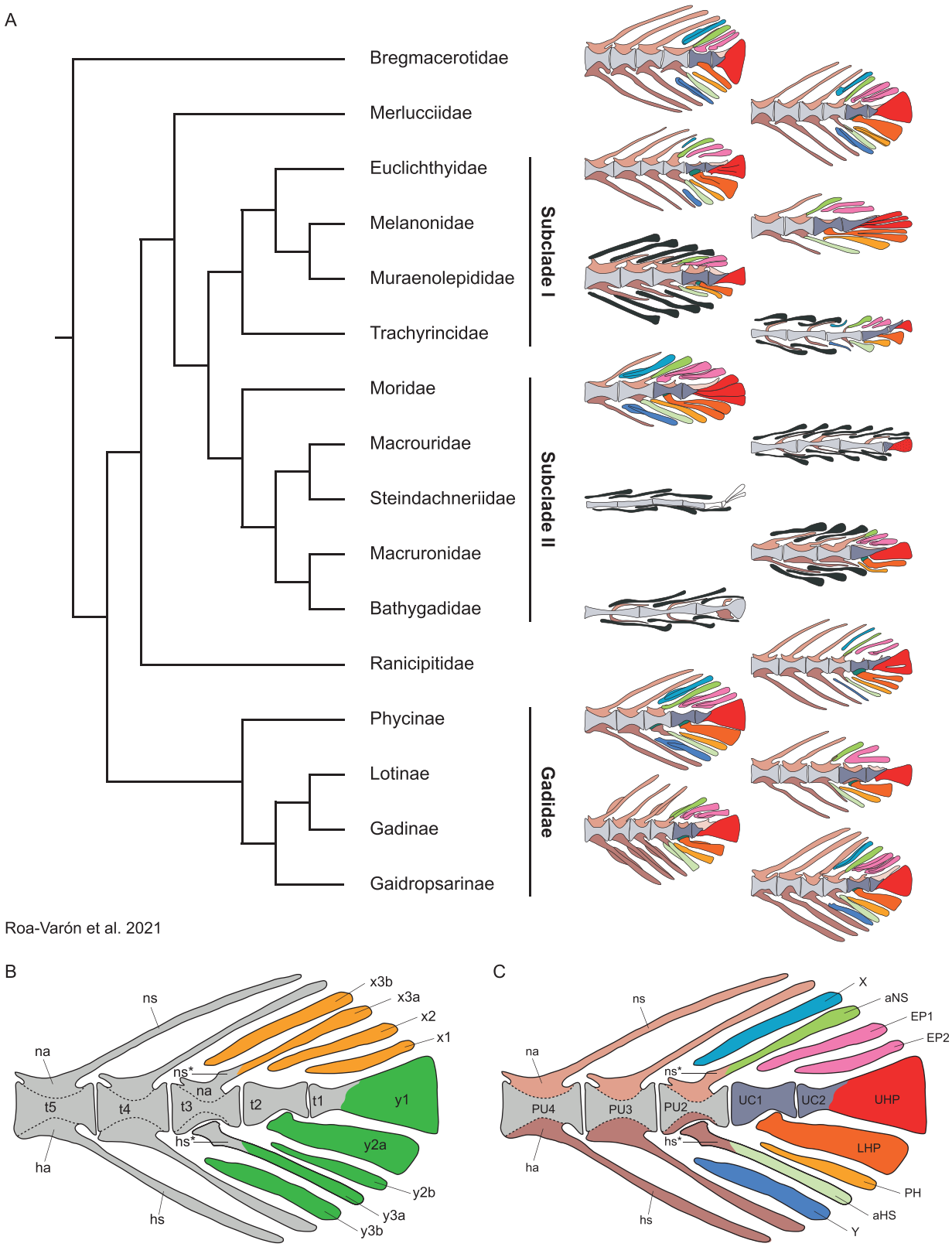

Figure 6. A, phylogenetic hypotheses of gadiforms of (Roa-Varón *et al.* 2021). Schematic drawings of the caudal-fin skeleton with one representative of each gadiform family/subfamily (taxonomic nomenclature following Nelson *et al.* 2016), respectively, are mapped on the trees: Bregmacerotidae, *Bregmaceros* sp.; Merlucciidae, *Merluccius merluccius*; Euclichthyidae, *Euclichthys polynemus* (Markle 1989, Patterson and Rosen 1989); Melanonidae, *Melanonus zugmayeri* (Howes 1993, Endo 2002); Muraenolepididae, *Muraenolepis microps*; Trachyrincidae, *Trachyrincus scabrus*; Moridae, *Gadella jordani*; Macrouridae, *Coryphaenoides rupestris*; Steindachneriidae, *Steindachneria argentea* (Borden *et al.* 2013); Macruronidae, *Macruronus novaezelandiae* (Howes 1991, Endo 2002); Bathygadidae, *Bathygadus melanobranchus* (Howes and Crimmen 1990); Ranicipitidae, *Raniceps raninus* (Dunn and Matarese 1984); Phycinae, *Phycis blennoides*; Lotinae, *Lota lota*; Gadinae, *Gadiculus argenteus*; Gaidropsarinae, *Gaidropsarus mediterraneus*. Colour code corresponds to terminology of (B), dark grey elements are

(subclade II after Roa-Varón *et al.* 2021). There are few differences between the two studies: the position of Merlucciidae, sister-taxon to the clade comprising Gadidae, subclade I, and subclade II in Han *et al.* (2021) but sister-taxon to subclade I and II in Roa-Varón *et al.* (2021), and Ranicipitidae, sister-taxon to Gadidae in Han *et al.* (2021) but sister-taxon to the clade comprising Merlucciidae, subclade I and subclade II in Roa-Varón *et al.* (2021).

With these new phylogenetic hypotheses, we can shed light on the evolution of the caudal-fin skeleton in gadiforms. Two terminal elements with unpaired ventral appendages are present in gadiforms, which changed within subclade II where, maybe, one terminal centrum remains in some macrourids and no terminal centra can be distinguished in *Steindachneria* and bathygadids. While in many gadiform species, ventral elements y1 and y2a are plate-like, partly separated elements can be found in subclades I (Euclichthyidae, Melanonidae) and II (Moridae), as well as in Ranicipitidae. Due to separated ventral elements associated with terminal centra in other Paracanthopterygii, i.e. upper hypurals in Zeiformes and Percopsiformes, and the tendency for hypurals to fuse instead of separate (Thieme *et al.* 2022), we conclude that separate ventral elements are most likely the ancestral character state in Gadiformes. Further studies on the caudal development of taxa with separated ventral elements will clarify this hypothesis. Further, y1 is generally fused to t1, whereas y2a is connected to t2 via cartilage in many gadiform taxa, which probably changed three times within the evolution of gadiforms, i.e. in Bregmacerotidae, Melanonidae, and Trachyrincidae. Other caudal elements, such as y2b, y3a, x1, x2, and x3a, are generally present in all gadiforms, except Marcouridae and *Steindachneria*, and Bathygadidae, where they presumably were lost. y3a and x3a, which are characterized by cartilaginous precursors and cartilaginous distal tips in adults, can also be observed in Percopsiformes and Zeiformes where the neural and haemal spine of preural centrum 2 have cartilaginous tips (Fujita 1990). y3b and x3b were presumably already present in ancestral gadiforms and lost multiple times within gadiforms, i.e. at least once within subclade I, once in subclade II, and at least once in gadids (Fig. 6). A caudal fin connected to the anal and dorsal fins presumably evolved at least twice within gadiforms, i.e. within subclade I and within subclade II.

With this new understanding of the caudal-fin evolution in Gadiformes, we can now evaluate previous hypotheses. Boulenger (1902) based his 'neocaudal' hypothesis on the assumption that Macrouridae are the most basal taxon within the Gadiformes and due to the absence of a caudal fin in this taxon, the caudal fin of other gadiforms had to evolve anew. As discussed above this hypothesis should be discarded, as the most common ancestor of all gadiforms presumably had a caudal-fin skeleton much like that of morids, melanonids, or ranicipitids. The 'pseudocaudal' hypothesis (Goodrich 1909, 1958) and the 'continuous caudal' hypothesis (Fahay and Markle 1984, Markle 1989) are equally based on the assumption that the dorsal and anal fins were connected to the caudal fin in a common ancestor of all gadiforms and terminal elements, therefore, correspond to pterygiophores. These hypotheses should also be discarded as no such connection of dorsal and anal fins with the caudal fin was present in ancestral gadiforms. Under these assumptions other arguments that claim the gadiform caudal fin is different from a common teleost caudal fin, such as the missing of a notochord flexion or the absence of uroneurals, have to be regarded as gadiform apomorphies derived from a 'true' teleost caudal fin.

CONCLUSION

To conclude, we homologize the caudal-fin elements of gadiforms (based on our neutral nomenclature, Fig. 6A) with the caudal-fin skeleton of other teleosts (Fig. 6B): Terminal centrum t1 equals ural centrum II. Terminal centrum t2 equals ural centrum I. Ventral element y1 equals the upper hypurals, i.e. maybe up to three hypurals, which in taxa such as *Moro mora* can be distinguished as single elements and are homologous to hypurals 3 to 5 in other teleosts. Ventral element y2a and the lower hypurals, i.e. up to two hypurals that in taxa such as Moridae, *Euclichthys*, *Raniceps*, and *Melanonus* can be distinguished and are homologous to hypurals 1 and 2. Ventral element y2b equals the parhypural to which no terminal centrum corresponds and, therefore, we conclude the absence of preural centrum 1 in gadiforms. Ventral element y3b equals an autogenous haemal spine of preural centrum 2. Dorsal elements x1 and x2 equal epurals. Dorsal element x3a equals an autogenous neural spine of preural centrum 2.

For x3b and y3b, which previously were named X- and Y-bones, no homologous structures are present in any closely related taxon. In *Oryzias* (Beloniformes) a similar structure, i.e. the extra caudal ossicle, is present, which is an evolutionary novelty in this taxon (Thieme *et al.* 2022). While it was hypothesized that the X- and Y-bones derived from pterygiophores (Boulenger 1902, Barrington 1937, Fahay and Markle 1984), their morphology, i.e. no cartilaginous proximal tip, and the absence of the connection of the dorsal or anal fins with the caudal fin in ancestral gadiforms disprove this theory. Other hypotheses stated that they may represent dorsal and haemal spines of a terminal centrum that was lost or never formed (Rosen and Patterson 1969:420), or that they could correspond to epurals and hypurals with a genetic programme being activated one somite more anterior than usually (Markle 1989). Although additional genetic data are needed to test these hypotheses, we herein conclude that X- and Y-bones are evolutionary novelties that probably evolved in ancestral Gadiformes and were lost multiple times, i.e. at least once in Gadidae, once or twice in subclade I, and once in subclade II, according to recent phylogenetic hypotheses (Han *et al.* 2021, Roa-Varón *et al.* 2021).

pterygiophores, beige elements represent the neural arch of ural centrum II, identity of white elements uncertain. B, neutral nomenclature for skeletal elements of the caudal fin in Gadiformes used in this study according to Figure 1; C, elements of the gadiform caudal-fin skeleton homologized with the teleostean caudal-fin skeleton. Abbreviations: aHS, autogenous haemal arch; aNS, autogenous neural arch; cc, cartilaginous connection; EP, epural; ha, haemal arch; hs, haemal spine; LHP, lower hypural plate; na, neural arch; neural spine; PH, parhypural; PU, preural centrum; UHP, upper hypural plate; UC, ural centrum; X, X-bone; Y, Y-bone.

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DATA AVAILABILITY

All specimens used in this study (Tab. 1) are deposited in museum collections and are accessible via the respective institutions.

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