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Timo Moritz, Jan Buchert, Nalani K Schnell

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TIMO MORITZ[1,2,*], JAN BUCHERT[1] and NALANI K. SCHNELL[3]

[1]*Deutsches Meeresmuseum, Katharinenberg 14–20, 18439 Stralsund, Germany*
[2]*Institute of Zoology and Evolutionary Research, Friedrich-Schiller-University Jena, Ebertstrasse 1, 07743 Jena, Germany*
[3]*Institut Systématique Evolution Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, Station Marine de Concarneau, Place de la Croix, 29900 Concarneau, France*

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Caudal fin skeletons of teleost fishes have been well-studied in the context of phylogenetic relationships. However, the small cartilages at the distal end of the diastema, the 'median caudal cartilages', have gained only little attention so far. For the first time we here report their taxa-dependent variable three-dimensional structure. We investigated 143 species of 62 teleost families for this study. The shape and arrangement of these cartilages is uniform in some systematic groups, e.g. Alepocephalidae, Platytroctidae or Myctophiformes; in other taxa there is high intrataxon variability, e.g. Stomiiformes or Aulopiformes. Shape, number and presence/absence may even vary in certain species, e.g. *Osmerus eperlanus*, *Thymallus thymallus* or *Gymnocorymbus ternetzi*. The function of median caudal cartilages remains unclear. It has been suggested that they might be related to fin-ray support, although an obvious relation to fin rays is lacking in several taxa. Their presence and size is not dependent on the size of the diastema. Median caudal cartilages seem to have evolved at the base of clupeocephalans and occur in many taxa up to about aulopiforms, as well as single beryciforms. It seems that they are often reduced at different systematic levels and may have re-evolved in some taxa.

ADDITIONAL KEYWORDS: caudal fin – Clupeocephala – diastema – morphology – Teleostei.

INTRODUCTION

Teleosts have many unique characters in their caudal fin skeleton, such as their principal configuration of two vertebral centra, a maximum of seven hypurals, of which the first two articulate with the first caudal centrum, or the possession of uroneurals. All these characters clearly support the monophyly of teleosts, but the caudal fin skeleton has undergone many evolutionary modifications in different taxa (Monod, 1968; Fujita, 1990), and thus often provides meaningful indicators of phylogenetic relationships (e.g. Patterson & Rosen, 1977; Arratia & Schultze, 1992; Johnson & Patterson, 1996; Arratia, 1997).

Despite the large number of studies including or focusing on the caudal fin skeleton in teleosts, cartilaginous elements are often overlooked or neglected. Prominent examples are the cartilages positioned in the distal area of the diastema. Such cartilages were not displayed and described in the otherwise comprehensive study of Monod (1968) on caudal fin skeletons of teleosts. The only other study of comparable extent by Fujita (1990) recorded such cartilages and listed them in an overview table, but did not draw detailed conclusions on functionality or phylogenetic significance of them. The latter author also provided a detailed nomenclature of cartilaginous elements in caudal fins of teleosts (Fujita, 1989) and used the term 'median caudal cartilage' (CMC) for the cartilages positioned in the distal area of the diastema. This term was already used by Markle (1976) in his study on alepocephaliforms. Other names for this element found in the literature are 'intercalary cartilage' (Cope, 1890) or 'median caudal radials' (Markle, 1976). Arratia & Schultze (1992) only

*Corresponding author. E-mail: timo.moritz@outlook.com

described them as 'cartilaginous plates supporting caudal fin rays' without providing a separate name.

Besides the note that median caudal cartilages are 'mainly restricted to rather primitive fish groups' (Fujita, 1989: 27), little interpretation was done on their phylogenetic importance until Johnson & Patterson (1996) used the respective cartilages as characters in their extensive morphological analysis of the interrelationships of basal euteleosts. Therein they used two characters referring to the CMCs: first, the presence or absence of CMCs, and second, their relation to caudal fin rays. Johnson & Patterson (1996) regarded the presence of CMCs as an apomorphy of euteleosts (including alepocephaliforms) and they found reductions of CMCs in six euteleostean lineages. Furthermore, they found two conditions of relationships between CMCs and fin rays: either, each CMC supports one fin ray, i.e. the upper CMC the lowest ray of the upper lobe of the caudal fin and the lower CMC the uppermost ray of the lower lobe, or alternatively, both CMCs support together the lowest ray of the upper lobe. Of these conditions Johnson & Patterson (1996) regarded the first as more primitive. Since this study, several new molecule-based phylogenetic hypotheses on basal teleosts have been presented (e.g. Near *et al.*, 2012; Betancur-R *et al.*, 2017; Straube *et al.*, 2018). In the present study, we investigated how far the presence/absence distribution and fin-ray support configurations agree with present phylogenetic hypotheses based on molecular analyses. Close examination of CMCs revealed more details and a higher diversity of these small cartilages. There are apparently more than two configurations in which CMCs can be involved in fin-ray support. Furthermore, all previous investigations studied CMCs only in lateral view (e.g. Markle, 1976; Fujita, 1990; Johnson & Patterson, 1996), depicting them as somewhat roundish cartilages, but overlooking a variety of the three-dimensional structure of CMCs in different taxa.

The present study gives an overview on the distribution of CMCs among teleosts, describes their relation to fin rays and their three-dimensional structure and proposes an evolutionary history of these structures in teleosts and in different teleostean lineages.

MATERIAL AND METHODS

Focusing on basal teleosts, 143 species from 62 families in 22 orders were investigated for the presence of median caudal cartilages (Table 1). Studied specimens are located at the ichthyological collections of the Deutsches Meeresmuseum (DMM), Stralsund, Germany, the Muséum national d'Histoire naturelle (MNHN), Paris, France, the Museum of Comparative Zoology (MCZ), Cambridge, USA, the National Museum of Nature and Science (NSMT), Tokyo, Japan, the Scripps Institution of Oceanography, San Diego (SIO), USA and the Smithsonian National Museum of Natural History (USNM), Washington, USA. All specimens were treated with the clearing and double-staining method according to a slightly modified protocol of Dingerkus & Uhler (1977) and Taylor & Van Dyke (1985).

In the study presented here, the 'median caudal cartilages' (CMCs) refer to the free cartilages that occur between or near the distal tips of the second and third hypurals (Fig. 1; Fujita, 1989). They usually appear as two separate elements, but sometimes there is only one (Fujita, 1989). In case there are small additional cartilages close by, they are referred to as 'accessory cartilages'.

To determine the relative size of the diastema, the vertical distance from the most ventral edge of hypural 1 to the most dorsal edge of the last hypural (see blue line in Fig. 1) was measured perpendicular to the body axis. The diastema between hypural 2 and 3 was measured along the same connecting line (see red line in Fig. 1). In some significant cases, the width of the CMCs in posterior view has been compared to the width of the hypurals (for orientation see Fig. 1B). Measurements were taken from photographs using ImageJ v.1.50i software. Measurements for SL were taken with a digital calliper; sizes up to 120 mm are given with one digit after the decimal point and above this size rounded to the next millimetre. Photographs were taken either using a Leica M165C stereomicroscope with a Leica DFC425 camera and the Leica Application Suite (v.4.3.0) software or using an Axiocam microscope camera attached to a ZEISS Discovery V20 stereomicroscope and processed with the Zeiss ZEN software. Anatomical nomenclature follows Fujita (1989, 1990) and the taxonomy follows Eschmeyer *et al.* (2018). Results are given in systematic order, principally following Nelson *et al.* (2016). For the phylogenetic relationships of major clupeocephalan clades we follow Straube *et al.* (2018) and Betancur-R *et al.* (2017).

RESULTS

THE OCCURRENCE OF CARTILAGES IN THE DIASTEMA

In all investigated species belonging to the Elopiformes, Osteoglossiformes, Clupeiformes, Gonorynchiformes, Cypriniformes, Siluriformes, Lepidogalaxiiformes, Esociformes, Galaxiidae, Ateleopodidae, Melamphaidae, Anoplogastridae, Diretmidae, Monocentridae, Trachichthyidae and

Table 1. Studied specimens; all cleared and double stained. Specimens are deposited at the Deutsches Meeresmuseum (DMM), Stralsund, Germany, the Muséum national d'Histoire naturelle (MNHN), Paris, France, the Museum of Comparative Zoology (MCZ), Cambridge, USA, the National Museum of Nature and Science (NSMT), Tokyo, Japan, the Scripps Institution of Oceanography (SIO), San Diego, USA, and the Smithsonian National Museum of Natural History (USNM), Washington, USA

Taxon	Number	SL (mm)	Registration
Elopidae			
Elops senegalensis Regan, 1909	1	40.2	DMM IE/11804
Elops senegalensis	2	29.3–38.2	DMM IE/11206
Osteoglossidae			
Osteoglossum bicirrhosum (Cuvier, 1829)	1	91.9	DMM IE/11035
Mormyridae			
Brienomyrus sp.	1	70.5	DMM IE/11059
Gnathonemus petersii (Günther, 1862)	1	65.4	DMM IE/11055
Hippopotamyrus pictus (Marcusen, 1864)	1	75.9	DMM IE/12203
Isichthys henryi Gill, 1863	2	16.5–31.6	DMM IE/11052
Mormyrops anguilloides (Linnaeus, 1758)	2	72.9–80.5	DMM IE/13294
Mormyrus caschive Linnaeus, 1758	1	72.6	DMM IE/12224
Petrocephalus bovei (Valenciennes, 1847)	2	51.7–56.0	DMM IE/13275
Petrocephalus pallidomaculatus Bigorne & Paugy, 1990	2	63.0–67.6	DMM IE/13279
Pollimyrus adspersus (Günther, 1866)	3	27.3–47.2	DMM IE/13274
Pollimyrus isidori (Valenciennes, 1847)	3	27.3–47.2	DMM IE/13274
Denticipitidae			
Denticeps clupeoides Clausen, 1959	2	30.0–30.6	DMM IE/11417
Engraulidae			
Anchoa mitchilli (Valenciennes, 1848)	1	40.0	DMM IE/11209
Engraulis encrasicolus (Linnaeus, 1758)	1	103.5	DMM IE/5845
Stolephorus chinensis (Günther, 1880)	2	55.6–72.2	DMM IE/11017
Clupeidae			
Clupea harengus Linnaeus, 1758	3	83.0–115.5	DMM IE/11027
Dorosoma cepedianum (Lesueur, 1818)	1	86.0	DMM IE/11019
Harengula jaguana Poey, 1865	1	36.4	DMM IE/11023
Pellonula leonensis Boulenger, 1916	2	25.2–31.0	DMM IE/11018
Sardina pilchardus (Walbaum, 1792)	2	107.5–111.6	DMM IE/11025
Sprattus sprattus (Linnaeus, 1758)	1	61.9	DMM IE/11026
Alepocephalidae			
Alepocephalus bicolor Alcock, 1891	1	190.0	DMM IE/13474
Alepocephalus rostratus Risso, 1820	2	114.2–141.0	DMM IE/13803
Alepocephalus rostratus	1	230.0	DMM IE/14846
Xenodermichthys copei (Gill, 1884)	1	110.8	DMM IE/10190
Xenodermichthys nodulosus Günther, 1878	4	146.0–151.0	DMM IE/14310
Platytroctidae			
Holtbyrnia anomala Kreft 1980	2	49.0–62.1	DMM IE/13490
Holtbyrnia anomala	2	101.8–130.0	DMM IE/13806
Holtbyrnia anomala	1	114.2	DMM IE/11744
Holtbyrnia anomala	1	137.0	DMM IE/12210
Holtbyrnia anomala	1	150.0	DMM IE/13802
Holtbyrnia macrops Maul, 1957	1	91.6	DMM IE/10137
Holtbyrnia macrops	1	137.0	DMM IE/10529
Maulisia argipalla Matsui & Rosenblatt, 1979	1	111.0	DMM IE/10459
Maulisia mauli Parr, 1960	1	116.2	DMM IE/10177
Normichthys operosus Parr, 1951	3	64.0–81.1	DMM IE/13808
Normichthys operosus	1	87.0	DMM IE/13804
Normichthys operosus	1	88.6	DMM IE/13804
Normichthys operosus	1	92.6	DMM IE/11040

Table 1. Continued

Taxon	Number	SL (mm)	Registration
Normichthys operosus	1	96.8	DMM IE/13807
Normichthys operosus	1	105.4	DMM IE/13805
Searsia koefoedi Parr, 1937	1	94.2	DMM IE/10068
Searsia koefoedi	1	103.0	DMM IE/13828
Chanidae			
Chanos chanos (Forsskål, 1775)	1	57.3	DMM IE/11074
Gonorynchidae			
Gonorynchus abbreviatus Temminck & Schlegel, 1846	1	81.8	DMM IE/11730
Phractolaemidae			
Phractolaemus ansorgii Boulenger, 1901	1	80.7	DMM IE/11045
Kneriidae			
Cromeria occidentalis Daget, 1954	1	22.0	DMM IE/13824
Cromeria occidentalis	1	22.4	DMM IE/13825
Kneria stappersii Boulenger, 1915	6	13.3–25.8	DMM IE/12025
Cyprinidae			
Barboides gracilis Brüning, 1929	6	8.7–10.2	DMM IE/12034
Chelaethiops bibie (Joannis, 1835)	3	37.4–44.8	DMM IE/12216
Ctenopharyngodon idella (Valenciennes, 1844)	1	45.0	DMM IE/11109
Danio rerio (Hamilton, 1822)	1	28.3	DMM IE/11770
Dawkinsia tambraparniei (Silas, 1954)	3	26.6–31.0	DMM IE/12072
Enteromius macrops (Boulenger, 1911)	4	33.0–44.6	DMM IE/13278
Gobio gobio (Linnaeus, 1758)	1	62.0	DMM IE/12051
Labeo coubie (Rüppell, 1832)	1	53.7	DMM IE/13276
Opsarius bernatziki (Koumans, 1937)	2	58.2–62.2	DMM IE/13291
Rutilus rutilus (Linnaeus, 1758)	3	17.9–18.1	DMM IE/12077
Tanichthys albonubes Lin, 1932	2	21.7–22.0	DMM IE/12075
Gyrinocheilidae			
Gyrinocheilus aymonieri (Tirant, 1884)	1	53.6	DMM IE/11808
Catostomidae			
Myxocyprinus asiaticus (Bleeker, 1864)	1	54.8	DMM IE/12176
Cobitidae			
Cobitis taenia (Kessler, 1876)	2	20.0–22.1	DMM IE/11108
Pangio sp.	1	60.7	DMM IE/11103
Balitoridae			
Barbatula barbatula (Linnaeus, 1758)	1	73.6	DMM IE/111753
Lefua costata (Kessler, 1876)	2	36.5–38.7	DMM IE/11107
Distichodontidae			
Distichodus rostratus (Günther, 1864)	1	53.4	DMM IE/11219
Distichodus rostratus	1	87.6	DMM IE/11223
Paradistichodus dimidiatus (Pellegrin, 1904)	1	46.3	DMM IE/11217
Citharinidae			
Citharinus eburneensis Daget, 1962	1	46.5	DMM IE/11224
Chilodontidae			
Chilodus punctatus Müller & Tröschel, 1844	1	43.7	DMM IE/13451
Alestidae			
Alestes baremoze (Joannis, 1835)	3	38.5–41.1	DMM IE/11110
Alestopetersius smykalai Poll, 1967	1	58.7	DMM IE/11092
Arnoldichthys spilopterus (Boulenger, 1909)	3	441.0–53.9	DMM IE/11097
Brycinus longipinnis (Günther, 1864)	4	11.5–11.8	DMM IE/11104
Brycinus longipinnis	2	71.4–72.7	DMM IE/11095
Brycinus macrolepidotus (Valenciennes, 1850)	1	79.0	DMM IE/11043
Hydrocynus forskahlii (Cuvier, 1819)	1	61.7	DMM IE/11082
Micralestes comoensis Poll & Roman, 1967	3	31.6–37.1	DMM IE/11101

Table 1. Continued

Taxon	Number	SL (mm)	Registration
Characidae			
Gymnocorymbus ternetzi (Boulenger, 1895)	3	25.4–26.9	DMM IE/11009
Gymnocorymbus ternetzi	1	25.7	DMM IE/11063
Gymnocorymbus. ternetzi	1	26.9	DMM IE/11064
Hemigrammus bleheri Géry & Mahnert, 1986	1	37.0	DMM IE/12065
Hemigrammus erythrozonus Durbin, 1909	1	17.3	DMM IE/11065
Hemigrammus erythrozonus	1	20.5	DMM IE/11066
Hemigrammus erythrozonus	2	20.8–21.1	DMM IE/11067
Serrasalmidae			
Metynnis hypsauchen (Müller & Troschel, 1844)	1	27.2	DMM IE/12010
Metynnis hypsauchen	1	39.7	DMM IE/12057
Pygocentrus nattereri Kner, 1858	3	11.7–13.7	DMM IE/12068
Pygocentrus nattereri	2	30.4–38.7	DMM IE/11072
Cynodontidae			
Raphiodon vulpinus Spix & Agassiz, 1829	2	104.0–123.0	DMM IE/11078
Hepsetidae			
Hepsetus odoe (Bloch, 1794)	1	84.5	DMM IE/12070
Amphiliidae			
Phractura clauseni Daget & Stauch, 1963	1	13.0	DMM IE/13426
Callichthyidae			
Corydoras aeneus (Gill, 1858)	1	22.6	DMM IE/11013
Loricariidae			
Ancistrus cf. *dolichopterus* Kner, 1854	9	6.3–10.9	DMM IE/13454
Sisoridae			
Erethistes hara (Hamilton, 1822)	1	38.3	DMM IE/11128
Malapteruridae			
Malapterurus electricus (Gmelin, 1789)	1	44.0	DMM IE/11126
Claroteidae			
Parauchenoglanis monkei (Keilhack, 1910)	2	11.2–13.9	DMM IE/11125
Parauchenoglanis monkei	2	22.4–36.5	DMM IE/12219
Bagridae			
Sperata aor (Hamilton, 1822)	2	50.6–58.6	DMM IE/11130
Lepidogalaxiidae			
Lepidogalaxias salamandroides Mees, 1961	1	30.4	DMM IE/14274
Argentinidae			
Argentina kagoshimae Jordan & Snyder, 1902	3	111.0–142.0	DMM IE/14348
Argentina sphyraena Linnaeus, 1758	1	122.0	DMM IE/11007
Argentina silus Ascanius, 1775	1	96.7	DMM IE/11031
Glossanodon semifasciatus (Kishinouye, 1904)	1	80.1	DMM IE/9526
Glossanodon semifasciatus	1	106.0	DMM IE/13713
Bathylagidae			
Bathylagus euryops Goode & Bean, 1896	2	47.5–54.4	DMM IE/13813
Bathylagus euryops	1	57.7	DMM IE/11803
Bathylagus euryops	4	66.5–75.4	DMM IE/13811
Bathylagus euryops	1	95.9	DMM IE/11034
Thymallidae			
Thymallus thymallus (Linnaeus, 1758)	38	12.1–28.0	DMM IE/11786
Thymallus thymallus	4	18.4–20.9	DMM IE/11799
Thymallus thymallus	2	31.9–38.0	DMM IE/14302
Thymallus thymallus	4	34.8–51.7	DMM IE/14321
Thymallus thymallus	2	36.6–47.7	DMM IE/15078
Thymallus thymallus	1	47.7	DMM IE/11088
Thymallus thymallus	2	49.4–54.3	DMM IE/11733

Table 1. Continued

Taxon	Number	SL (mm)	Registration
Thymallus thymallus	2	76.0–83.1	DMM IE/11732
Thymallus thymallus	1	96.3	DMM IE/11820
Coregonidae			
Coregonus maraena (Bloch, 1779)	8	22.5–32.2	DMM IE/13722
Coregonus maraena	5	30.8–47.0	DMM IE/13723
Salmonidae			
Salmo trutta (Linnaeus, 1758)	3	17.3–18.2	DMM IE/11368
Salmo trutta	3	17.6–34.9	DMM IE/11369
Salmo trutta	1	27.9	DMM IE/11002
Salmo trutta	1	91.9	DMM IE/11042
Salmo trutta	1	114.6	DMM IE/11766
Esocidae			
Esox lucius (Linnaeus, 1758)	3	11.0–13.0	DMM IE/11089
Esox lucius	4	18.9–37.1	DMM IE/11798
Esox lucius	1	84.8	DMM IE/11015
Retropinnidae			
Retropinna tasmanica McCulloch, 1920	2	31.3–31.9	DMM IE/13831
Retropinna semoni (Weber, 1895)	2	28.0–40.3	DMM IE/12059
Osmeridae			
Hypomesus olidus (Pallas, 1814)	4	55.0–64.0	DMM IE/13716
Mallotus villosus (Müller, 1776)	1	112.2	DMM IE/13829
Mallotus villosus	1	132.0	DMM IE/12211
Osmerus eperlanus (Linnaeus, 1758)	5	8.2–35.0	DMM IE/11090
Osmerus eperlanus	3	11.6–15.1	DMM IE/11801
Osmerus eperlanus	6	13.1–16.4	DMM IE/13724
Osmerus eperlanus	4	21.9–38.2	DMM IE/13725
Osmerus eperlanus	1	26.1	DMM IE/11790
Osmerus eperlanus	1	64.3	DMM IE/11086
Osmerus eperlanus	1	72.6	DMM IE/11005
Osmerus eperlanus	1	73.6	DMM IE/11741
Osmerus eperlanus	1	77.6	DMM IE/11740
Osmerus eperlanus	1	103.9	DMM IE/11039
Salangidae			
Protosalanx chinensis (Basilewsky, 1855)	3	84.8–104.1	DMM IE/13712
Salanx acuticeps (Regan, 1908)	2	37.7–52.3	DMM IE/11087
Salanx acuticeps	5	38.1–52.2	DMM IE/11748
Stomiidae			
Astronesthes lucifer Gilbert, 1905	3	45.0–73.8	DMM IE/11805
Aristostomias xenostoma (Regan & Trewavas, 1930)	1	83.0	USNM 296715
Astronesthes niger Richardson, 1845	2	26.0–37.0	MCZ 133101
Astronesthes niger	1	29.0	MCZ 147083
Bathophilus vaillanti (Zugmayer, 1911)	1	101.0	USNM 234150
Chauliodus sloani (Bloch & Schneider, 1801)	1	106.2	DMM IE/11137
Eustomias obscurus (Vaillant, 1884)	1	147.0	USNM 206711
Eustomias sp.	3	27.0–33.0	MCZ 62637
Grammatostomias dentatus (Goode & Bean, 1896)	1	76.0	USNM 234036
Malacosteus australis (Kenaley, 2003)	1	110.0	USNM 296675
Photonectes albipennis (Döderlein, 1882)	2	58.8–96.4	DMM IE/13715
Photostomias sp.	2	21.0–32.0	MCZ 155694
Photostomias sp.	1	92.0	USNM 296650
Stomias boa (Risso, 1810)	1	114.4	DMM IE/11822
Phosichthyidae			
*Ichthyococcus irregularis (*Rechnitzer & Böhlke 1958)	2	27.0–42.0	SIO 93–183

Table 1. Continued

Taxon	Number	SL (mm)	Registration
Vinciguerria lucetia (Garman, 1899)	2	45.0–54.0	SIO 95–123
Vinciguerria sp.	1	11.0	NSMT-PL 691
Sternoptychidae			
Argyropelecus sp.	1	44.5	DMM IE/11117
Argyropelecus sp.	1	9.9	NSMT-PL uncat.
Argyropelecus sp.	1	13.3	NSMT-PL 728
Maurolicus muelleri (Gmelin, 1789)	4	40.2–49.9	DMM IE/12197
Polyipnus spinosus Günther, 1887	2	27.5–33.7	DMM IE/11802
Polyipnus spinosus	3	24.4–35.9	DMM IE/13714
Sternoptyx sp.	2	8.8–9.5	NSMT-PL 730
Gonostomatidae			
Cyclothone sp.	1	20.8	MNHN uncat.
Diplophos sp.	1	39.9	NSMT-PL 643
Manducus maderensis (Johnson, 1890)	1	40.8	MCZ 82180
Sigmops elongatus (Günther, 1878)	1	175.0	MNHN 20031394
Triplophos hemingi (McArdle, 1901)	2	169.0–187.0	DMM IE/12621
Galaxiidae			
Galaxias maculatus (Jenyns, 1842)	2	24.6–30.5	DMM IE/13717
Galaxias occidentalis (Ogilby, 1899)	1	68.0	DMM IE/12062
Lovettia sealii (Johnston, 1883)	1	51.3	DMM IE/13718
Ateleopodidae			
Ateleopus japonicus Bleeker, 1853	1	220.0	DMM IE/9518
Aulopidae			
Hime japonica (Günther, 1877)	1	84.2	DMM IE/9516
Synodontidae			
Harpadon microchir Günther, 1878	2	165.0–190.0	DMM IE/12048
Saurida brasiliensis Norman, 1935	1	82.0	DMM IE/11004
Saurida gracilis (Quoy & Gaimard, 1824)	2	103.9–119.7	DMM IE/15079
Trachinocephalus myops (Forster, 1801)	3	77.4–101.2	DMM IE/12027
Chlorophthalmidae			
Chlorophthalmus nigromarginatus Kamohara, 1953	3	84.5–111.2	DMM IE/13720
Evermannellidae			
Coccorella atlantica (Parr, 1928)	1	64.0	NSMT-P 99762
Scopelarchidae			
Rosenblattichthys alatus (Fourmanoir, 1970)	1	86.2	DMM IE/12788
Paralepididae			
Arctozenus risso (Bonaparte, 1840)	19	20.4–30.5	DMM IE/11797
Arctozenus risso	1	147.0	DMM IE/11138
Lestrolepis japonica (Tanaka, 1908)	2	105.5–106.9	DMM IE/11724
Neoscopelidae			
Neoscopelus microchir Matsubara, 1943	2	87.6–139.0	DMM IE/14351
Myctophidae			
Benthosema glaciale (Reinhardt, 1837)	2	61.6–67.7	DMM IE/11136
Diaphus watasei Jordan & Starks, 1904	1	93.5	DMM IE/13710
Lampadena speculigera Goode & Bean, 1896	1	93.5	DMM IE/10198
Lampanyctus crocodilus (Risso, 1810)	1	94.6	DMM IE/11030
Lampanyctus crocodilus	3	80.3–88.7	DMM IE/13287
Symbolophorus veranyi (Moreau, 1888)	1	86.7	DMM IE/11738
Polymixiidae			
Polymixia berndti (Gilbert, 19059	2	73.1–99.5	DMM IE/13296
Batrachoididae			
Halobatrachus didactylus (Bloch & Schneider, 1801)	1	55.2	DMM IE/4144

Table 1. Continued

Taxon	Number	SL (mm)	Registration
Melamphaidae			
Poromitra megalops (Lütken, 1878)	2	56.3–71.6	DMM IE/10150
Scopelogadus beanii (Günther, 1887)	2	69.6–77.9	DMM IE/12215
Berycidae			
Beryx splendens Lowe, 1834	1	111.0	DMM IE/13772
Anoplogastridae			
Anoplogaster cornuta (Valenciennes, 1833)	1	104.4	DMM IE/4878
Diretmidae			
Diretmus argenteus Johnson, 1864	1	82.6	DMM IE/15071
Diretmus argenteus	1	88.4	DMM IE/15072
Anomalopdiae			
Anomalops katoptron (Bleeker, 1856)	1	63.0	DMM IE/13721
Monocentridae			
Monocentris japonica Houttuyn, 1782	1	44.6	DMM IE/13707
Trachichthyidae			
Aulotrachichthys prosthemius (Jordan & Fowler, 1902)	3	59.5–77.3	DMM IE/13290
Hoplostethus mediterraneus Cuvier, 1829	1	90.9	DMM IE/12199
Percidae			
Perca fluviatilis	3	75.7–91.2	DMM IE/14267

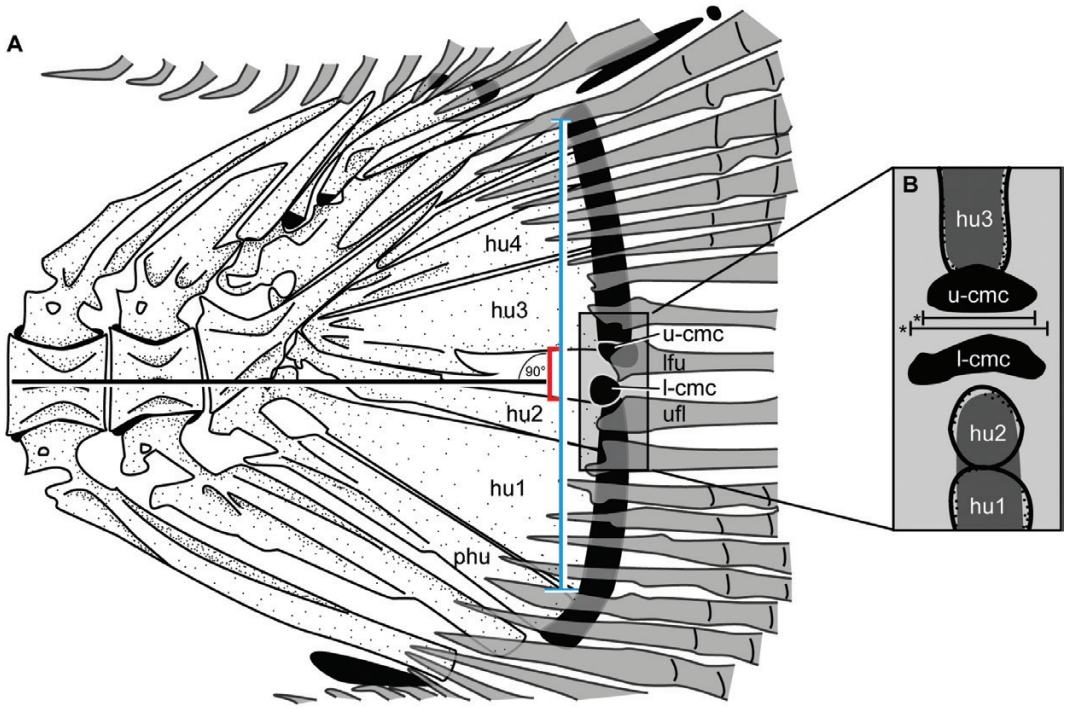

Figure 1. Drawing of the caudal skeleton of *Osmerus eperlanus*, DMM IE/11005, 72.6 mm SL: A, lateral view, the black line indicates the body axis, the blue line the vertical distance from the most ventral edge of hypural 1 to the most dorsal edge of the last hypural taken perpendicular to the body axis, and the red line the distance between hypural 2 and hypural 3 along the same connecting line (blue line); B, posterior view. The two lines marked with an * show the width of the upper and lower median caudal cartilages respectively. Abbreviations: hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; phu, parhypural; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

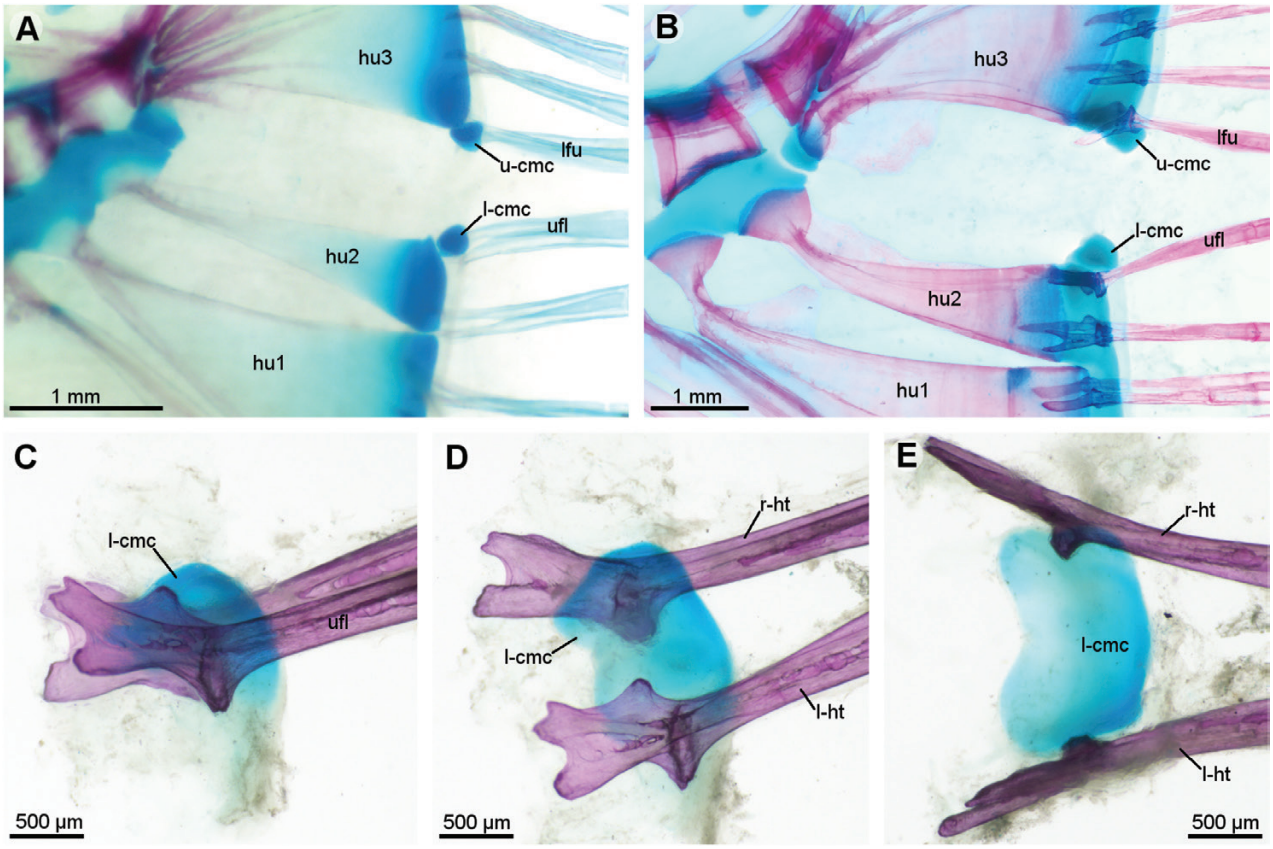

Figure 2. Cleared and stained caudal fins in the area of the diastema of Alepocephalidae: A, *Xenodermichthys copei*, DMM IE/10190, 110.8 mm SL, lateral view; B, *Alepocephalus rostratus*, DMM IE/13803, 114.2 mm SL, lateral view; C–E, isolated lower median caudal cartilage with associated ray of *A. rostratus*, DMM IE/14846, 230 mm SL, lateral (C), dorso-lateral (D) and dorsal (E) views. Abbreviations: hu, hypural; l-cmc, lower median caudal cartilage; l-ht, left hemitrich; lfu, lowest ray of upper caudal lobe; r-ht, right hemitrich; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

Batrachoididae, no median caudal cartilages have been detected in the diastema. All other groups with at least some representatives showing CMCs are described below.

Alepocephalidae (Alepocephaliformes) (Fig. 2)

Principally, two different arrangements of median caudal cartilages can be found in Alepocephaliformes, each typical for Alepocephalidae or Platytroctidae. Members of Alepocephalidae have two rather small cartilages (Fig. 2A, B): one at the dorsodistal tip of hypural 2 and one at the ventrodistal tip of hypural 3. Each cartilage supports one fin ray of the caudal fin. The hemitrichs of the respective fin rays are widely splayed and bear a peg on their inner side articulating either in lateral grooves of the CMCs or in the area between CMC and neighbouring hypural plate (Fig. 2C–E). The cartilages are concave on their anterior facet (Fig. 2D, E) where they articulate on the edges towards the diastema of hypural 2 and hypural 3, respectively. In posterior view, the cartilages are wider than the hypural plates (see Fig. 1B for orientation and measurement method). Such pegs are not unique to the fin rays articulating with CMCs, but can also be found in the one to three neighbouring fin rays, depending on the taxon. The situation with two relatively small cartilages each supporting a fin ray was principally found in all members of Alepocephalidae studied, with only slight variations, e.g. direct articulation of fin rays on the CMCs or in-between CMC and hypural plate.

Platytroctidae (Alepocephaliformes) (Fig. 3)

The situation found in Platytroctidae clearly differs from the one in Alepocephalidae. Here, two large cartilages are present and, accordingly, virtually bridge the diastema (Fig. 3). The upper and lower CMC almost contact each other; in this contact area they are both closely associated with the lowest fin ray of the upper caudal lobe (Fig. 3A, E, F, G). The lower CMC further

supports the upper ray of the lower lobe in almost the same way as in Alepocephalidae with the ray articulating in the area where the lower CMC meets hypural 2. The cartilages are wider in lateral dimension than the hypural plates on which they articulate with an anterior articulatory facet (Fig. 3B–D). Seen posteriorly (Fig. 3C, D), a complex three-dimensional structure becomes observable: the cartilages are kidney- or U-shaped, contacting each other on their ends. The articulating hemitrichs of the lowest fin ray of the upper caudal lobe are positioned with a medial peg, comparable to that in Alepocephalidae, in the area where the two cartilages approach each other. This situation is principally present in all studied specimens of Platytroctidae with only slight differences in relative size of the cartilages (Fig. 3).

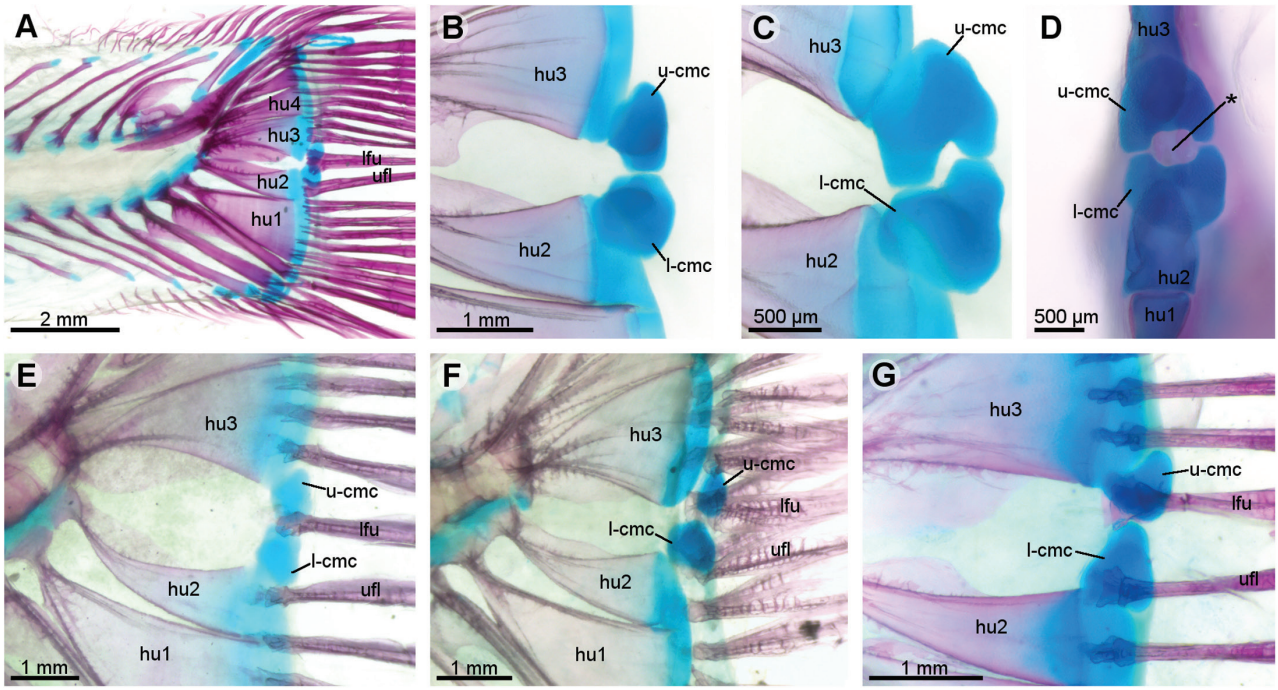

Figure 3. Cleared and stained caudal fins of Platytroctidae: A, *Holtbyrnia anomala*, DMM IE/13490, 62.1 mm SL, lateral overview; B–D, *Holtbyrnia anomala*, DMM IE/11744, 114.2 mm SL, details of CMCs with fin rays removed, lateral (B), posterior-lateral (C) and posterior (D) views; E, *Maulisia argipalla*, DMM IE/10459, 111.0 mm SL, lateral view; F, *Normichthys operosus*, DMM IE/13804, 87.0 mm SL, lateral view; G, *Searsia koefoedi*, DMM IE/13828, 99.7 mm SL, lateral view. Abbreviations: *, ligament between CMCs; hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

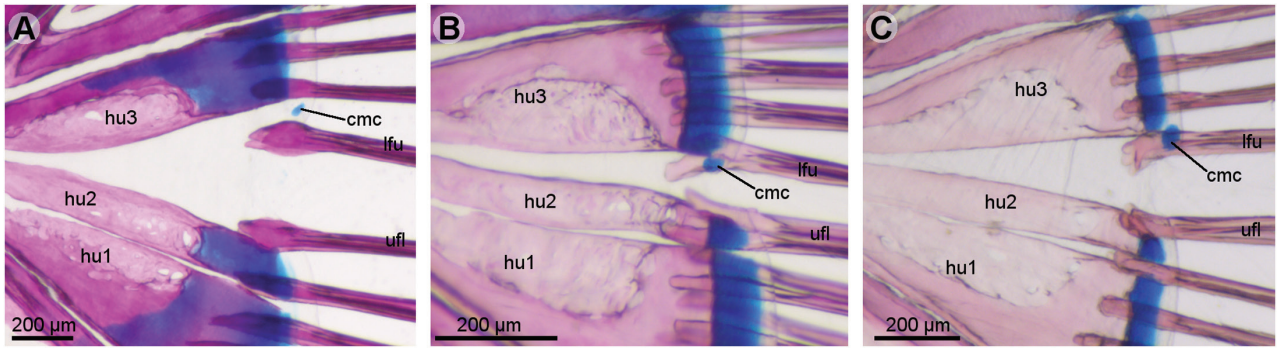

Figure 4. Cleared and stained caudal fins in the area of the diastema of Characiformes: A, *Gymnocorymbus ternetzi*, DMM IE/11063, 25.7 mm SL; B, *Hemigrammus erythrozonus*, DMM IE/11065, 17.3 mm SL; C, *Hemigrammus erythrozonus*, DMM IE/11066, 20.5 mm SL; all lateral views. Abbreviations: cmc, median caudal cartilage; hu, hypural; lfu, lowest ray of upper caudal lobe; ufl, upper most ray of lower caudal lobe.

Characiformes (Fig. 4)

Out of the 18 species, representing eight families, only two characid species have median caudal cartilages. However, not all investigated specimens of those two species showed such cartilages. In *Gymnocorymbus ternetzi* five out of seven specimens had a very small comma-like cartilage at the lower distal edge of hypural 3 (Fig. 4A). It does not appear to be associated with the lowest ray of the upper caudal lobe, which inserts more ventral in the diastema. In *Hemigrammus erythrozonus* a roundish to oval, small cartilage can be present at about the same position (Fig. 4B, C). However, in this species the lowest ray of the upper caudal lobe inserts in this area, so that the cartilage is somewhere between the bases of the hemitrichs. The hemitrichs in both species may be prolonged in anterior direction, but do not show any medially directed pegs pointing to each other.

Argentinidae (Argentiniformes) (Fig. 5)

In *Argentina silus* there are two CMCs showing a clear difference in size: the lower is about double to triple the size of the upper one (Fig. 5A–D). Together they support one fin ray of the dorsal lobe positioned in between both cartilages, plus a fin ray of the lower lobe in direct contact with the ventral part of the lower CMC. Both fin rays have dorsoventrally widened bases in comparison to the neighbouring rays. The fin rays contacting the upper or lower cartilage both show prominent medially directed pegs, but these pegs are more pronounced in the ray of the upper lobe (Fig. 5E). The pegs of this fin ray originate on the dorsal margin of the hemitrichs and point to the area between the upper CMC and the cartilaginous distal part of hypural 3. This lowest fin ray of the upper lobe shows tighter connections to the upper cartilage. The cartilage is roughly rectangular in lateral view, almost round posteriorly and dorsally it becomes visible that the cartilage is convex on its distal part and concave on its proximal facet, allowing articulation on the lower corner of hypural 3 (Fig. 5C). When seen posteriorly, this upper cartilage has the same width as the hypural plates. The bases of the associated fin ray do not contact this cartilage directly: the distance between these bases is larger than the width of the cartilage.

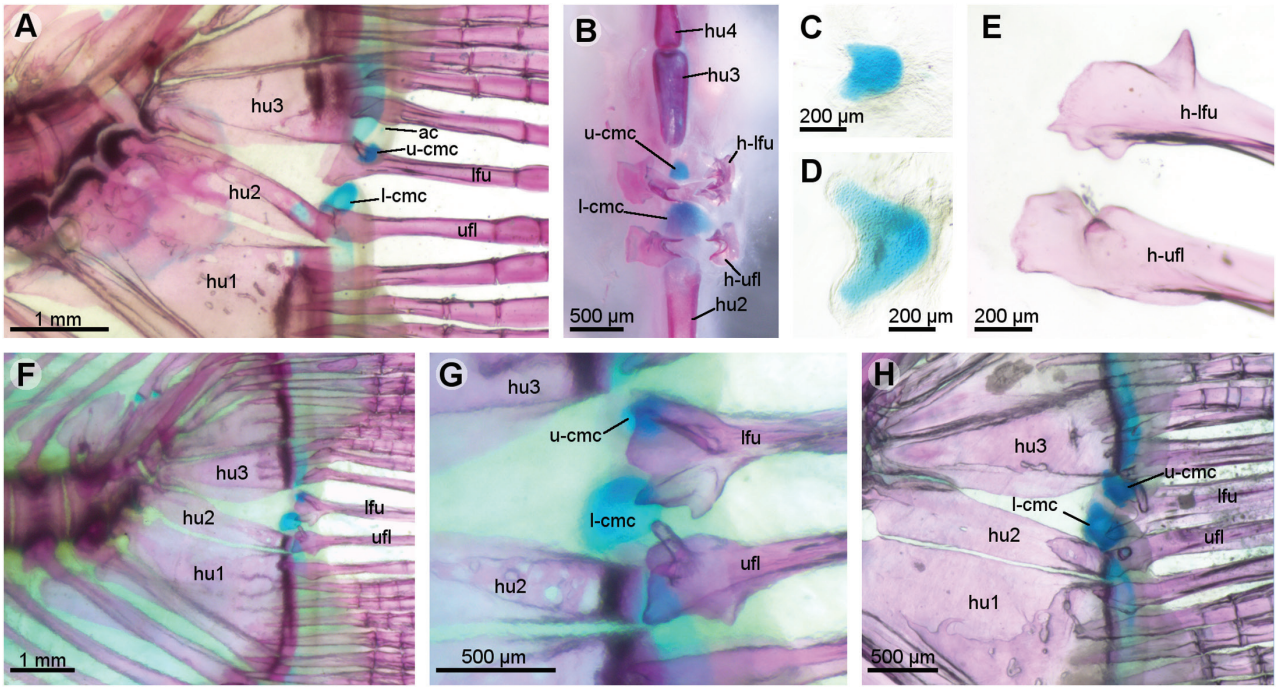

Figure 5. Cleared and stained caudal fins in the area of the diastema of Argentinidae: A–E, *Argentina silus*, DMM IE/11031, 96.7 mm SL, overview lateral (A), median caudal cartilages from posterior all rays removed except bases of associated rays (B), upper median caudal cartilage in dorsal view (C), lower median caudal cartilage in dorsal view (D), right hemitrichs of lowest ray of upper caudal lobe and upper most ray of lower lobe in medial view (E); F–G, *Argentina kagoshimae*, DMM IE/14348, 111.0 mm SL, overview (F) and detail in lateral view (G); H, *Glossanodon semifasciatus*, DMM IE/13713, 106.0 mm SL, lateral view. Abbreviations: ac, accessory cartilage; h-lfu, hemitrich of lowest ray of upper caudal lobe; h-ufl, hemitrich of upper most ray of lower caudal lobe; hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

However, both cartilages are embedded in stable connective tissue. The lower cartilage is clearly wider than the hypural plates and it makes direct contact with the bases of its associated fin ray. The lower CMC is somewhat triangular to rectangular when seen laterally, dorsoventrally flattened ovoid when seen posteriorly and dorsally somewhat boomerang-shaped (Fig. 5D). This allows a stable articulation on the upper edge of hypural 2. In lateral reflected light, a strong connective tissue, maybe a ligament, becomes visible, stretching from the upper tip of the lower CMC to the upper CMC. This 'ligament' is about as wide as the upper CMC. In the other argentinid species studied, *A. sphyraena*, *A. kagoshimae* and *Glossanodon semifasciatus*, the situation for the CMCs and their associated fin rays seems to equal that of *A. silus* (Fig. 5F, G). In *A. kagoshimae* there is a pronounced inward-directed peg at the base of the upper fin ray of the lower lobe (Fig. 5F, G). In *Glossandon semifasciatus* (Fig. 5H) the two CMCs are larger, filling a significant part of the diastema. Together they support the lowest fin ray of the upper lobe. The upper fin ray of the lower lobe is placed at the contact zone of the lower CMC and hypural 2. The upper CMC is roughly boomerang-shaped in dorsal view, with blunt tips facing anteriorly; it is about 1.5 times as wide as the hypurals in posterior view. The lower CMC resembles a bar, rectangular when seen posteriorly and almost square when viewed laterally, but with tips in the anterioventral corner and an articulatory groove for the upper margin of hypural 2 in between the tips of both sides. It is slightly wider than the upper CMC in posterior view. The articulatory pegs of the lower ray of the upper lobe are quite large, extending medially in a right angle and contacting the posterior border of the upper CMC.

Bathylagidae (Argentiniformes) (Fig. 6)

The situation in *Bathylagus euryops* is like *Argentina* in that the lower CMC is larger than the upper one (Fig. 6A–C). However, the size differences between the

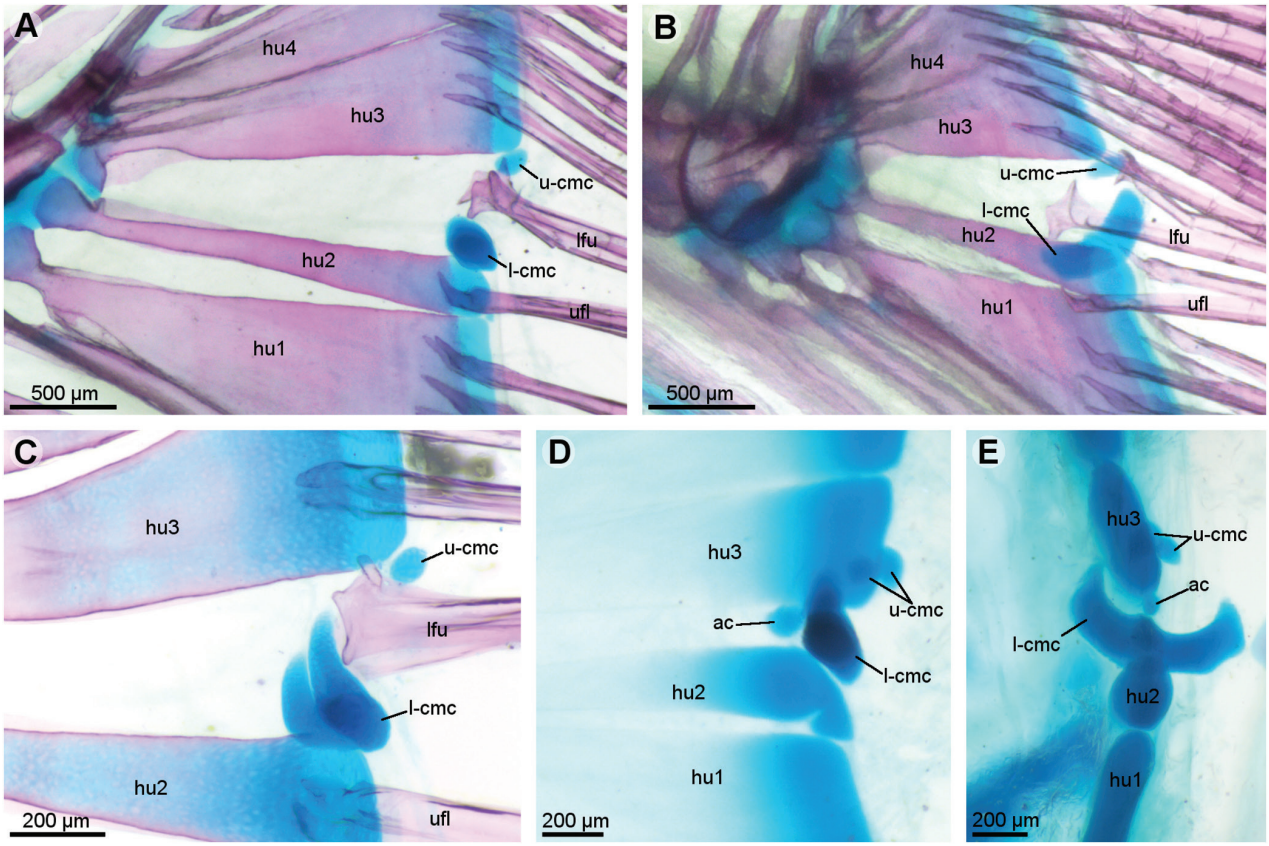

Figure 6. Cleared and stained caudal fins in the area of the diastema of *Bathylagus euryops* (Bathylagidae): A–B, DMM IE/13811, 72.4 mm SL; lateral (A) and posterior-lateral (B) views; C, DMM IE/13813, 47.5 mm SL, lateral view; D–E, DMM IE/11803, 57.7 mm SL, lateral (D) and posterior (E) views. Abbreviations: ac, accessory cartilage; hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

two is much more pronounced: where the lower CMC is about three to four times the width of the hypural plates and shows a complex three-dimensional structure, the upper CMC is very small, ball-like and, in some specimens, a much reduced to a hardly visible remnant (Fig. 6B, E). There is one fin ray that is dorsally in contact with hypural 3 and ventrally with the lower CMC; its large base occupies the upper half of the diastemal gap (Fig. 6C). The upper CMC is slightly variable in its position: at about the level of the upper rim of the central fin ray, at the lower edge of hypural 3 or even dorsally to that on the distal margin of hypural 3. Due to its small size, it seems that there is no direct relation to the central ray or any other rays. The lower CMC principally resembles a bracket or a crescent moon, horizontally positioned on the upper edge of hypural 2, with its tips curved dorsally (Fig. 6E). The size of the cartilage, especially the extension and curvature of the tips, varies among individuals. In two specimens there are two upper CMCs at the same dorsoventral position, forming a pair left and right of the medial plain (Fig. 6D, E). Furthermore, in one of these, and one other specimen, there is an additional small, round cartilage in the diastema anterior to the lower CMC (Fig. 6D).

Salmoniformes (Fig. 7)

In all three studied genera representing the three families in this order, i.e. Thymallidae, Coregonidae and Salmonidae, the configuration is similar: the lowest ray of the upper caudal lobe articulates with hypural 3 and the uppermost ray of the lower lobe articulates with hypural 2 (Fig. 7A, B). In the diastema there are one or two CMCs (Fig. 7; see also Fig. 24A–I). The variation in number does not depend on the species. For example, our *T. thymallus* specimens were all from the same parents and raised under the same conditions; out of 14 specimens between 30 and 97 mm SL, five had one CMC and nine had two CMCs. If only one cartilage is present, it is large, ranging from half the height of the diastema to about as high as the diastema; it is roundish or triangular with blunt edges in lateral view and upright-oval when seen posteriorly. There seems to be no relation to fin rays.

Retropinnidae (Fig. 8)

In *Retropinna tasmanica* the diastema is narrow, but the edges of hypural 2 and 3 are rounded, thus forming an indentation in the otherwise almost continuous posterior margin of the hypural plates. Posterior to the hypurals, a single CMC is present; its dorsoventral extension ranges between 50 to 100% of the height of hypural 2 (in lateral view). The CMC is rounded to slightly triangular, pointing with its tip to the diastema (Fig. 8A). It seems of minor importance for the support of fin rays; there may be some interaction with the uppermost ray of the lower lobe. A similar situation is present in a 28.0 mm SL specimen of *R. semoni*: here the cartilage is more elongated in the dorsoventral direction, thus having a more pronounced triangular shape and the position is more anterior with about half of its length anterior to the posterior margin of the hypurals. It almost reaches the level of the ossified parts of the hypural plates (Fig. 8B). The dorsal and ventral facets of the triangular CMC exhibit emarginations into which the diastemal-directed edges of hypural 2 und 3 articulate. Its dorsal and ventral tips seem to be involved in the support of one fin ray each (Fig. 8B).

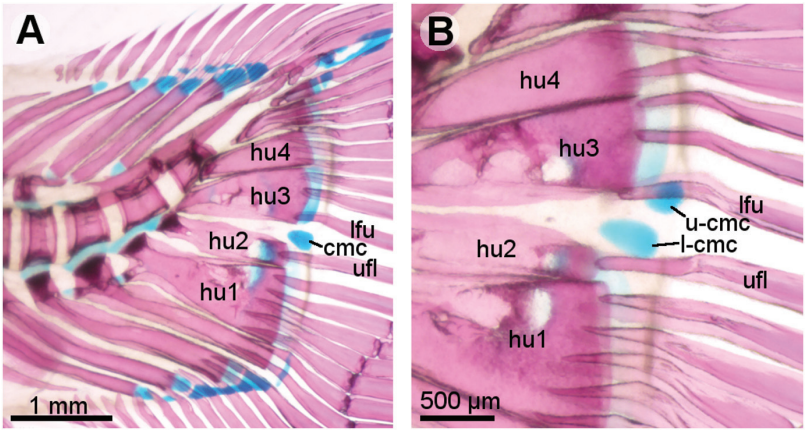

Figure 7. Cleared and stained caudal fins in the area of the diastema of *Thymallus thymallus* (Thymallidae), DMM IE/11733: A, 54.3 mm SL; B, 49.9 mm SL; all lateral views. Abbreviations: cmc, median caudal cartilage; hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

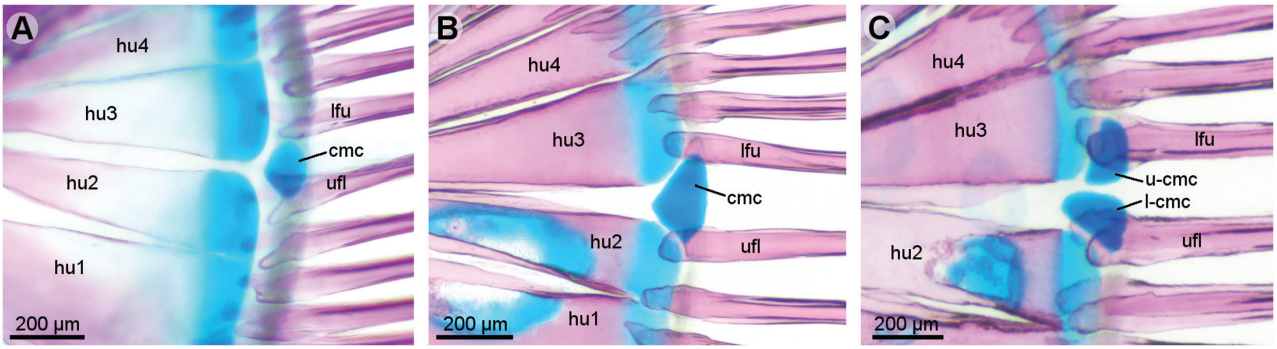

Figure 8. Cleared and stained caudal fins in the area of the diastema of *Retropinna* (Retropinnidae): A, *Retropinna tasmanica*, DMM IE/13831, 31.9 mm SL; B, *R. semoni*, DMM IE/12059, 28.0 mm SL; C, *Retropinna semoni*, DMM IE/12059, 40.3 mm SL; all lateral views. Abbreviations: cmc, median caudal cartilage; hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

The situation becomes more complicated with a larger specimen, i.e. 40.3 mm SL, of the same species in which two separate CMCs are present in about the same position as the single cartilage in the smaller specimen (Fig. 8C). Each cartilage is closely associated to one fin ray. Their facets directed to the hypurals are slightly concave enabling articulation. Independent of amount, size and exact position of the cartilages, their width in the horizontal plane is about the same or even slightly larger than that of the hypural plates. None of the caudal fin rays show medially directed articulatory pegs.

Osmeridae (Osmeriformes) (Fig. 9)

There are two CMCs in *Osmerus eperlanus*. Both have about the same size, width and shape: they are crescent-shaped and have about double to triple the width of the hypural plates (Fig. 9A–G). The lower CMC might be slightly larger than the upper (Fig. 9G). However, the anatomical orientation differs: the upper CMC, lying inside the diastema on the lower distal edge of hypural 3, is almost parallel to the body axis with its tips pointing anteriorly. The lower CMC, on the distal edge of hypural 2, also lying in the diastema, is oblique to the body axis with its tips pointing anterior-ventrally. The upper CMC is associated with the lowest ray of the upper caudal lobe and the lower CMC with the uppermost ray of the lower lobe. Both rays are placed directly or ventrally on the CMCs and none of the rays possess medially directed pegs (Fig. 9E). In shape, position, orientation and fin-ray association, the situation in *Hypomesus olidus* (Fig. 9H–I) is very similar to that in *Osmerus*.

In contrast to *Osmerus* and *Hypomesus*, the cartilage did not stain well in *Mallotus villosus*. Nevertheless, it is clearly visible that there is a single, large CMC over the complete height of the diastema (Fig. 9J). Together with the neighbouring hypural plates, this CMC supports the lowest ray of the upper lobe and the uppermost ray of the ventral lobe. The CMC is clearly wider than the hypural plates with anterodorsal and anteroventral grooves for fitting on the neighbouring hypural plates. Medially directed pegs on the articulating fin rays are absent.

Salangidae (Osmeriformes) (Fig. 10)

In *Salanx acuticeps* and *Protosalanx chinensis* two CMCs are present (Fig. 10). They are usually of similar size with the upper one only slightly smaller than the lower one. In some individuals, not depending on species, the upper CMC is very small (Fig. 10A). The cartilages are roughly triangular when seen from the posterior side with their edges bent anteriorly, thus forming a cap on the diastemal edge of hypural 2 and 3, respectively. Each CMC supports a fin ray: the lowest of the upper lobe and the upper most of the lower lobe (Fig. 10B, C). There are no medially directed pegs on the rays in the studied salangids.

Sternoptychidae (Stomiiformes) (Fig. 11)

Polyipnus spinosus possesses two large and prominent CMCs (Fig. 11A–C). They are somehow like an upright brick with a clear notch on the diastemal side. Thus, there are two tips facing the respective tips of the other CMC. There seems to be a strong type of connective tissue between those tips of the opposing CMCs (Fig. 11C). In posterior view the CMCs appear massive and have about double the width of the hypural plates. The lowest ray of the upper caudal lobe articulates on the dorsal third of the upper CMC; the uppermost ray of the lower lobe in contrast articulates in the area where the lower CMC meets the fused hypural 1 and 2. There are no medially directed processes on the

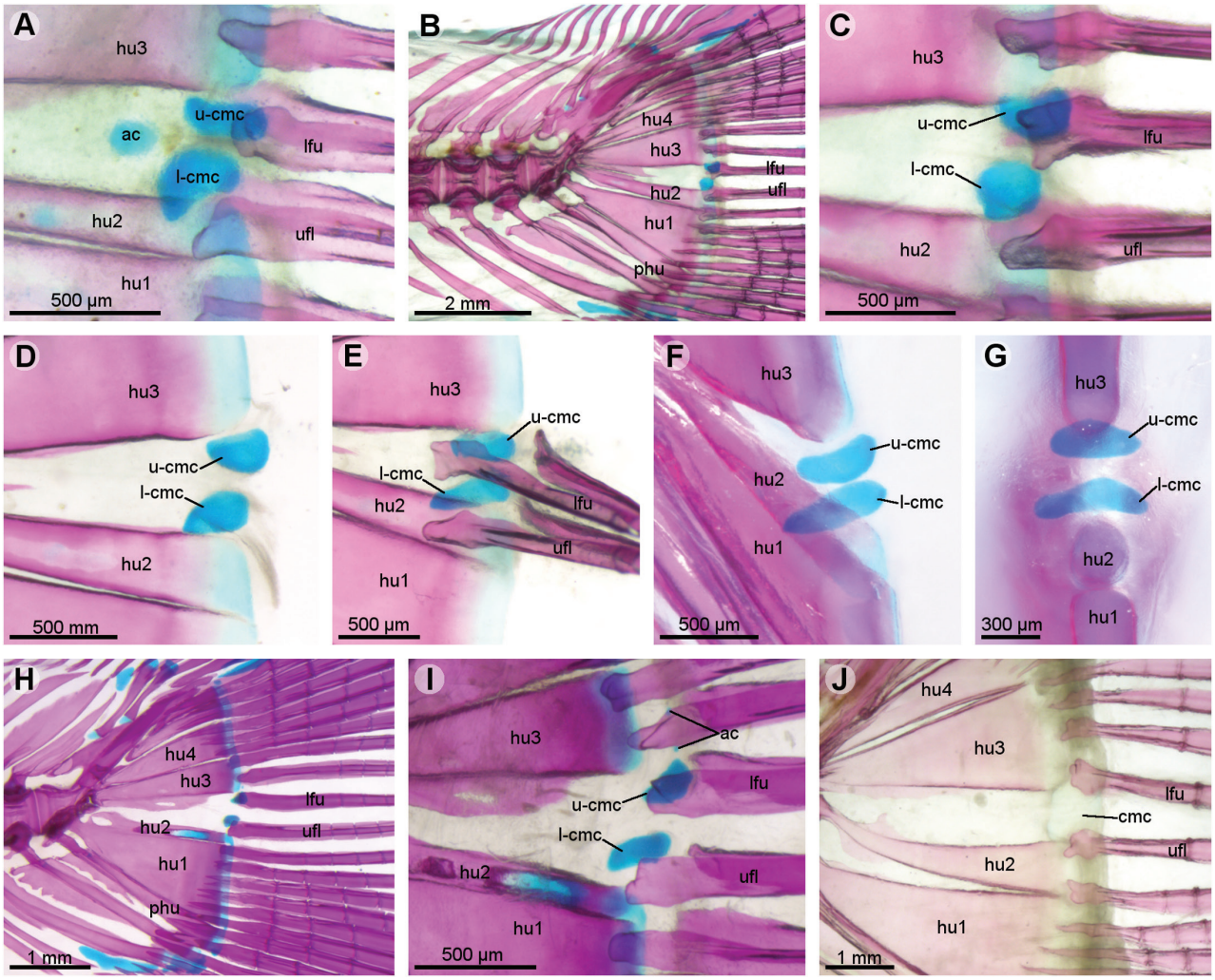

Figure 9. Cleared and stained caudal fins of Osmeridae: A, *Osmerus eperlanus*, DMM IE/11005, 72.6 mm SL, lateral view; B–G, *Osmerus eperlanus*, DMM IE/11740, 77.6 mm SL, overview (B), median caudal cartilages with (C) and without rays (D) in lateral view, median caudal cartilages with all but associated rays removed from posterior-lateral view (E), median caudal cartilages without rays from dorso-posterior-lateral view (F) and from posterior view (G); H–I, *Hypomesus olidus*, DMM IE/13716, 55.0 mm SL, overview (H) and medial caudal cartilages (I) in lateral view; J, *Mallotus villosus*, DMM IE/12211, 132 mm SL, median caudal cartilage, lateral view. Abbreviations: ac, accessory cartilage; cmc, median caudal cartilage; hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; phu, parhypural; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

bases of these rays. Besides the large CMCs, there are several additional small and unpaired cartilages along the distal margin of hypural 1 + 2 and 3. They are ball-like, not as wide as the hypural plates and should probably be called post-hypural cartilages following Fujita (1989).

The single adult specimen of *Argyropelecus* in this study did not stain well for cartilage (Fig. 11D). However, we can present some data, because there are also two well-expressed CMCs. In this case, the upper one is larger than the lower one. The upper one is slightly bean-shaped in lateral view and brick-shaped when seen from the posterior side. The lower CMC is slightly bean-shaped laterally and ball-shaped in posterior view. Only the lower CMC has a slight notch on the diastemal side. The uppermost ray of the lower lobe articulates on the lower CMC. On the upper CMC there are two rays articulating: the lowest ray of the upper lobe on the ventral half of the CMC and the second lowest ray on the dorsal end of the CMC. *Sternoptyx* appears unique in having a large cartilage bordering the diastema posteriorly and large parts of the hypurals (see below under Development of median caudal cartilages; Fig. 25G, H).

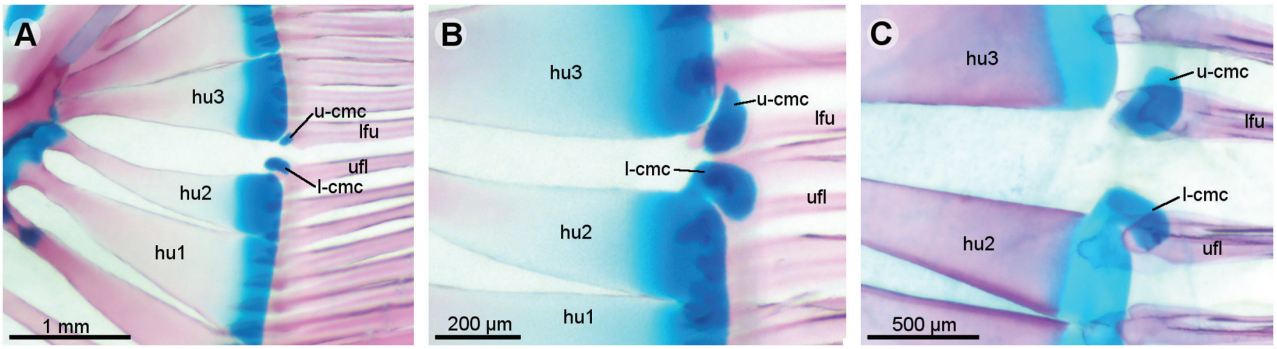

Figure 10. Cleared and stained caudal fins in the area of the diastema of Salangidae: A, *Salanx acuticeps*, DMM IE/11748, 43.0 mm SL; B, *Salanx acuticeps*, DMM IE/117480, 51.0 mm SL; C, *Protosalanx chinensis*, DMM IE/13712, 103.4 mm SL; all lateral views. Abbreviations: cmc, median caudal cartilage; hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

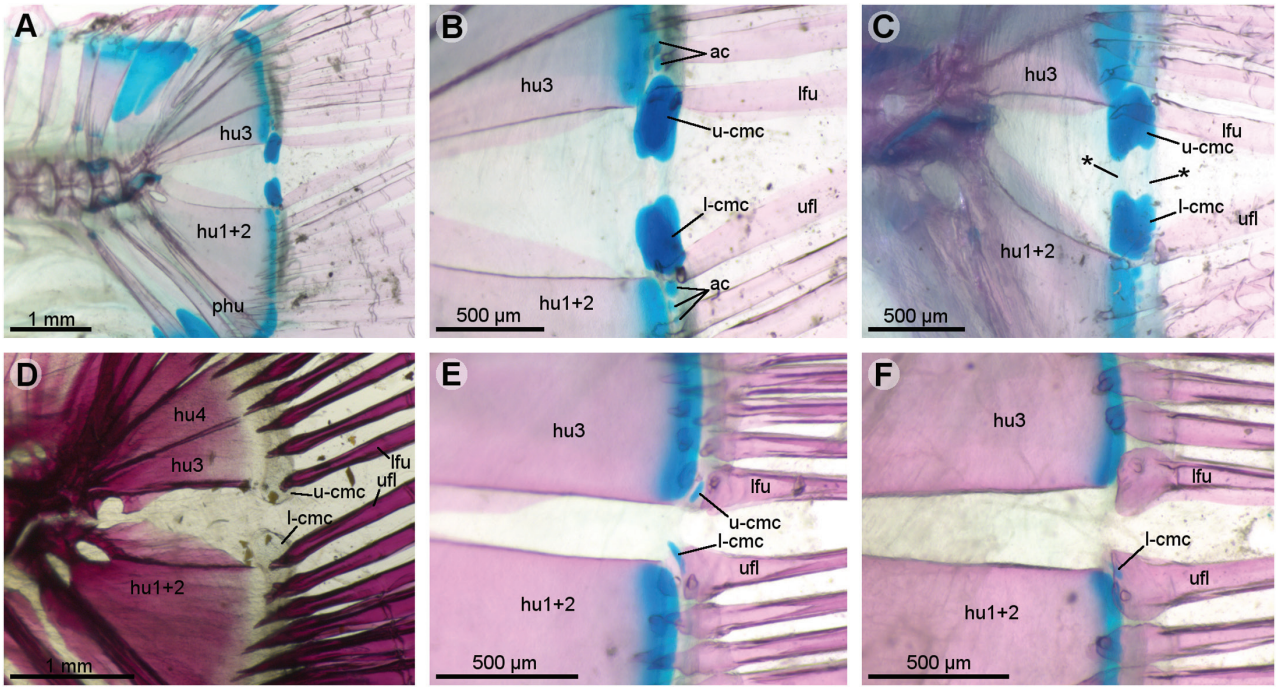

Figure 11. Cleared and stained caudal fins in the area of the diastema of Sternoptychidae: A–C, *Polyipnus spinosus*, DMM IE/13714, 35.9 mm SL, in lateral (A–B) and posterior-lateral (C) view; D, *Argyropelecus* sp. DMM IE/1117, 44.5 mm SL, lateral, cartilage not stained, lateral view; E, *Maurolicus muelleri*, DMM IE/12197, 40.2 mm SL, lateral view; F, *Maurolicus muelleri*, DMM IE/12197, 45.9 mm SL, lateral view. Abbreviations: *, ligament between CMCs; ac, accessory cartilage; hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; phu, parhypural; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

In *Maurolicus muelleri* there are two rather small CMCs (Fig. 11E) of which the upper one is missing in some specimens (Fig. 11F). They are comma-shaped and, in contrast to most other CMCs, positioned in the rostro-caudal plane, not extending laterally. The width of the CMCs does not exceed the width of the hypural plates. The CMCs seem to be in anatomical association with the most median rays of the caudal lobes, but these rays seem not to depend on the CMCs in terms of their attachment, which equals that of the other caudal rays on the hypural plates.

Gonostomatidae (Stomiiformes) (Fig. 12)

In *Sigmops elongatus* there are two large and prominent CMCs (Fig. 12A). They almost contact each other

within the diastema and are connected via a strong ligament (Fig. 12B). In lateral view they are ovoid and the upper CMC is slightly larger than the lower CMC (Fig. 12A). The lowermost fin ray of the upper lobe directly articulates on the ventral portion of the upper CMC; the penultimate fin ray of this lobe articulates at, or close to, the dorsal margin of the upper CMC. In posterior view the upper CMC is roughly quadrate in shape with two little pads, left and right, that seem to serve as articular facets for the fin rays. These pads are more pronounced on the lower CMC giving it an upside-down crown shape with a tip pointing upwards in posterior view. The uppermost ray of the lower lobe articulates with these downward-pointing pads (Fig. 12B). The anterior side of the CMCs is concave, thus forming a cap on the diastemal edge of hypural 2 and 3, respectively, and they are only slightly wider than the hypural plates. In *Cyclothone* sp. there are two small CMCs, roundish in lateral (Fig. 12C) and posterior views (Fig. 12D). Their anterior facet is concave and therewith they sit like little caps at the diastemal corners of the dorsal and ventral hypural plates. The lowermost ray of the upper caudal fin lobe articulates directly with the upper CMC. The uppermost ray of the lower lobe articulates only with the ventral edge of the lower CMC. The CMCs are about the same width as the hypural plates.

In *Manducus maderensis, Diplophos* sp. and *Triplophos hemingi* no CMCs have been observed.

Phosichthyidae (Stomiiformes) (Fig. 13)

In *Ichthyococcus irregularis* there is one single, elongated cartilage posterior to the diastemal edges of hypural 2 and hypural 3 (Fig. 13A), occupying the space of the CMCs and therewith presumably presenting a single CMC, possibly due to an ontogenetic fusion of two CMCs. In lateral view, anterior to the bean-shaped CMC, there is an accessory small, round cartilage. The dorsal and ventral edges of the CMC articulate each

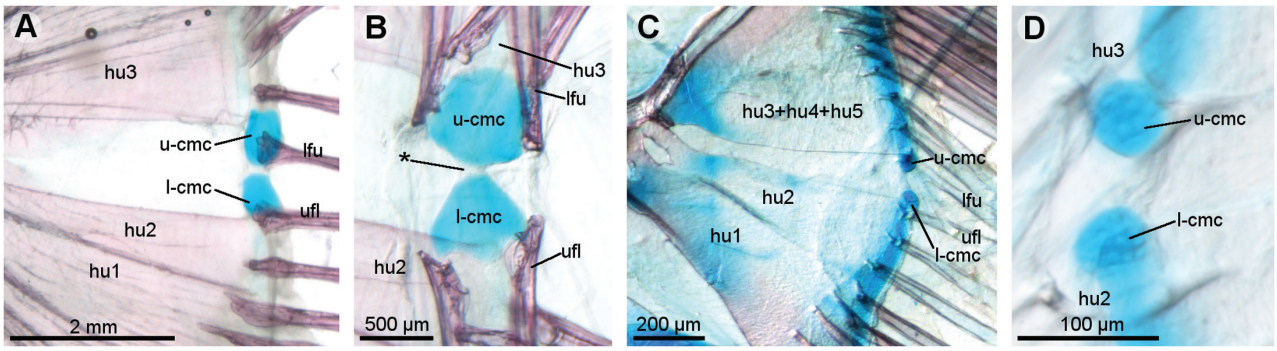

Figure 12. Cleared and stained caudal fins in the area of the diastema of Gonostomatidae: A–B, *Sigmops elongatus*, MNHN 20031394, 175 mm SL, in lateral (A) and posterior (B) views; C–D, *Cyclothone* sp., MNHN uncat., 20.8 mm SL, in lateral (C) and posterior (B) views. Abbreviations: *, ligament between CMCs; hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

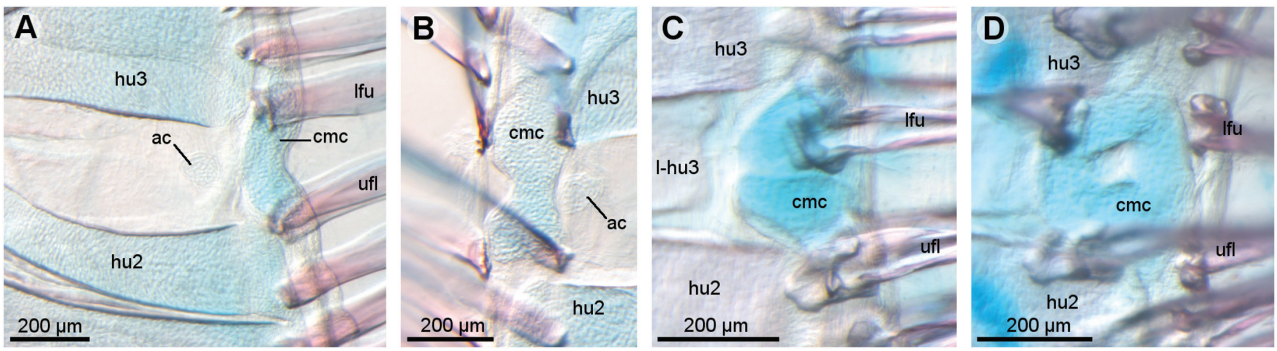

Figure 13. Cleared and stained caudal fins in the area of the diastema of Phosichthyidae: A–B, *Ichthyococcus irregularis*, SIO 93–183, 42.0 mm SL, in lateral (A) and posterior (B) views; C–D, *Vinciguerria lucetia*, SIO 95–123, 45.0 mm SL, in lateral (C) and posterior (D) views. Abbreviations: ac, accessory cartilage; cmc, median caudal cartilage; hu, hypural; l-hu3, lamellar outgrowth of hypural 3; lfu, lowest ray of upper caudal lobe; ufl, upper most ray of lower caudal lobe.

with a caudal fin ray. In posterior view the CMC is dumbbell-shaped and has about the same width as the hypural plate (Fig. 13B).

In *Vinciguerria lucetia* there is also one single cartilage occupying the space of the CMCs between hypural 2 and hypural 3 (Fig. 13C). A major part of the diastema is filled by bony lamellar outgrowths of hypural 3. Only the posterior part of the diastema is spared by the outgrowth and houses the single CMC (Fig. 13C). It is irregularly shaped in lateral view with a horizontal area where the cartilage seems less dense. One might even think there is a dorsoventral separation. However, in posterior view it becomes obvious that there is only one single, doughnut-shaped cartilage (Fig. 13D). The outline of the hole in the cartilage shines through in lateral view and accounts for the misleading separation line and the less dense cartilage in the horizontal area. The lowermost caudal fin ray of the upper lobe articulates with the dorsal half of the cartilage, whereas the uppermost caudal fin ray of the lower lobe articulates with only the ventral margin of the cartilage.

Stomiidae (Stomiiformes) (Fig. 14)

In *Astronesthes lucifer* there are two prominent CMCs (Fig. 14A–D). They are like massive caps on the distal diastemal edges of hypural 2 and hypural 3 with laterally extending arms bending in the hypural direction. Thus, articulation on the margins of hypural plate 2 and 3 is facilitated by a notch in the anterior–posterior direction on the mid-parts of the cartilages, while at the same time the arms encompass the hypural plates laterally. Each CMC supports one ray that articulates with the dorsalmost part of the upper CMC and the ventralmost part of the lower CMC, respectively. In the largest specimen, 73.9 mm SL, there are two additional very small ball-like cartilages anterior to the CMCs on the diastemal margin of the hypurals (Fig. 14B).

In *Aristostomias xenostoma* (Fig. 14E, F) and *Bathophilus vaillanti* (Fig. 14G, H) there are two prominent CMCs in the diastema. In both species the upper CMC is slightly smaller than the lower one and they are both roundish in lateral view. In latero-posterior view the upper CMC in *A. xenostoma* resembles a bean with the slightly concave side facing hypural 3 (Fig. 14F). The lower CMC in *A. xenostoma* is roughly boomerang-shaped with blunt tips facing ventrally, therewith embracing the sides of hypural 2 with its lateral arms (Fig. 14F). In *B. vaillanti* the CMCs are slightly bean-shaped in posterior view, embracing the edge of hypural 2 and hypural 3 with their concave side facing anteriorly (Fig. 14H). The CMCs in *A. xenostoma* and *B. vaillanti* are connected by strong connective tissue (Fig. 14H). In *A. xenostoma* there is no direct articulation between any caudal fin ray and the CMCs. The lowermost caudal ray of the upper lobe articulates with the ventral edge of hypural 3, whereas the uppermost caudal ray of the lower lobe articulates with hypural 2. In *B. vaillanti* (Fig. 14G) the lowermost caudal ray of the upper lobe articulates with hypural 3 and the upper CMC, its proximal tip points ventrally, therewith embracing the upper CMC. The uppermost caudal ray of the lower lobe articulates with hypural 2 and the lower CMC, its proximal tip points dorsally, therewith embracing the lower CMC. There are no medial pegs on the caudal rays in *A. xenostoma* and *B. vaillanti*. The CMCs are only slightly overlapping the edges of the hypurals in width. Hypural 3 gains in width more dorsally; hypural 2 more ventrally and at that point the width of the CMCs and the width of the hypurals are about the same (Fig. 14D, H).

There are also two CMCs present in the diastema of *Chauliodus sloani* (Fig. 14I–K). They are of similar size with the upper one being slightly larger. In lateral view the lower CMC is roundish, and when seen in posterior view its shape resembles a bar or handle about double the width of a hypural plate. It seems somehow related to the upper ray of the lower lobe, but there is little connective tissue. In lateral view the upper CMC has an upright ovoid outline, but when seen from posterior side, its strongly curved, bean-like shape becomes visible. The concave part of the 'bean' is facing ventrally towards the diastema. Two rays are articulating on this cartilage: in its lower half the lowest ray of the upper lobe and at its dorsal tip the penultimate ray of the upper lobe. None of the fin-ray bases show medially directed pegs.

In *Grammatostomias dentatus* there are two small CMCs (Fig. 14L). The upper CMC is bigger than the lower one, cordate in posterior view and with the tip pointing ventrally. The lower CMC is bean-shaped in posterior view, with its concave facet directed towards hypural 2. Neither cartilage has a direct articulation with caudal fin rays.

In *Eustomias obscurus* the upper and lower CMCs are roundish in lateral view and V-shaped in posterior view (Fig. 14M). In the upper CMC, which is smaller than the lower one, it becomes evident in posterior view that the left and right parts of the V are separate and not fused, thus actually representing two, bilateral cartilages. The CMCs are connected by a strong ligament (Fig. 14M) and have no direct articulation with caudal fin rays.

In *Photonectes albipennis* there is only a single CMC (Fig. 14N), resembling the lower CMC in *Chauliodus*. It is positioned like a cap on the inner distal edge of hypural 2. An association with the uppermost ray of the lower lobe seems not very tight, if present at all.

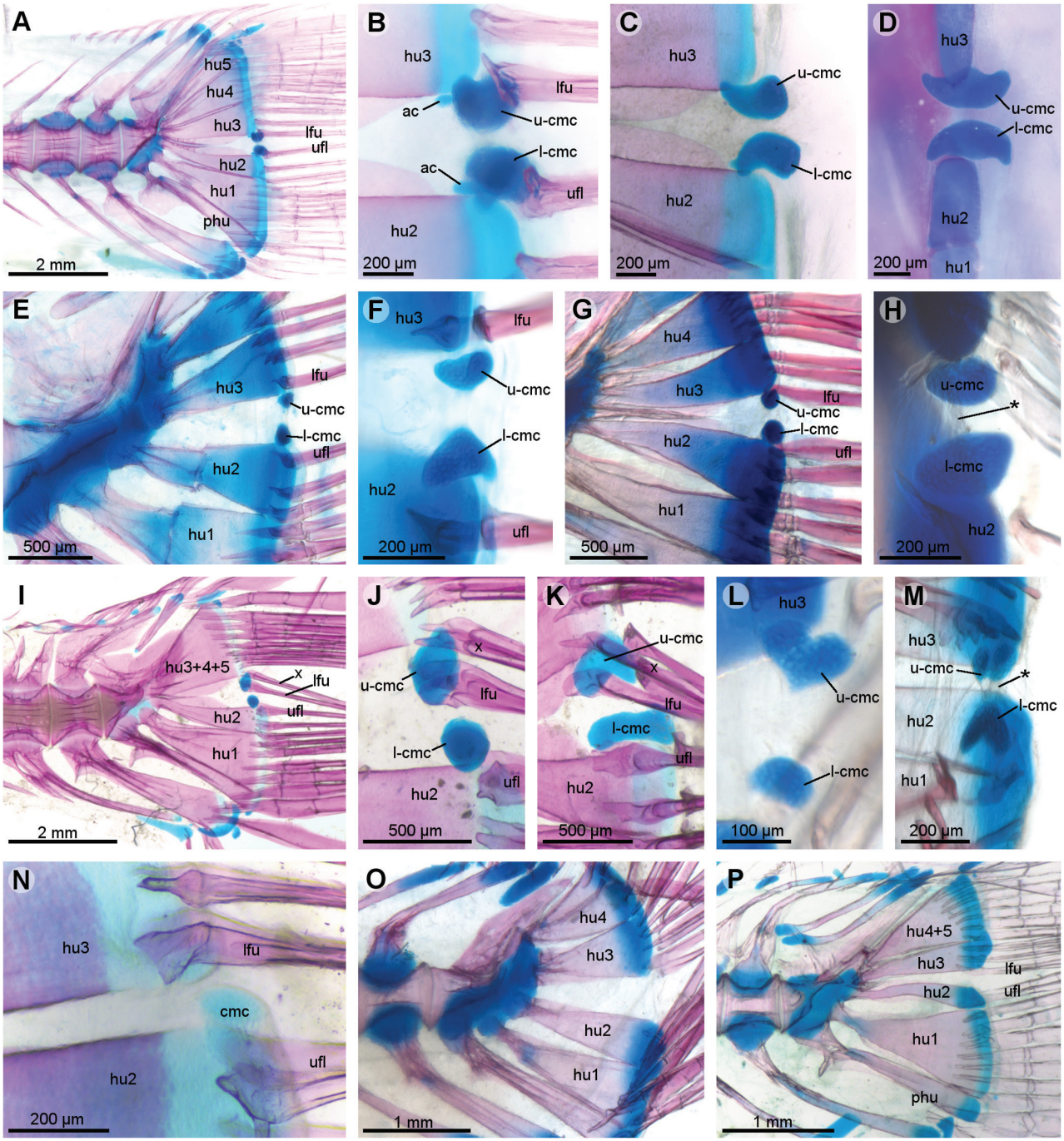

Figure 14. Cleared and stained caudal fins in the area of the diastema of Stomiidae: A–D, *Astronesthes lucifer*, DMM IE/11805, 73.8 mm SL, overview lateral (A), median caudal cartilages lateral (B), from posterior-lateral without fin rays (C), from posterior without fin rays; E–F, *Aristostomias xenostoma*, USNM 296715, 83.0 mm SL, overview lateral (E), posterior-lateral; G–H, *Bathophilus vaillanti*, USNM 234150, 101.0 mm SL, overview lateral (G), posterior view (H); I–K, *Chauliodus sloani*, DMM IE/11137, 106.2 mm SL, overview lateral (I), detail lateral (J), posterior-lateral (K); L, *Grammatostomias dentatus*, USNM 234036, 76.0 mm SL, posterior view; M, *Eustomias obscurus*, USNM 206711, 147 SL, posterior-lateral; N, *Photonectes albipennis*, DMM IE/13715, 96.4 mm SL, lateral; O, *Malacosteus australis*, USNM 296675, 110.0 mm SL, lateral; P, *Stomias boa*, DMM IE/11822, 114.4 mm SL. Abbreviations: *, ligament between CMCs; ac, accessory cartilage; hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; phu, parhypural; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe; x, second lowest ray of upper caudal lobe.

CMCs are absent in *Malacosteus australis* (Fig. 14O) and *Stomias boa* (Fig. 14P). Here the interior most rays of the caudal lobes articulate with hypural 2 and hypural 3, respectively.

Paralepididae (Aulopiformes) (Fig. 15)

In *Arctozenus risso* there are two large CMCs (Fig. 15A, B). Their three-dimensional structure is complex: in lateral view they have a somewhat rectangular to irregular shape. Seen from the posterior side, they are slightly cordate with their tips pointing to, and almost contacting, each other. There seems to be strong connective tissue between those tips. As the CMCs have articulatory facets on their anterior part they look slightly bean-shaped when seen from above. The lowest ray of the upper lobe articulates in the contact area of the upper CMC with hypural 3. The uppermost ray of the lower lobe articulates on hypural 2, hardly having any contact to the lower CMC. In *Lestrolepis japonica* there is only a single CMC on the distal diastemal edge of hypural 2 (Fig. 15C). It forms a cap on the hypural edge and has about the same width as the hypural plate and a small, medial, anteriorly directed tip (Fig. 15C). When seen from posterior it is somewhat cordate with its tip pointing dorsally and anteriorly (Fig. 15D). There is no association to any caudal fin ray visible.

Evermannellidae (Aulopiformes) (Fig. 16A, B)

In *Coccorella atlantica* there are two CMCs (Fig. 16A). In lateral view they are teardrop-shaped with the tips pointing away from each other. The upper CMC is smaller in size than the lower CMC. There is no articulation with caudal fin rays. In posterior view the CMCs are wider than the hypural plates, forming a bracket with swollen endings to the left and right and therewith forming a posteriorly facing concavity (Fig. 16B).

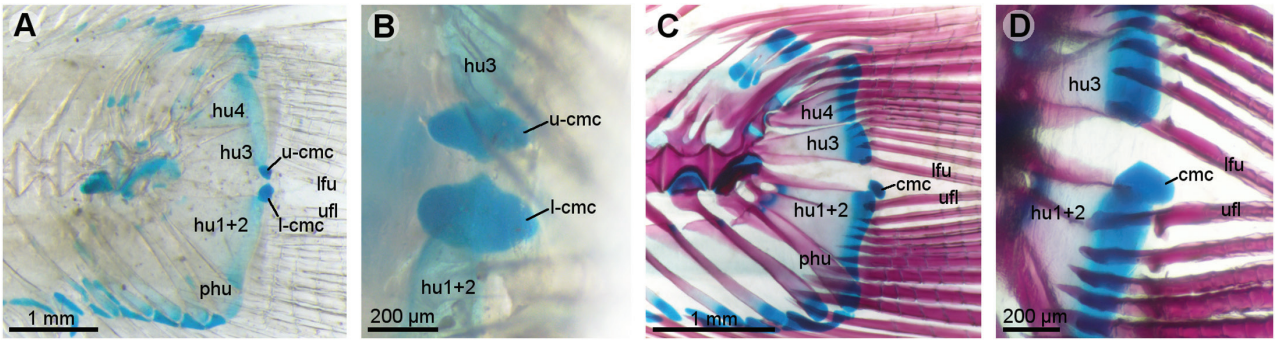

Figure 15. Cleared and stained caudal fins of Paralepididae: A–B, *Arctozenus risso*, DMM IE/11138, 147 mm SL, bone poorly stained, overview lateral (A), median caudal cartilages, posterior view (B); C–D, *Lestrolepis japonica*, DMM IE/11724, 106.9 mm SL, overview lateral (C), median caudal cartilage from posterior-lateral view (D). Abbreviations: cmc, median caudal cartilage; hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; phu, parhypural; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

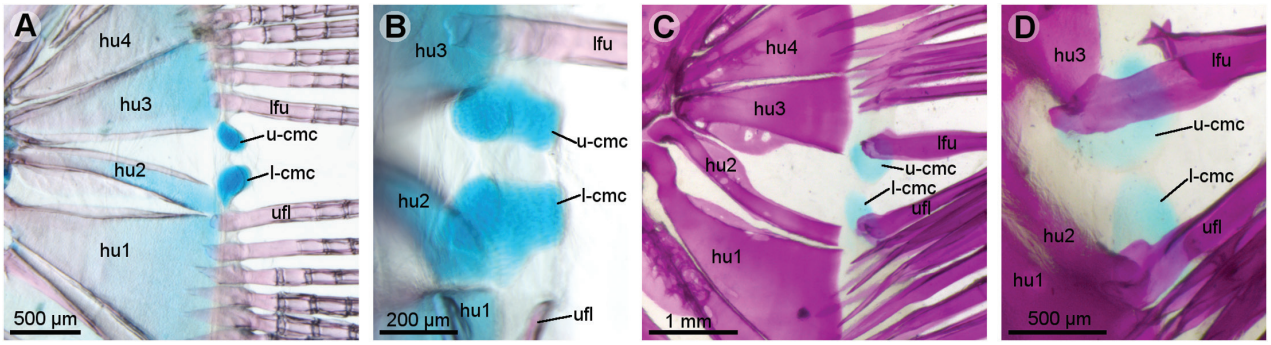

Figure 16. Cleared and stained caudal fins of Evermannellidae and Scopelarchidae: A–B, *Coccorella atlantica* (Evermannellidae), NSMT-P-99762, 64.0 mm SL, lateral (A) and posterior (B) views; C–D, *Rosenblattichthys alatus* (Scopelarchidae), DMM IE/12788, 86.2 mm SL, lateral (C) and posterior-lateral (D) views. Abbreviations: hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; phu, parhypural; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

Scopelarchidae (Aulopiformes) (Fig. 16C, D)

In *Rosenblattichthys alatus* two prominent CMCs are present (Fig. 16C). In lateral view the lower is slightly oval with upright orientation and the upper one, which is larger, has a somewhat roundish to downward-pointing triangular shape. Both cartilages have articulatory facets towards their hypural plates, giving the upper CMC a bean-shaped appearance in dorsal view. In posterior view it becomes evident that the upper CMC is wider, about two times the width of the hypurals, whereas the lower, egg-shaped CMC has only hypural width (Fig. 16D). Strong connective tissue stretches between the approaching tips of the CMCs. The most median fin rays of the caudal lobes articulate in the areas where the CMCs contact the distal cartilages of the hypural plates. There are no inward-directed pegs on the bases of these rays; in contrast there are rather small laterally directed pegs, probably for the attachment of ligaments.

Chlorophthalmidae (Aulopiformes) (Fig. 17)

In *Chlorophthalmus nigromarginatus* there are two CMCs (Fig. 17). In all studied specimens these cartilages did not stain very well, i.e. even in specimens where other cartilages in the area of the caudal fin like those at the base of procurrent rays stained well, the CMCs are only poorly dyed. The upper CMC is formed like a cap at the distal lower edge of hypural 3 (Fig. 17A–C), is clearly wider than the hypural plate and appears crown-like when seen in posterior view with one central posterior and two lateral spikes (Fig. 17D). The lower CMC is roundish, placed on the upper distal edge of hypural 2 and contacts the upper CMC. In posterior view it is narrower than the upper CMC, but has about the same width as the hypurals (Fig. 17D). Ventrally, there is an articulatory facet, where it is in contact with hypural 2. The lowest ray of the upper caudal lobe articulates on the upper CMC; the uppermost ray of the lower lobe articulates in the contact area of the lower CMC and hypural 2.

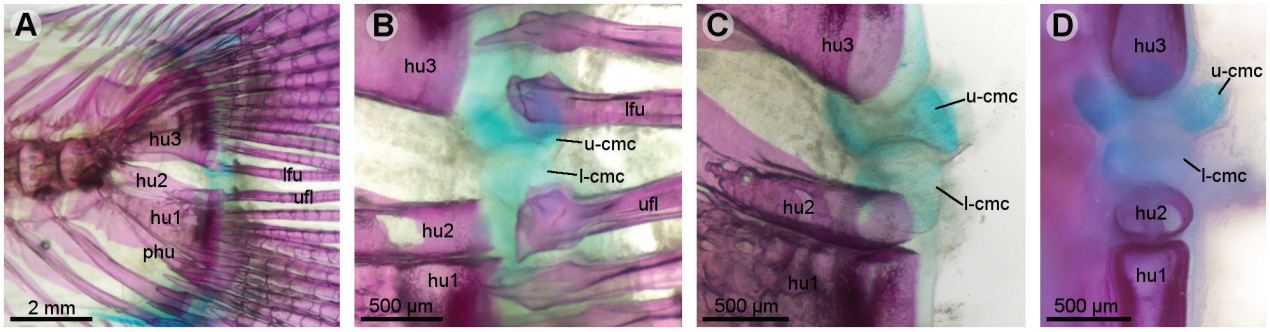

Figure 17. Cleared and stained caudal fins of *Chlorophthalmus nigromarginatus* (Chlorophthalmidae), DMM IE/13720, 93.5 mm SL: A, overview lateral; B, detail on median caudal cartilages lateral view; C, posterior-lateral view without rays; D, posterior view. Abbreviations: hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; phu, parhypural; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

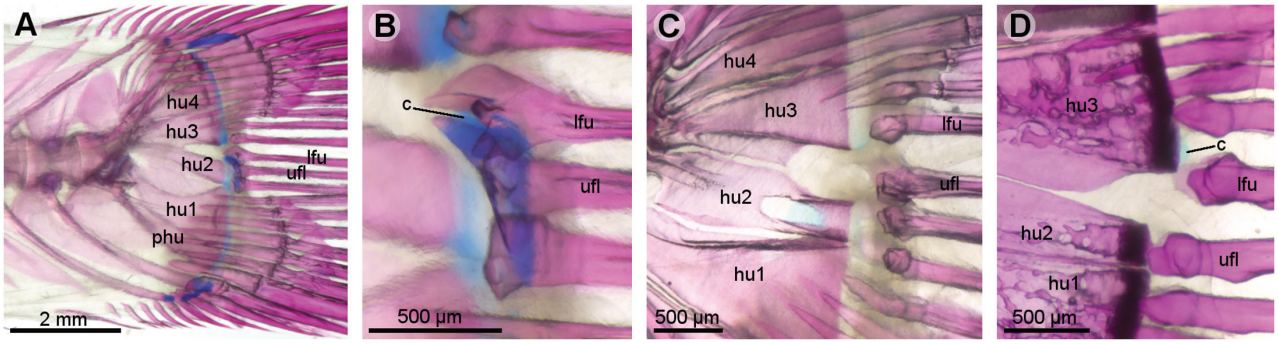

Figure 18. Cleared and stained caudal fins of Synodontidae and Aulopidae: A–B, *Saurida brasiliensis* (Synodontidae), DMM IE/11004, 82.0 mm SL, overview (A), median caudal cartilage (B); C, *Trachinocephalus myops* (Synodontidae), DMM IE/12027, 77.7 mm SL; D, *Hime japonica* (Aulopidae), DMM IE/9516, 84.2 mm SL. Abbreviations: c, cartilage; hu, hypural; lfu, lowest ray of upper caudal lobe; phu, parhypural; ufl, upper most ray of lower caudal lobe.

Synodontidae (Aulopiformes) (Fig. 18A–C)

In our specimen of *Saurida brasiliensis* there is a single, large cartilage situated on the distal diastemal edge of hypural 2, from where it tapers ventrally with a median process all along the distal margin of hypural 2 (Fig. 18A, B). The bases of the upper three caudal fin rays of the lower lobe are different from the regular caudal fin rays: a dorsally directed process of the second uppermost ray of the lower lobe fits into a notch formed by a dorsal and ventral process of the base of the uppermost ray from the same lobe. The second ray has also a ventrally tapering process that overlaps the base of the ray ventral to it (third ray counted from the diastema). The respective cartilage serves as support for these three rays. It nevertheless remains unclear if this cartilage is a CMC due to its position or even if this finding in our *S. brasiliensis* specimen shows the regular condition: the same fin-ray configuration was found in our two specimens of *Saurida gracilis*, but in these specimens, cartilage did not stain well, so we refrain from drawing a conclusion on the identity and bearing of this cartilage in *S. brasiliensis*.

In *Trachinocephalus myops* a diastema is well visible, but there are no CMCs (Fig. 18C). The lowest ray of the upper caudal lobe articulates directly in the diastema, but without cartilaginous support (Fig. 18C). In *Harpadon microchir* the distal part of hypural 3 has a laminar extension that restricts the diastema caudally. There are also no CMCs present.

Aulopidae (Aulopiformes) (Fig. 18D)

In *Hime japonica* a small cartilaginous area can be seen at the lower distal edge of hypural 3 (Fig. 18D). However, there is no indication that this cartilaginous structure represents an entity comparable to a CMC. It appears to belong directly to hypural 3, thus there are no CMCs present in this species.

Myctophidae (Myctophiformes) (Fig. 19)

In the myctophids a major part of the diastema is filled by bony lamellar outgrowths of the neighbouring hypurals, mainly of hypural 3. However, the posterior part of the diastema is not closed by these outgrowths.

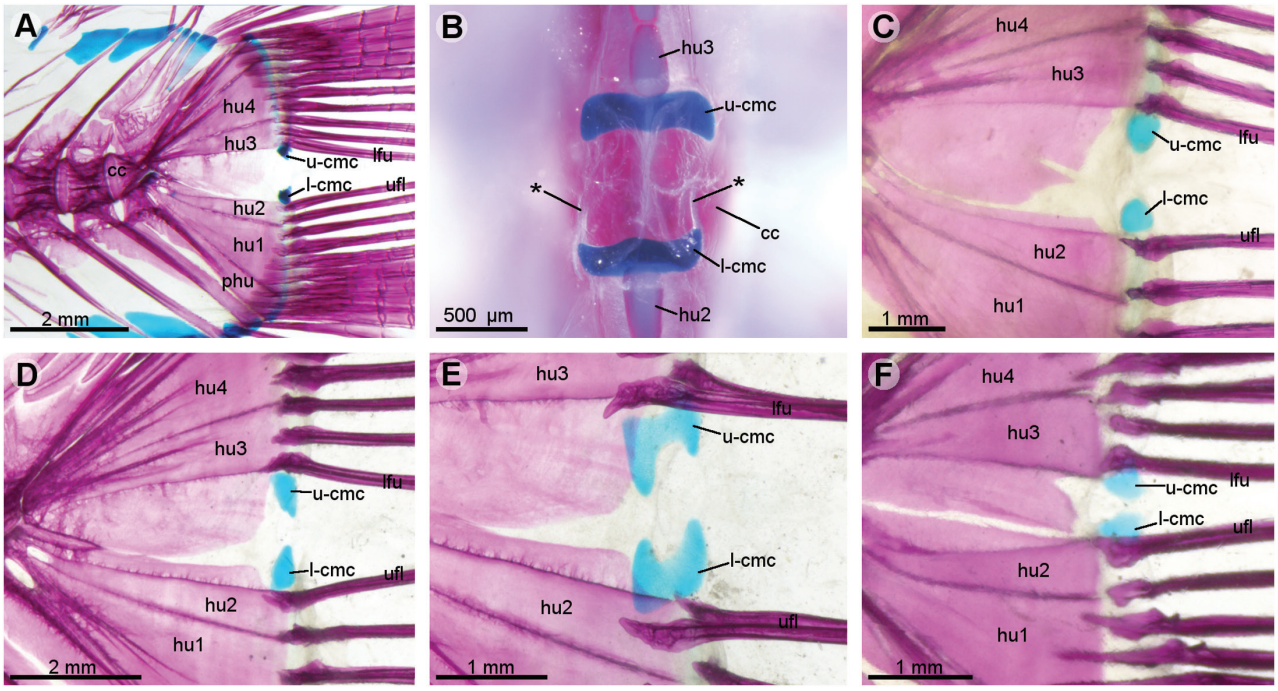

Figure 19. Cleared and stained caudal fins of Myctophidae: A–B, *Benthosema glaciale*, DMM IE/11136, 61.6 mm SL, overview lateral (A), median caudal cartilages in posterior view without fin rays (B); C, *Lampadena speculigera*, DMM IE/10198, 93.5 mm SL, lateral view; D–E, *Lampanyctus crocodilus*, DMM IE/11030, 94.6 mm SL, overview lateral (D), median caudal cartilages in posterior-lateral view (E); F, *Symbolophorus veranyi*, DMM IE/11738, 86.7 mm SL, lateral view. Abbreviations: *, ligament between CMCs; hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; phu, parhypural; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

All studied members of the family Myctophidae have two well-expressed CMCs in this posterior part of the diastema (Fig. 19A, C, D, F). In *Benthosema glaciale* the CMCs are, in posterior view, bracket- to W-shaped with their exterior tips facing towards each other (Fig. 19B). There is a band of strong connective tissue between these tips of the upper and lower CMC (Fig. 19B). The cartilages are relatively wide, more than three times the hypural width. Their middle parts articulate with the diastemal edges of hypural 2 and hypural 3, respectively. The most interior rays of the caudal lobes are placed close to the bases of the CMCs, but there seems to be no tight connection. These rays have only low medially directed bulges equalling those of the other rays. Specialized articulatory pegs are absent.

The situation is principally the same in other myctophid species (Fig. 19C–F). In *Lampadena speculigera* there are small medially directed pegs in the interior-most fin rays of the caudal lobes. In *Lampanyctus crocodilus* the tips of the bracket-shaped CMCs are elongated bridging a major part of the diastema (Fig. 19D, E). In *Diaphus watasei* and *Symbolophorus veranyi* (Fig. 19F) the CMCs are triangular in lateral view. In some specimens (not depicted here), there are very small bean-shaped accessory cartilages directly anterior to the CMCs.

Neoscopelidae (Myctophiformes) (Fig. 20)

In *Neoscopelus* two CMCs are present, being less complex and smaller (Fig. 20) than in myctophids (Fig. 19). The upper CMC is positioned like a cap on the posterior-ventral edge of hypural 3. It is slightly bean-shaped when seen laterally, with its concave side facing the hypural edge (Fig. 20A, B); when seen dorsally it is about one and a half times the width of a hypural plate and is cordate with its tip pointing caudally in between the bases of the lower ray of the upper caudal lobe. In posterior view the upper CMC is handlebar-shaped with enlarged rounded ends resulting in concave facets on the dorsal and ventral side (Fig. 20C). This cartilage clearly supports the base of the lower ray of the upper lobe. The lower CMC is only slightly wider than the upper one (Fig. 20C). In lateral view it is roundish with its ventral facet slightly flattened where it sits on the posterior-dorsal margin of hypural 2 (Fig. 20B). Seen from dorsal or posterior it is bar-like (Fig. 20C). The upper ray of the lower caudal lobe articulates in the area where the lower CMC contacts hypural 2. There are no explicit medially directed pegs on the bases of the caudal fin rays present; only the dorsal margin of the base of the lowermost ray of the upper lobe bends peg-like medially towards the contact zone of the upper CMC with hypural 3. In the smaller of the two investigated specimens there was an additional, but very small cartilage anterior to the lower CMC, on the dorsal margin of hypural 2.

Anomalopidae (Trachichthyiformes) (Fig. 21A–C)

In *Anomalops katoptron* there are two well-expressed CMCs (Fig. 21A, B). Both are rather simple in their shape, just cap-like with a notch for their articulation on the hypurals. In posterior view they are like a bar and have about double the width of the hypural plates (Fig. 21C). The lower CMC is slightly larger than the upper one. The lowest ray of the upper caudal lobe articulates in the area, where the upper CMC sits on hypural 3. The uppermost ray of the lower lobe articulates on hypural 2 slightly distant from the lower CMC and thus this CMC seems not to be involved in supporting fin rays. There are no medially directed pegs on the bases of the central fin rays. We did not find CMCs in the other trachichthyiform families studied: Trachichthyidae, Diretmidae (Fig. 21F), Anoplogastridae and Monocentridae.

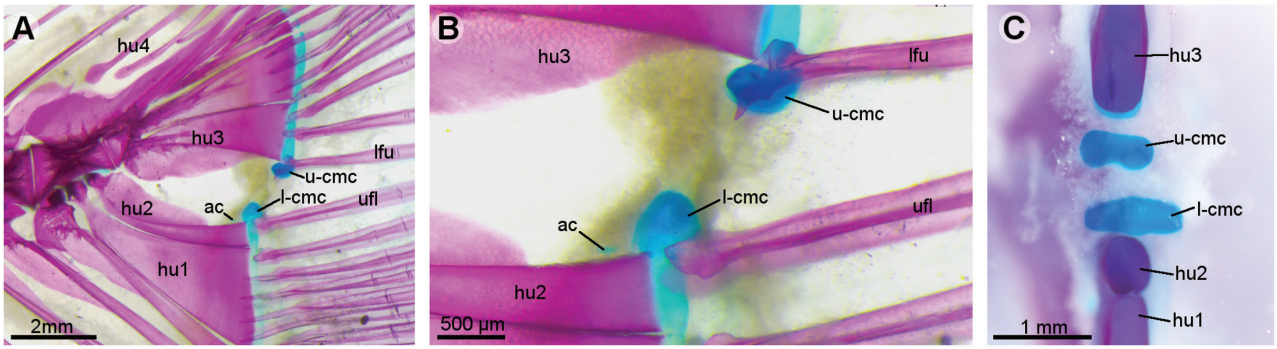

Figure 20. Cleared and stained caudal fin of *Neoscopelus microchir*, DMM IE/14351, 87.6 mm SL: A, overview lateral; B, detail, lateral view; C, detail, posterior view, fin rays removed, upper CMC slightly displaced ventrally due to preparation. Abbreviations: ac, accessory cartilage; hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

Berycidae (Beryciformes) (Fig. 21D, E)

Beryx splendens shows two CMCs (Fig. 21D, E) of which the lower is larger and well-visible. The shape of both CMCs resembles those found in *Anomalops*, only the upper CMC is slightly smaller and positioned between the bases of the lowest rays of the upper lobe. The bases possess inward-directed pegs, but they do not contact the CMC. The lower CMC is not closely associated with the upper ray of the lower lobe. Along the distal margin of the hypural plates a strong band of connective tissue runs from the dorsal and ventral sides to the diastema, where they bend anteriorly. The CMCs are positioned in the thickened ends of these strands.

Polymixiidae (Fig. 22)

In *Polymixia* there is a small cartilaginous nodule with few, neighbouring, very small, roundish or irregular cartilages on the distal diastemal edge of hypural 3

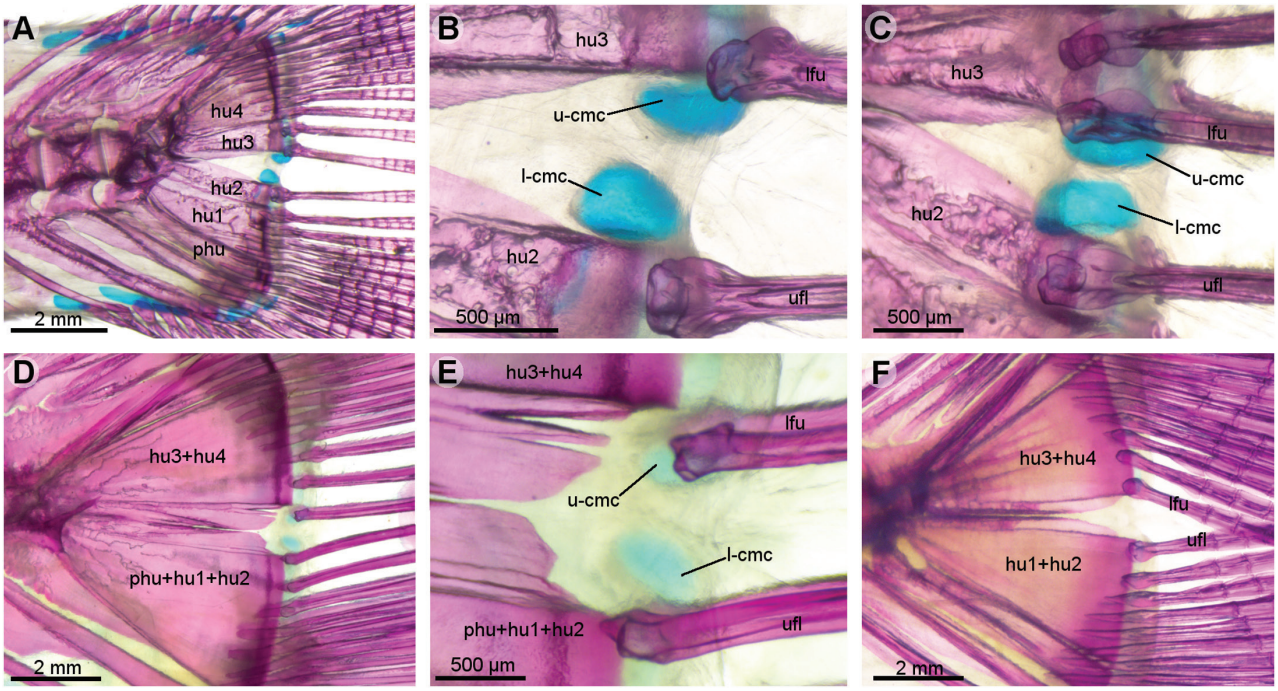

Figure 21. Cleared and stained caudal fins of Anomalopidae, Berycidae and Diretmidae: A–C, *Anomalops katoptron* (Anomalopidae), DMM IE/13721, 63.0 mm SL, overview lateral (A), CMCs, lateral view (B), CMCs, posterior-lateral view (C); D–E, *Beryx splendens*, DMM IE/13772, 111.0 mm SL, overview lateral (D), CMCs, lateral view (E); F, *Diretmus argenteus*, DMM IE/15071, 82.6 mm SL, overview lateral. Abbreviations: hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; phu, parhypural; ufl, upper most ray of lower caudal lobe; u-cmc, upper median caudal cartilage.

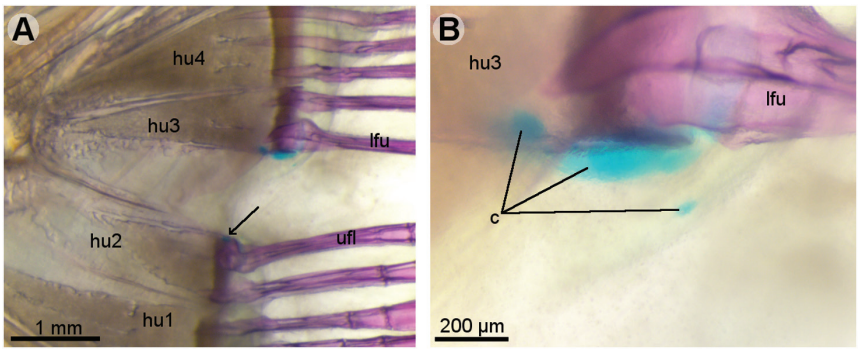

Figure 22. Cleared and stained caudal fin of *Polymixia berndti* (Polymixiidae), DMM IE/13296, 99.5 mm SL: A, area of diastema; B, lower distal edge of hypural 3. Arrow pointing to minute cartilaginous patch on hypural 2. Abbreviations: c, cartilage; hu, hypural; lfu, lowest ray of upper caudal lobe; ufl, upper most ray of lower caudal lobe.

(Fig. 22B). Furthermore, there is a minute cartilaginous patch on the distal diastemal edge of hypural 2 (Fig. 22A). These cartilaginous patches are in very close contact with the hypurals and do not form well-defined entities.

Size of diastema and presence of median caudal cartilages

Some species show highly specialized caudal fins without any diastemal gap. However, most species have a diastema, but not necessarily cartilaginous structures in that area. Thirty-two individuals of 27 species with CMCs and 25 individuals of 25 species without CMCs were measured to examine the size relationships of the diastema and its cartilages, if present (Fig. 23; see Fig. 1 for measuring method). In specimens with CMCs, the size of the diastema ranged between 2.7 and 23.4% of the total hypural height, with an average of 13.0%. In specimens without CMCs, the diastemal gap ranged from 8.0 to 29.7%, with an average of 15.9%. There is no functional relationship between size of the diastema and presence/absence of CMCs among teleosts.

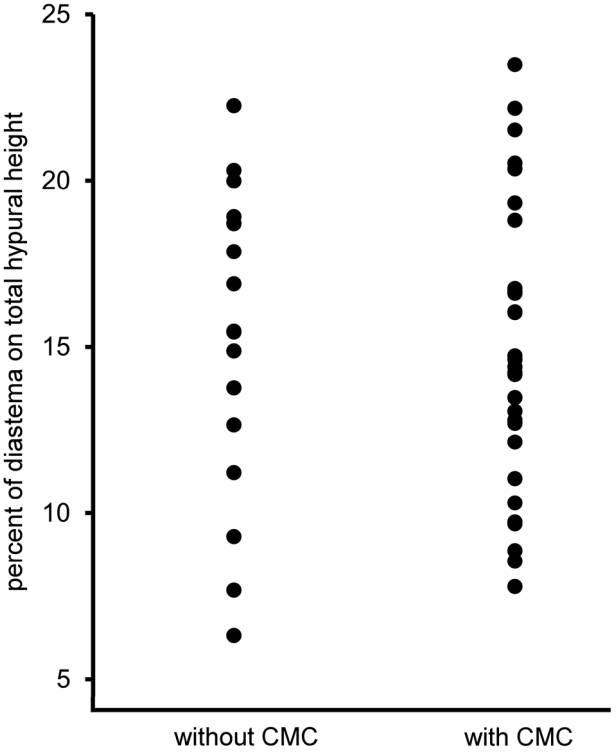

Figure 23. Presence vs. absence of median caudal cartilages in relation to size of the diastema. Data from 25 specimens of 25 species without and 32 specimens from 27 species with median caudal cartilages.

Development of medial caudal cartilages

Little information on the development of CMCs can be currently presented. Most information is available for salmoniform species (Fig. 24A–I). Here, the single or two CMCs develop relatively late in comparison to other elements of the caudal fin. All hypurals are at least partly ossified before the first traces of CMCs appear (Fig. 24B, E, H). This happens in *Salmo* and *Thymallus* shortly before the ural centra form. In *Coregonus* the two ural centra are already present when the first trace of a CMC appears (Fig. 24H). First appearance of CMCs happens in *Coregonus* at about 27–30 mm SL, in *Thymallus* and *Salmo* between 19 and 25 mm SL. The CMCs form as a new structure in the diastema and do not originate as part of the hypural cartilages. They start as a small cartilage that grows during ontogeny (Fig. 24B, C, E, F, H, I) until they reach their assumed final size, shape and place in the larger specimens depicted here. In cases where only one CMC develops, it appears in the ventral part of the diastema, close to the edge of hypural 2.

The development of CMCs in *Osmerus* is similar (Fig. 24J, K): they appear relatively late in comparison to other caudal fin elements. In *Arctozenus risso* juveniles of about 30 mm SL, the lower CMC is present in some specimens (Fig. 24L), but not in all. It is formed as a simple bar embraced by the bases of the left and right hemitrich of the uppermost ray of the lower lobe. In many specimens of about the same size, no CMC is present, whereas in few, the upper CMC is present as a small ball between the bases of the lowest ray of the upper lobe.

In the stomiid *Photostomias* the lower CMC appears between 21 and 32 mm SL (Fig. 25A, B) and it develops before the upper CMC (Fig. 25B). At this stage all hypurals are preformed of cartilage, but show no sign of ossification yet. There is one cartilaginous epural and the ossified uroneural, but there are no ossified vertebral centra. In a 92 mm SL specimen, all hypurals, caudal vertebrae and the single epural (with the tips still cartilaginous) are ossified, and two prominent CMCs are present in the diastema (Fig. 25C). We lack intermediate developmental stages to determine the exact size at which the upper CMC appears. The same development of the CMCs during early ontogeny was observed in *Astronesthes niger* and *Eustomias* sp. (not illustrated here). In the phosichthyid *Vinciguerria* there is just a single CMC. This cartilage is present in a 9 mm SL specimen (Fig. 25D). At this stage the hypurals have just started to ossify, but no ural centra are formed yet. In the sternoptychid genus *Argyropelecus*, the lower CMC develops before the upper CMC. At this stage (9.9 mm SL; Fig. 25E) the hypurals, the parhypural and one ural centrum have already partly ossified. In our 13.3 mm SL specimen all caudal vertebrae have formed and the upper

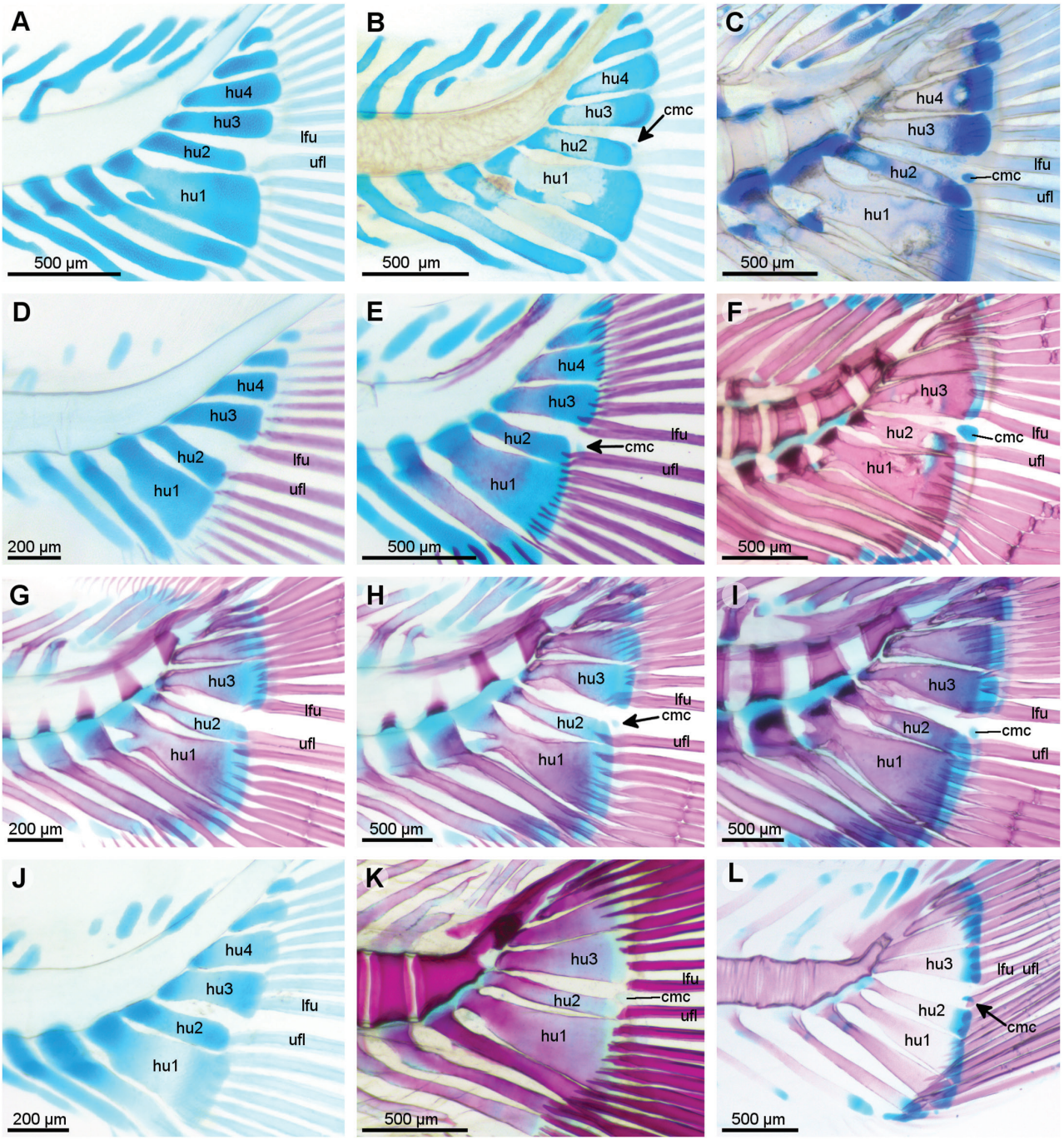

Figure 24. Development of medial caudal cartilages: A, *Salmo trutta*, DMM IE/ 11368, 17.3 mm SL; B, *Salmo trutta*, IE/11369, 18.1 mm SL; C, *Salmo trutta*, DMM IE/11002, 27.9 mm SL; D, *Thymallus thymallus*, DMM IE/11786, 14.2 mm SL; E, *Thymallus thymallus*, DMM IE/11799, 19.1 mm SL; F, *T. Thymallus*, DMM IE/11733, 50.3 mm SL; G, *Coregonus maraena*, DMM IE/13722, 27.1 mm SL; H, *Coregonus maraena*, DMM IE/13722, 29.2 mm SL; I, *Coregonus maraena*, DMM IE/13723, 36.1 mm SL; J, *Osmerus eperlanus*, DMM IE/11090, 14.3 mm SL; K, *Osmerus eperlanus*, DMM IE/13725, 21.9 mm SL; L, *Arctozenus risso*, DMM IE/11797, 29.8 mm SL. Abbreviations: cmc, median caudal cartilage; hu, hypural; lfu, lowest ray of upper caudal lobe; ufl, upper most ray of lower caudal lobe.

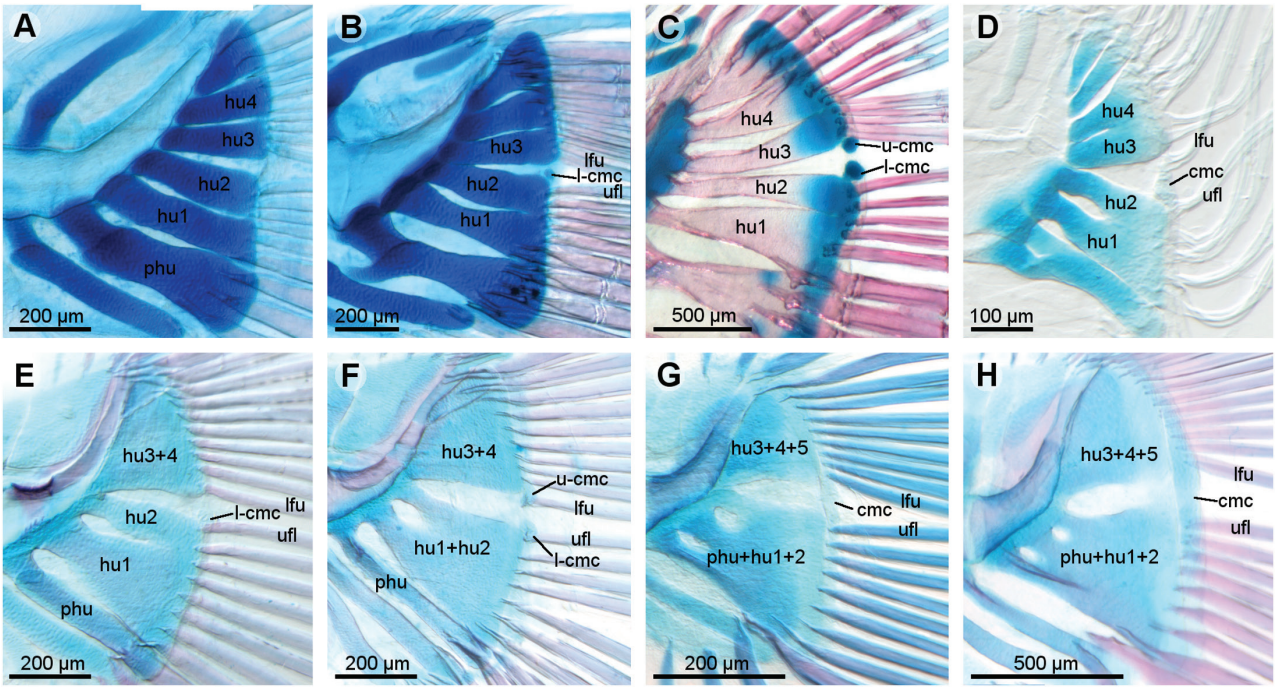

Figure 25. Development of medial caudal cartilages: A, *Photostomias* sp., MCZ 155694, 21 mm SL; B, *Photostomias* sp., MCZ 155694, 32 mm SL; C, *Photostomias* sp., USNM 296650, 92.0 mm SL; D, *Vinciguerria* sp., NSMT-PL 691, 9 mm SL; E, *Argyropelecus* sp., NSMT-uncat., 9.9 mm SL; F, *Argyropelecus* sp., NSMT-PL 728, 13.3 mm SL; G, *Sternoptyx* sp., NSMT-PL 730, 8.8 mm SL; H, *Sternoptyx* sp., NSMT-PL 730, 9.5 mm SL. Abbreviations: cmc, median caudal cartilage; hu, hypural; l-cmc, lower median caudal cartilage; lfu, lowest ray of upper caudal lobe; phu, parhypural; u-cmc, upper median caudal cartilage; ufl, upper most ray of lower caudal lobe.

CMC is also present (Fig. 25F). In the sternoptychid genus *Sternoptyx* there is one single, enlarged CMC. Our smallest specimen (8.8 mm SL) already shows this single cartilage (Fig. 25G). At this stage the urostyle and hypurals already started to ossify. In a 9.5 mm SL specimen the single CMC has elongated in dorsoventral direction (Fig. 25H).

For the other investigated groups there is almost no information on the development available. In the smallest alepocephaliforms, sternoptychids and bathylagids available in this study, the CMCs are already present. In the smaller specimens of *Polyipnus spinosus*, the CMCs show a simpler, almost ball-like shape without the typical notch on the diastemal side found in bigger specimens.

DISCUSSION

THE FUNCTION OF MEDIAN CAUDAL CARTILAGES

So far, only very few statements on the function of CMCs have been made. Johnson & Patterson (1996) distinguished two types of CMCs based on the way they support caudal fin rays, thereby implying that the function of CMCs is to support fin rays. This certainly holds true in many cases, e.g. for Alepocephalidae, Platytroctidae, Argentinidae, Osmeridae and some Stomiiformes. However, in several other taxa there seems little or no involvement of CMCs in fin-ray support. If they were necessary to mechanically bridge the diastema, one would expect to find a relation between size of the diastema and presence of CMCs. However, such a relation was not found in our study (Fig. 23), but it seems that in some taxa, like myctophiforms, *Polyipnus* and *Anomalops*, CMCs plus their associated strong connective tissue serve in stabilizing the caudal fin.

One could speculate that the functional division of an upper and lower lobe is kept by the movable CMC–ligament connection and at the same time giving a robust protection against excessive separation of the two lobes. In order to more closely investigate the ligaments in some of our cleared and stained specimens, we transferred some of them into ethanol and used polarized light. We found substantial variability in the morphology and arrangement of the ligaments and their relation to the CMCs. It is beyond the scope of this paper to document the ligaments in all investigated taxa and, therefore, we only document their diversity with some examples

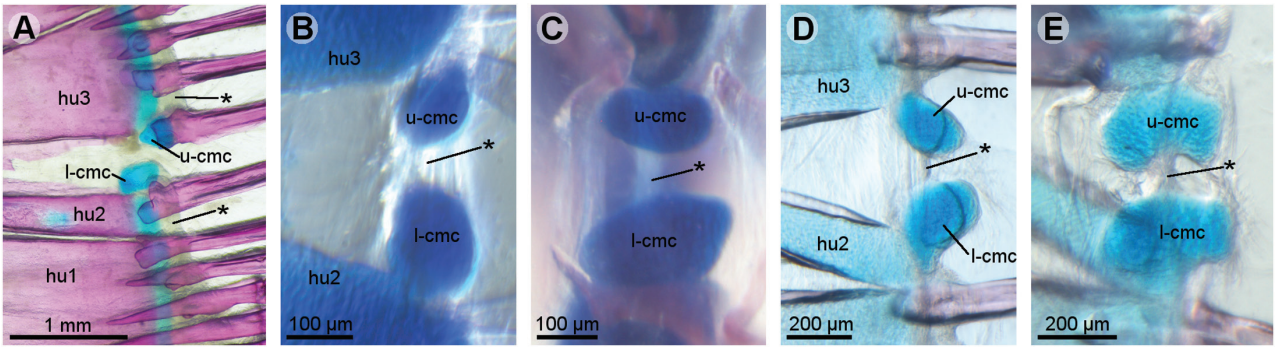

Figure 26. Ligaments related to median caudal cartilages: A, *Osmerus eperlanus* (Osmeridae), DMM IE/15080, 111.8 mm SL, lateral view; B–C, *Bathophilus vaillanti* (Stomiidae), USMN 234150, 101.0 mm SL, lateral (D) and posterior (E) view; D–E, *Coccorella atlantica* (Evermannellidae), NSMT-P 99762, 64.0 mm SL, lateral (D) and posterior (E) views. Abbreviations: *, ligaments between CMCs; hu, hypural; l-cmc, lower median caudal cartilage; u-cmc, upper median caudal cartilage.

(Fig. 26). In salmoniforms, retropinnids, *Osmerus* (Fig. 26A) and *Beryx* the CMCs apparently develop in strong bands of connective tissue running along the distal margins of the hypurals, either from the dorsalmost hypural to hypural 3 and then extending anteriorly into the diastema or running from hemal spines incorporated into the caudal fin along the parhypural and hypural 1 to hypural 2, where it also bends anteriorly into the diastema. Both strands end in the diastema and when CMCs are present they are positioned directly in the ends of these strands (Fig. 26A). Therefore, in those taxa, CMCs might serve as an anchor for a band of strong connective tissue stretching along the posterior ends of the hypural plates. Such connective tissue strands are also present, but less pronounced, in, for example, several Stomiiformes and the evermannellid *Coccorella atlantica*. In some Stomiiformes (Figs 12B, 14H, M, 26B, C) and *C. atlantica* (Fig. 26D, E) the CMCs are connected by a strong ligament that spans the diastema and connects the CMCs on their diastemal side (Fig. 26B–E, marked with an *). In *Polyipnus* (Fig. 11A–C), myctophiforms (Fig. 19) and *C. atlantica* there are two further ligaments connecting the laterally positioned processes of the CMCs with each other. In most investigated species, the two median fin rays are connected to each other by ligaments that are bilaterally present (Fig. 26C, E). Altogether the morphology of the CMC-related ligaments might be as similarly diverse as the CMCs themselves and surely needs a separate comprehensive investigation.

In some taxa only very small cartilages are present, which may represent CMCs and for which it seems questionable if they serve any mechanical function. This impression is reinforced by variable expressions, or even complete absence, of CMCs in some but not all specimens of certain species, e.g. *Osmerus eperlanus*, *Thymallus thymallus* and *Retropinna*. All speculations need to be further tested in future studies. In summary, it seems that in a primitive state, CMCs served as fin-ray supporting structures, but gained additional functions in the course of evolution or lost their significance, resulting in total or almost complete reduction.

Ontogeny of median caudal cartilages

From the little information so far available it seems clear that CMCs develop as separate entities and not as part of another cartilage, e.g. of hypural plates. They develop late in ontogeny when most other structures of the caudal fin skeleton have already appeared. In *Mallotus villosus* the first occurrence of a CMC is reported at a standard length of 20.5 mm (Doosey & Domke, 2014: fig. 3D). Arratia & Schultze (1992) supposed that single cartilages in adult salmoniforms are the product of ontogenetic fusion. More adult salmoniforms should be studied, but our data suggest that it is due to individual variation, independent of the size of the specimen. Generally, the ontogeny of CMCs presently is much understudied. Little information is available for stomiiforms and aulopiforms, and no information was presented for alepocephaliforms, argentiniforms, myctophiforms, *Beryx*, *Anomalops* and *Polymixia*. However, the limited information can already be helpful in the identification of larval material at genus level. For example, some larval phosichthyids, gonostomatids and sternoptychids resemble each other and there exists no single set of larval characters that would allow separation of all species at family level (Watson, 1996). However, with our limited stomiiform material available in this study, we were able to show that two CMCs are present in our investigated gonostomatids, except for those species previously placed in their

own family, the Diplophidae (e.g. Nelson, 2006) and now included in the Gonostomatidae (Betancur, 2017) in which CMCs are lacking. In phosichthyid genera only one CMC is present. Sternoptychids have either one or two present, but each configuration and three-dimensional structure of the CMCs is genus-specific. Another example can be taken from the Aulopiformes; in *Lestrolepis* there is never an upper CMC, whereas it is usually present in *Arctozenus*; therewith the configuration of CMCs seems to distinguish some taxa from an early stage on. Further studies have to test this statement and present more details on more specimens and more taxa within certain groups.

Occurrence and evolution of median caudal cartilages among teleosts

Elopomorpha and Osteoglossomorpha, the two most basal teleost groups, lack median caudal cartilages (Schultze & Arratia, 1988; Hilton & Britz, 2010). They first appear in clupeocephalan lineages with prominent forms in alepocephaliforms (as part of the Otomorpha) and several euteleost taxa (Fig. 27). Among otomorphs CMCs have never been found in clupeomorphs. In Ostariophysi there are so far only very few records of cartilages in the diastema. If present, they are always minute and found in taxa imbedded in clades of non-CMC species, i.e. the characids *Gymnocorymbus*

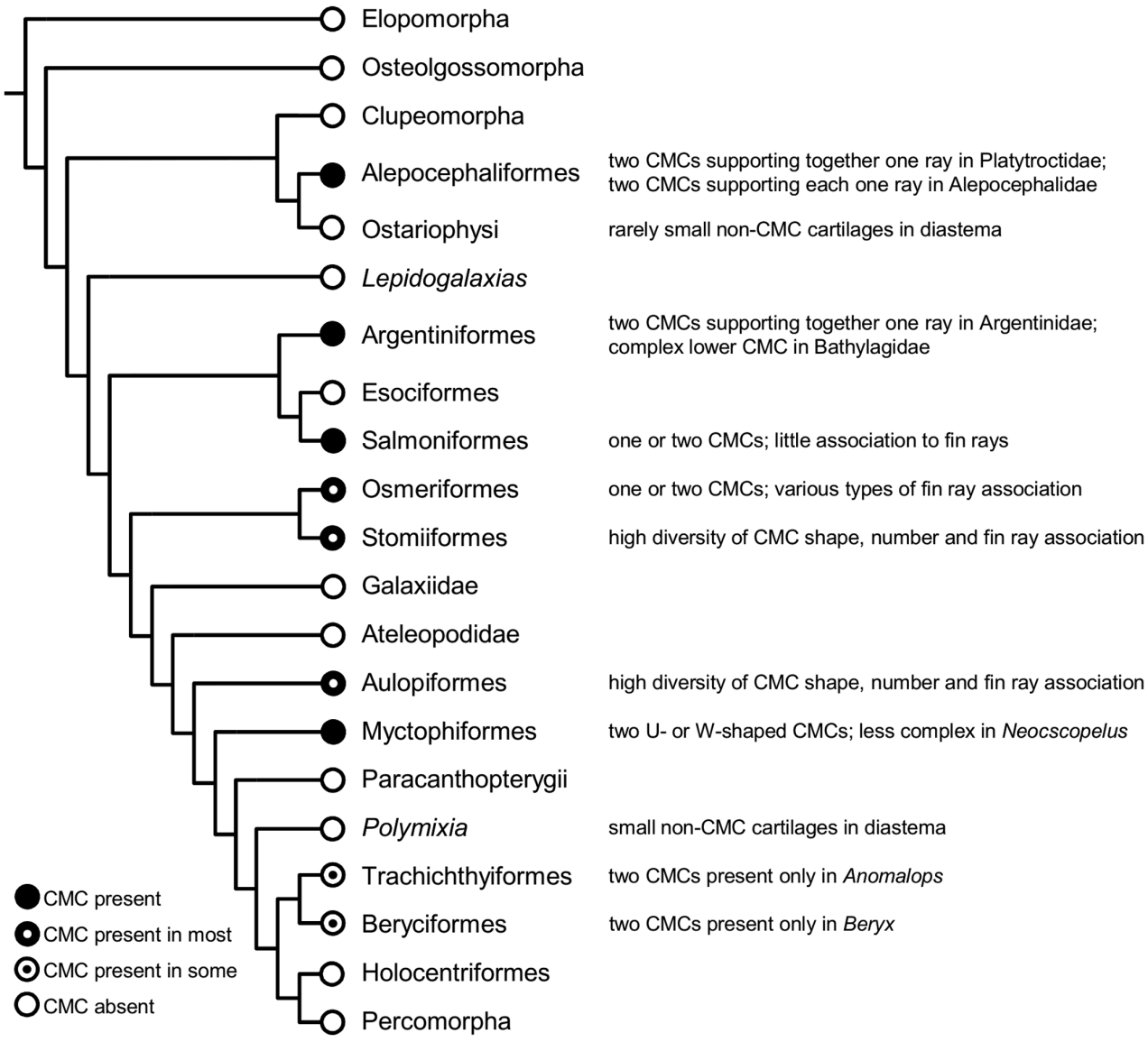

Figure 27. Overview on the phylogenetic distribution of median caudal cartilages (CMCs) mapped on a simplified tree based on Betancur *et al.* (2017) and Straube *et al.* (2018).

ternetzi and *Hemigrammus erythrozonus* (this study) or the cyprinid *Tanakia tanago* (Fujita, 1990). Even if these structures are called CMCs due to their position close to or in the diastema, it seems obvious that these cartilages cannot be homologous to CMCs of various euteleost groups or alepocephaliforms. In this context, the findings of Cope (1890) must be mentioned. He displayed a CMC (called 'intercalary cartilage') for *Salmo trutta* and *Salmo salar*, as a large cartilage filling the complete diastema. Probably biased by these findings he displayed respective large cartilages also in the caudal fins of *Barbus barbus* (Cyprinidae) and *Perca fluviatilis* (Percidae) (Cope, 1890: plates 27 and 28). No hint was found in other studies on caudal fins (e.g. Fujita, 1990; Keivany, 2016) or in our own material that large CMCs may be present in any cyprinid or perciform taxon. Therefore, we interpret the large diastemal cartilages depicted by Cope (1890) for *Barbus* and *Perca* as erroneous.

CMCs can be found in all families of alepocephaliforms: Alepocephalidae, Platytroctidae and Bathylaconidae (for *Bathylaco nigricans* see: Markle, 1976). All alepocephaliform taxa investigated in the present study show CMCs. Markle (1976) reported two CMCs for the alepocephalid genera *Alepocephalus*, *Asquamiceps*, *Bathyprion*, *Leptochilichthys*, *Mirognathus, Rouleina, Talismania* and *Bajacalifornia*, with each CMC supporting one ray. Only in *Bajacalifornia* are the CMCs large and in contact with each other. In the alepocephalid genus *Narcetes* there are two large CMCs that together support a single ray. The latter represents the situation otherwise described for platytroctids in *Mentodus* (Markle, 1976). They have relatively large CMCs, not necessarily contacting each other, but supporting together a single ray. The situation almost equals that in the bathylaconid *Bathylaco nigricans*: the CMCs are quite large, contacting each other and together supporting one fin ray (Markle, 1976). For the alepocephalids *Conocara*, *Einara*, *Leptoderma*, *Photostylus* and *Xenodermichthys* Markle (1976) noted the absence of CMCs. Johnson & Patterson (1996: 288) confirmed this absence for *Leptoderma* and *Photostylus.* For *Leptoderma,* showing a highly reduced caudal fin skeleton, this is not surprising, but the other taxa should be carefully reassessed, as at least for *Xenodermichthys* the herein reported results contradict these findings: all specimens of both species from the genus, *X. copei* and *X. nodulosus*, clearly showed CMCs as typical for Alepocephalidae.

Johnson & Patterson (1996) regarded the alepocephalid configuration with two cartilages each supporting one ray as primitive and the condition with two, usually larger, cartilages supporting together one ray as derived. This makes sense from an anatomical point of view, especially when compared to the present results: the lower fin-ray of the upper lobe slightly shifted its position ventrally, the cartilages kept their position, but are enlarged, and the upper ray of the lower lobe shifted its position only slightly ventrally, compared to other alepocephaliforms, thus being anchored close to the ventral part of the lower CMC (Figs 2, 3). Treating the latter condition as more 'basal', also fits the hypothesis presented by Begle (1992) in which the platytroctids are nested deep inside the alepocephalids *s.l.* However, that study was heavily criticized by Johnson & Patterson (1996) who presented a phylogenetic hypothesis with Alepocephalidae and Platytroctidae being sister-groups. This rough division in two clades was also supported by molecular studies (Lavoué *et al.*, 2008; Poulsen *et al.*, 2009). However, support values for most basal nodes are very low in both studies, so a detailed interpretation remains open, until well-founded phylogenetic hypotheses on alepocephaliforms are available. In any case, it seems that the derived configuration developed more than once in alepocephaliforms: in platytroctids, in *Narcetes* deeply nested inside alepocephalids and maybe in *Bathylaco*, a genus with a presently insufficiently resolved position.

In euteleosts the most 'basal' taxon, *Lepidogalaxias*, does not show any CMC. The remaining euteleosts are divided in Protacanthopterygii, Stomiatii and Galaxiiformes plus Neoteleostei (Straube *et al.*, 2018). In Protacanthopterygii very similar configurations to the platytroctids are present in argentiniforms: two large cartilages support together the lowermost fin-ray of the upper caudal lobe in *Argentina* and *Glossanodon* (this study; Fujita, 1990), the microstomatids *Microstoma* and *Nansenia*, and the opisthoproctid *Bathylychnops* (Johnson & Patterson, 1996). The lower CMC is also involved in the support of the uppermost ray of the lower lobe, at least in the herein investigated groups. In *Bathylagus euryops* the situation is slightly altered in the way that the upper CMC is very small and the lower CMC is much enlarged with a complex three-dimensional structure. The upper ray of the lower lobe is shifted ventrally and not in contact with the lower CMC anymore. Fujita (1990: 239–240) depicted the caudal skeletons of *Bathylagus ochotensis* and *B. milleri* (now *Pseudobathylagus*), but did not give much detail on the CMCs nor indicate fin-ray position in the respective illustrations. Nevertheless, this depiction seems to correspond to our findings of *B. euryops*; at least it is clearly shown that the lower CMC is much larger than the upper one. The drawing of *Pseudobathylagus milleri* by Johnson & Patterson (1996: 288) does not show any upper CMC, although the authors interpreted this situation as two CMCs each supporting one ray. We cannot follow this view based on their drawing (fig. 14B), which is not compatible to the drawing of Futjita (1990) and our findings in *Bathylagus euryops*.

The very similar situation in argentiniforms and platytroctids raises two major questions: first, the already above-mentioned question on the more primitive situation for fin-ray support by CMCs, and second, how the contradicting morphological and molecular findings for the position of alepocephaliforms can be explained. Following recent molecular phylogenetic hypotheses (e.g. Straube *et al.*, 2018), the more parsimonious explanation would be that the platytroctid–argentiniform situation represents the 'basal' condition and that Alepocephalidae *s.s.* altered this state. In any case, evolutionary explanations are much more complex when placing alepocephaliforms into otomorphs, as proposed by molecular findings (e.g. Betancur-R *et al.*, 2017; Straube *et al.*, 2018), instead of regarding them as euteleosts, as proposed by morphological findings (e.g. Greenwood & Rosen, 1971; Johnson & Patterson, 1996). Also, other characters so far regarded as synapomorphies of Alepocephaliformes and Argentiniformes, i.e. their specialized epibranchial organ (called crumenal organ) or a special pattern in the anterior epineurals, must be explained as convergent developments. While feeding adaptations like specialized epibranchial organs more easily might be interpreted as convergent evolutions, the epineural pattern or the very similar CMC configuration, are difficult to explain. Both characters seem to have no important ecological meaning, nor do they serve as an adaptation for the same habitat, i.e. the deep sea. The conflict of molecular and morphological data regarding the systematic position of alepocephaliforms remains unsolved or is even increased by detailed studies of the CMCs and will certainly be the focus of future studies.

In the sister-group of Argentiniformes, the Salmoniformes plus Esociformes, CMCs have apparently been lost in Esociformes. In Salmoniformes they are very variable in their expression, with alternatively one or two CMCs in the same species (Fig. 7). Fin-ray support seems not to play any role here; the CMCs just fill the diastemal gap. The situation reported here corresponds to the findings of Arratia & Schultze (1992) and Fujita (1990). The former depicted *Oncorhynchus mykiss* (with one and two CMCs), *Salmo salar* (one CMC), *Salvelinus fontinalis* (one CMC), *Prosopium williamsoni* (one CMC), *Thymallus arcticus* (two larger CMCs plus two additional small cartilages) and *T. thymallus* (one CMC). Fujita (1990) depicted the following species: *Oncorhynchus masou* (one CMC), *O. mykiss* (his *Salmo gairdneri*; one CMC), *Salvelinus leucomaenis* (his *S. pluvius*; one small CMC), *Coregonus maraena* (two CMCs) and *Thymallus arcticus* (two CMCs). Interestingly, he also investigated *Oncorhynchus rhodurus*, which is now treated as a synonym of *O. masou*. His *O. rhodurus* specimen showed two CMCs, whereas his *O. masou* specimen showed only a single CMC. Therefore, the variability of one or two, rarely more, CMCs seems to characterize all the salmoniforms, as Arratia & Schultze (1992) noted.

The Stomiatii, i.e. Stomiiformes and Osmeriformes, show a high variability in their CMC shape and number. In the present study, CMCs were lacking in those gonostomatid species that have been sometimes united as diplophids, i.e. *Manducus maderensis*, *Triplophos hemingi* and *Diplophos* sp. (Nelson, 2006). Also, Fujita (1990) did not find CMCs in *Diplophos orientalis*. In the gonostomatids *s.s.*, of which we investigated *Sigmops elongatus* and *Cyclothone* sp., two CMCs are present; this corroborates Fujita (1990) who studied *Sigmops elongatus* (his *Gonostoma elongatum*) and *Cyclothone atraria*. These findings might present another hint that Gonostomatidae as presently understood should be divided into two separate families.

The general situation of gonostomatids *s.s.* much resembles that in sternoptychids, which usually have two CMCs of differing size, each supporting one ray. *Polyipnus* additionally has a more complex shape of the CMCs, much resembling the situation found in myctophids. Futjita (1990) reported a single, large CMC for *Sternoptyx* and two CMCs for *Argyropelecus sladeni*, supported by our findings on *Sternoptyx* sp. and *Argyropelecus* sp. For phosichthyids, Fujita (1990) reported two CMCs in *Polymetme,* and a large CMC in *Vinciguerria* and *Ichthyococcus*, which he interpreted as a fusion of two CMCs. Fujita (1990) furthermore found two separate CMCs in the following investigated stomiid species: *Chauliodus sloani*, *Astronesthes lucifer*, *A. cyaneus*, *A. indicus*, *A. chrysophekadion*, *Leptostomias multifilis*, *Photonectes albipennis*, *Echiostoma barbatum*, *Flagellostomias boureei* and *Photostomias guernei*. In *Idiacanthus antrostomus* only a single CMC was present, and in both investigated species of *Stomias* CMCs, were absent (Fujita, 1990). As mentioned above, statements on the three-dimensional structures on CMCs in stomiiforms are not possible based on the drawings of Fujita (1990), but the results presented here do not contradict any of his findings and show a high variability in size, shape and fin-ray support. The Stomiiformes seem to need a more detailed study on their CMC morphology for any general statements on family level and to draw any conclusion on the evolution of these structures in this taxon.

In osmerids the CMC configuration shows considerable variability. Doosey & Domke (2014: 361) stated that '*Mallotus villosus* has a single median caudal cartilage' and refer to Fujita (1989), although the specimen in their figure 4A clearly possesses two CMCs. Their specimen in figure 4B indeed has a single CMC; in the other figures, cartilage staining does not

allow clear statements. Our specimen of *M. villosus* also showed a single CMC, but in *Hypomesus* and salangids there are two, and in *Osmerus* two plus an additional cartilage in some specimens. Shapes of the CMC seem less complex than, for example, in stomiiforms, and in most cases the two CMCs each support one fin ray. Fujita's (1990) findings are congruent with our findings with *Osmerus mordax*, *Hypomesus nipponensis*, *H. japonicus* and *Plecoglossus altivelis*, each having two CMCs, each supporting one fin ray. Only his drawing of a salangid, *Salangichthys ishikawae*, differs from our salangids in having only a single, large (in lateral view), cordate CMC (Fujita, 1990). Retropinnids, having one or two CMCs within the same species, resemble the situation in *Osmerus* regarding their position and support for fin rays; they differ from the similarly variable salmoniforms regarding the fin-ray supporting function.

Recent molecular studies placed the Galaxiiformes (*s.s.*, i.e. without retropinnids and *Lepidogalaxias*) as sister-group to neoteleosts (Near *et al.*, 2012; Straube *et al.*, 2018). In our specimens of *Lovettia sealii*, *Galaxias occidentalis* and *G. maculatus* we did not find any trace of CMCs. Fujita (1990) also reports the last species. Due to the much reduced caudal fin skeleton, the absence of CMCs in ateleopodiforms is not surprising. The situation in Aulopiformes seems similarly complicated as in stomiiforms. Combining the present study with the results of Fujita (1990) gives the following picture: two cartilages, each supporting one ray, are present in *Paralepis* (Paralepididae), *Omosudis* (Omosudidae), *Alepisaurus* (Alepisauridae), *Benthalbella* (Scopelarchidae) and most chlorophthalmids; only *Chlorophthalmus oblongus* has a single, large cartilage where the others have two. The CMCs of chlorophthalmids are remarkable due to their large size filling the complete diastemal distance. Only the lower CMC is present in *Lestrolepis* (Paralepididae), *Scopelosaurus* (Notosudidae) and *Bathypterois* (Ipnopidae), and CMCs are absent in Aulopidae and most Synodontidae (i.e. *Harpadon*, *Trachinocephalus* and *Synodus*). Fujita (1990) also listed and displayed *Saurida undosquamis* and *S. elongata* as having no CMCs; our specimen of *S. brasiliensis* showed a cartilage with the unusual arrangement of supporting three fin rays at one time. The identity of this cartilage remains to be studied. Recently, Keivany (2016) depicted the caudal skeleton of *Synodus synodus*, including its cartilages; therein also no CMCs have been detected. Thus, it seems that also in aulopiforms this study has not yet covered the complete spectrum of variability of CMC in terms of shape, amount and fin-ray support.

All investigated myctophiforms showed two rather complex CMCs. *Neoscopelus* apparently has a more simple, likely basal, condition with two CMCs each supporting a fin ray. The three-dimensional shape of the CMCs in *Neoscopelus* is rather simple, especially in comparison to myctophids. All studied species of the latter showed two CMCs with opposing lateral prolongations. Also, all myctophids studied by Fujita (1990) have two CMCs, except for *Centrobranchus*, which has a single, large cartilage in this area and, generally, a much derived caudal fin with many fusions. CMCs also have been reported for three species of *Triphoturus* (Rubio-Rodriguez *et al.*, 2016). More statements on myctophiform CMCs are not possible based on the lateral drawings of Fujita (1990) and Rubio-Rodriguez *et al.* (2016), except perhaps for the impression that the upper and lower CMC of a respective species always are about of the same size. It seems likely that all myctophiforms show similar conditions as for the herein reported species: two similarly sized CMCs, almost mirrored, have pronounced, diastemal directed processes that are connected by strong connecting tissue, and each CMC supports a single ray on its diastema-averted portion.

Among Acanthomorpha (= Acanthomorphata of Betancur-R *et al.*, 2017) CMCs have only been reported in the beryciforms *Anomalops* and *Beryx* (Fujita, 1990). There are two simply bean-shaped CMCs (Fig. 21); the upper CMC seems to be involved in supporting the lowest ray of the upper lobe, whereas the lower CMC is only close to the articulation of the upper ray of the lower lobe, but apparently not involved in any supporting function. In both species, two strands of connective tissue running along the distal margins of the hypural plates bend into the diastema. The CMCs are positioned in the ends of these strands. Also, the findings presented here for *Polymixia* are remarkable. There are cartilages that should be named CMCs due to their position in the diastema, but their real origin remains unclear. The presence of CMCs in the acanthomorphs *Polymixia* and *Anomalops* seems remarkable and at the present state of phylogenetic hypothesis (e.g. Betancur-R *et al.*, 2017) the homology of these cartilages with the CMCs of basal clupeocephalans would implicate multiple reductions of CMCs among basal acanthomorphs. On the other hand, the evolutionary history of CMCs in clupeocephalans showed that they often have been reduced in various taxa.

In summary, CMCs originated at the base of the clupeocephalans have been reduced several times, at least in clupeomorphs, Ostariophysi, esociforms, galaxiforms, ateleopodids, stomiiforms and aulopiforms (Fig. 27). Originally, they seem to have supported fin rays, but apparently lost this function sometimes or took over additional functions. This hypothesis seems reasonable due to the complex structures of CMCs found in certain taxa, even if it is not yet clear which specific functions are fulfilled by these cartilages.

They are not needed just to 'bridge' the diastema, and they appear late in ontogeny compared to other structures of the caudal fin – at least for the few taxa where ontogenetic information is available. If the well-formed CMCs of *Beryx* and *Anomalops*, and probably also the small cartilages in the diastema of *Polymixa*, are homologous to 'real' CMCs, more reductions must be assumed. Future studies should investigate the ontogeny of CMCs in more taxa. The diversity of these cartilages should be studied in stomiiformes and aulopiformes, which may lead to a more complete picture of these minute, but fascinating structures at the literal end of so many fishes.

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