

IDENTIFICATION GUIDE TO THE
CLUPEIFORMES
OF THE INLAND WATERS OF AFRICA

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JOS SNOEKS

ONLINE SERIES

'ZOOLOGICAL DOCUMENTATION'



Cover: dried ndakala (endemic sardine) from Lake Tanganyika (Kigoma, Tanzania). Photo © RMCA.

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Identification guide to the Clupeiformes of the inland waters of Africa

Tobias Musschoot, Gert Boden, Jos Snoeks

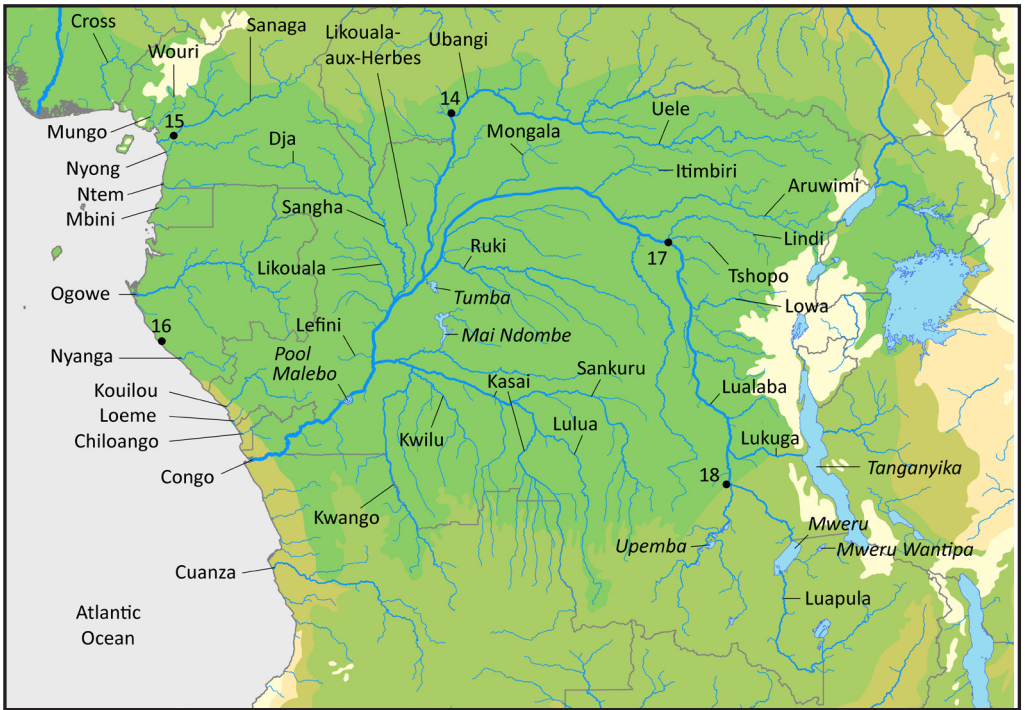


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Overview of main water bodies and localities used in the text. Lakes and reservoirs in italics.

1. Alexandria, 2. Dakhla, 3. Banc d'Arguin National Park, 4. Jebba, 5. Benguela, 6. Walvis Bay, 7. False Bay, 8. Krysna, 9. Port Alfred, 10. Durban, 11. Driefontein, 12. Majunga, 13. Port Tudor, 14. Bangui, 15. Edea, 16. Sette Cama, 17. Kisangani, 18. Ankoru. Map based on the Global Ecological Zones dataset (see FAO 2012).

1. Introduction

1.1. Clupeiformes: general characters

Clupeiformes are an order of bony fishes with a very wide distribution that includes herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. Most species are marine and live in schools in coastal areas. However, a number of species enter brackish and fresh waters, and some even live permanently in fresh-water rivers and/or lakes. In Africa, they are especially well represented in the fresh waters of West Africa, the Lower Guinea ichthyofaunal province and the Congo basin. They are largely absent in the fresh waters of the Nile basin, East Africa and southern Africa, except for the Zambezi basin where they have been introduced. Clupeiformes are currently divided into five to seven families with about 418 valid species (Nelson *et al.* 2016; Fricke *et al.* 2020).

Clupeiformes are one of the most economically important fish groups in the world. Among the 14 major species and genera of the marine capture production of finfish in 2018, five belong to the Clupeiformes. They constitute about 17% of total marine capture production (FAO 2020). In addition to their direct use for human food and as a source of animal feed, they play an important role in the ecosystems they inhabit, as small and abundant prey for all kinds of predators. In the inland waters of Africa, several taxa are of large economic interest. This is less so the case in West Africa, but in certain lakes in East and southern Africa (Kivu, Tanganyika, Mweru, Kariba), clupeids constitute a major part of capture fisheries (Laë & Lévêque 2006).

After more than three decades, the statement of Whitehead (1985), a specialist in clupeiform fishes, still holds. He argued that a rational exploitation of these fishes has often been impossible and that both biological and fisheries studies must be underpinned by sound taxonomy. To contribute to that end, he produced a number of catalogues for FAO (Whitehead 1985; Whitehead *et al.* 1988). We hope that this identification guide will extend these efforts to the inland waters of Africa.

Clupeiformes are moderately sized or small fishes usually with a fusiform body. They have no spines in the fins, a single short dorsal fin, no adipose fin, abdominally placed pelvic fins and a forked caudal fin. They are also characterised by the

presence of a series of abdominal scutes (modified scales) anterior and posterior to the pelvic fins. A pelvic scute with ascending arms is always present just in front of the pelvic fins (except in Chirocentridae where it is absent). Almost all species are completely covered with cycloid scales, except for those of the genera *Thrattidion* and *Sierrathrissa*, in which scales are partly lost. There is only a rudimentary lateral line canal anteriorly on the flanks, except in the Denticipitidae, where the lateral line is well-developed all along the flanks.

1.2. Methodology

This guide focusses on the clupeiform species from the African inland waters, including Madagascar and the islands between Madagascar and mainland Africa. It includes typical freshwater species, but also a number of species predominantly occurring in marine waters that are often found in brackish and sometimes even fresh waters. The selection of the species to be included was not a trivial exercise and is based on the categories outlined by Whitfield (1994; 1999; 2005; 2007). In this guide, we incorporated all species that are included in any of the freshwater or estuarine categories, and also the marine migrants, but not the marine stragglers. As such, a total of 39 species was recorded. In order to reduce the possibility of mis-identifying species found in brackish waters, estuaries and lagoons, we compiled an additional list that includes two categories of species: the marine stragglers listed by Whitfield (1994; 2005; 2007) and marine species that occur along the African coasts for which the data in FishBase indicate that they enter inshore, brackish waters (even outside Africa), but without depending on these environments for any essential part of their life cycle (such as food, growth or reproduction) (see Table 1). All taxa from Table 1 have also been integrated in the identification keys (and marked with an asterisk *). They are however not further discussed in the text. We acknowledge that potentially other marine species, not included in Table 1 and the keys, may exceptionally be found in African inland waters. However, integrating all coastal marine species is beyond the scope of this work.

A few records that were not incorporated in Table 1 need some more explanation.

- *Nematalosa nasus* was reported from a single juvenile from Durban Bay by Smith (1949), but no other specimens were caught afterwards (Whitehead & Wongratana 1986a). Nelson & Rothman (1973) questioned its presence in South

Africa (Natal) while Whitehead (1985) mentioned the species to be absent from South Africa. Possibly the specimen reported by Smith (1949) was transferred with ballast water. The specimen from Somalia in Nelson & Rothman (1973), which is the second report of *Nematalosa nasus* from Africa, was reidentified by Nelson & McCarthy (1995) as *Nematalosa resticularia*, a marine species occurring mainly in the Persian Gulf.

- The report of *Tenuulosa toli* from Mauritius by Fricke (1999) is based on two syntypes of *Alausa argyrochloris*. However, Whitehead (1967a) already showed that the original description of Valenciennes (1847) is based only on a single specimen from Bombay (currently Mumbai, India), which he placed in synonymy with *Hilsa (Tenuulosa) toli*. Kottelat (2013) selected this specimen (MNHN 2738) as lectotype of *Alausa argyrochloris*. The other two specimens mentioned in the original description, recorded by Quoy & Gaymard from 'Île-de-France' (currently Mauritius), were incorrectly treated as types and found to be misidentifications, tentatively reidentified as *Sardinella jusieui* (Whitehead 1967a), and later as possibly *Sardinella dayi* (Whitehead & Bauchot 1985).
- Reports of *Tenuulosa ilisha* (distributed in the Indian Ocean from the Persian Gulf eastward to Myanmar) from Zanzibar (Günther 1868) and Madagascar (Angot 1950; Fricke *et al.* 2018) appear to be unsubstantiated and most probably refer to *Hilsa kelee*. This was confirmed for the Zanzibar specimens by Whitehead (1965a). Since the description of these by Günther (1868) served as a basis for the identification of the Malagasy specimens, they are considered as *H. kelee* as well.

Nematalosa nasus, *Tenuulosa toli* and *T. ilisha* are consequently not included in this guide as they do not occur in the area under consideration.

A large part of the information in this book was extracted from FishBase. The FishBase for Africa team in the Royal Museum for Central Africa, Tervuren, within the FishBase Consortium, assumes the task of updating the information on African fresh and brackish water species in the database and has made a special effort in recent years to get the information on Clupeiformes in FishBase up to date. This information has been edited and, if necessary, complemented for the purpose of this book.

Distribution maps are limited to African inland waters, including Madagascar and the islands between Madagascar and mainland Africa. They are based on data taken from the GBIF, FishBase, OBIS and AMNH databases, and the RMCA collections. Only records based on preserved specimens are retained (black dot for native occurrences, black triangle for introductions). The locality of primary types is added on the map (star) if primary types are from the area under consideration and if locality details/coordinates are available. Erroneous localities are indicated with an 'X' and questionable reports with a question mark. Exceptionally, literature reports (open dot) and observations without preserved specimens (square) are also included. Corresponding HydroBasins (Lehner & Grill 2013) level 6 polygons were plotted for confirmed point locations. Inferred distributions, linking these areas, were also based on HydroBasins level 6, except in a few cases where these distributions appeared to be unrealistically large. For these cases, HydroBasins levels 8 and exceptionally 9 were used. River networks are based on the HydroSHEDS 15 arc-seconds dataset (Lehner *et al.* 2008), while lakes are based on the RWDB2 Rivers and Surface Water Body Outlines from the African Water Resources Database (see Jenness *et al.* 2007a, 2007b). For ease of comparison, distributions were plotted on nine standardised maps covering various areas of Africa (see Figure 1-1).

Species and genera descriptions include the most important features, focussing on diagnostic characters. An overview of meristic data is given in Table 2.

Common names were taken from FishBase and include globally used names (with an indication of the language of the name) and local names (with an indication of the country where the name is used).

Museum acronyms follow Sabaj (2020). AMNH: American Museum of Natural History (New York, USA); KAUM-I: Kagoshima University Museum, Ichthyology (Kagoshima, Japan); MNHN: Muséum national d'Histoire naturelle [National Museum of Natural History] (Paris, France); NHMUK: Natural History Museum (London, UK); NRM: Naturhistoriska Riksmuseet [Swedish Museum of Natural History] (Stockholm, Sweden); RMCA: Royal Museum for Central Africa (Tervuren, Belgium); SAIAB: South African Institute for Aquatic Biodiversity (Grahamstown, South Africa); SMF: Senckenberg Forschungsinstitut und Natur-

museum [Senckenberg Research Institute and Natural History Museum] (Frankfurt am Main, Germany); UMMZ: University of Michigan Museum of Zoology (Ann Arbor, Michigan, USA).

Abbreviations used: DRC: Democratic Republic of the Congo; TL: total length; SL: standard length; HL: head length; Common names: E = English, F = French, S = Spanish.

Table 1. List of marine stragglers based on Whitfield (1994; 2005; 2007) and own data (see text). Distribution based on FishBase (Froese & Pauly 2021).

Family	Species	Distribution
Chirocentridae	<i>Chirocentrus dorab</i>	Indo-Pacific
Clupeidae	<i>Amblygaster sirm</i>	Indo-West Pacific
	<i>Sardina pilchardus</i>	Northeast Atlantic Ocean southward to Senegal, and the Mediterranean Sea
	<i>Sardinella aurita</i>	Atlantic Ocean and Mediterranean Sea
	<i>Sardinella melanura</i>	Indo-West Pacific
	<i>Sardinella rouxi</i>	Eastern Atlantic Ocean
	<i>Sardinops sagax</i>	Indo-Pacific
	<i>Sprattus sprattus</i>	Northeast Atlantic Ocean to Morocco, and the Mediterranean Sea
Dussumieriidae	<i>Etrumeus whiteheadi</i>	Southeast Atlantic Ocean to Western Indian Ocean (Angola, Namibia, South Africa)
Engraulidae	<i>Encrasicholina heteroloba</i>	Indo-Pacific
	<i>Encrasicholina devisi</i>	Indo-Pacific
	<i>Engraulis encrasicolus</i>	Eastern Atlantic Ocean
	<i>Engraulis capensis</i>	Southeast Atlantic Ocean
	<i>Stolephorus belaerius</i>	Western Indian Ocean
	<i>Stolephorus insularis</i>	Indo-Pacific
	<i>Thryssa setirostris</i>	Indo-Pacific
Spratelloididae	<i>Spratelloides delicatulus</i>	Indo-Pacific

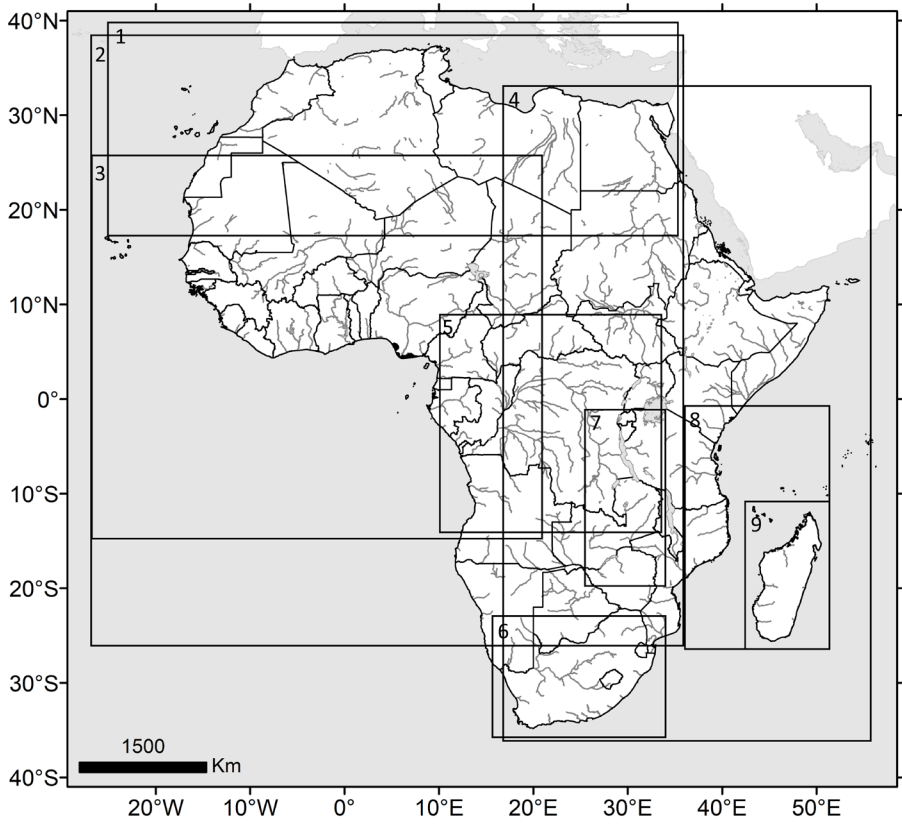


Figure 1-1. Overview of the nine standardised maps used for the distribution maps.
 1) Northern Africa: *Alosa*; 2) Northern and Western Africa: *Sardinella maderensis*; 3) West African Coast: *Denticeps*, *Ilisha*, *Ethmalosa*, *Laeviscutella*, *Odaxothrissa ansorgii*, *O. mento*, *Pellonula*, *Sierrathrissa*, *Thrattidion*; 4) East African Coast: *Stolephorus*, *Thryssa*, *Pellona*, *Herklotsichthys*, *Hilsa*; 5) Congo basin: *Congothrissa*, *Microthrissa*, *Nannothrissa*, *Odaxothrissa losera*, *Potamothrissa*; 6) South Africa: *Gilchristella*; 7) Lake Tanganyika and Zambezi: *Limnothrissa*, *Stolothrissa*; 8) Madagascar and Kenyan coast: *Spratellomorpha bianalis*; 9) Madagascar: *Sauvagella*.

Table 2. Overview of meristics; see FishBase (Froese & Pauly 2021) for updated information and literature sources. All species in the table have a pelvic scute, but depending on the source (Whitehead 1985; Gourène & Teugels 1989; ...), this scute may or may not be included in the number of prepelvic or postpelvic scutes. * pelvic scute only; ** includes pelvic scute with lateral arms; *** based on two paratypes (RMCA 2001-66-P-1-2)

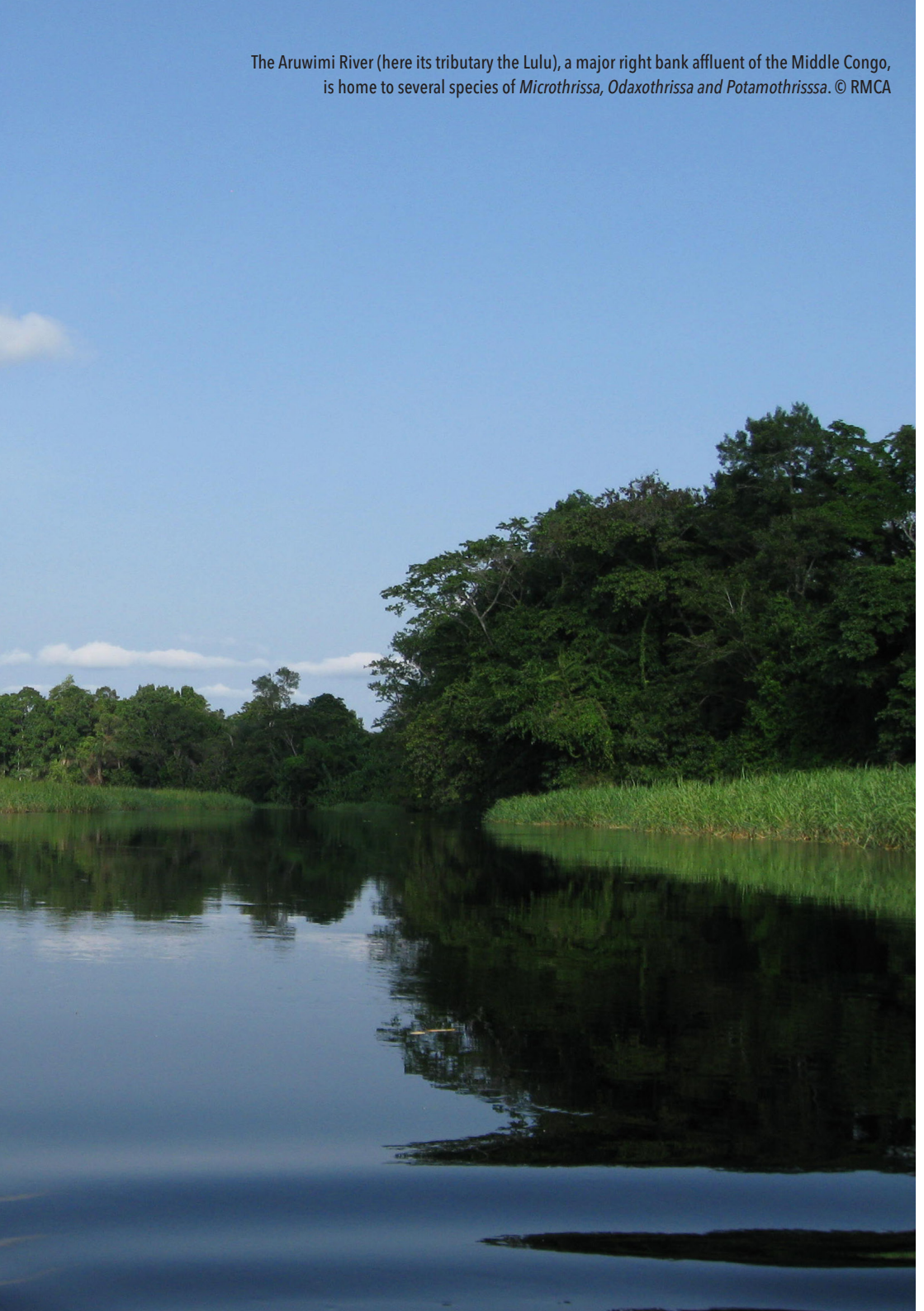
			total number of rays		
			dorsal fin	anal fin	pectoral fin
		<u>Denticipitidae</u>			
1		<i>Denticeps clupeoides</i>	8-9	23-27	11-12
		<u>Engraulidae</u>			
2		<i>Stolephorus holodon</i>	15-17	20-23	12-14
3		<i>Stolephorus zephyrus</i>	15-17	20-22	13-14
4		<i>Thryssa baelama</i>	14-16	29-34	13-14
5		<i>Thryssa vitrirostris</i>	13-14	34-44	12-13
		<u>Pristigasteridae</u>			
6		<i>Ilisha africana</i>	14-17	45-50	12-14
7		<i>Pellona ditchela</i>	16-19	34-42	14-18
		<u>Clupeidae</u>			
8		<i>Alosa algeriensis</i>	18-22	20-25	?
9		<i>Alosa alosa</i>	18-21	22-27	15-16
10		<i>Alosa fallax</i>	16-22	19-26	15-17
11		<i>Congothrissa gossei</i>	14-16	15-17	11-12
12		<i>Ethmalosa fimbriata</i>	16-19	19-25	15-15
13		<i>Gilchristella aestuaria</i>	14-15	20-20	11-12
14		<i>Herklotsichthys quadrimaculatus</i>	16-21	15-21	14-17

	scales	number of scutes		lower gill rakers
pelvic fin	lateral series	prepelvic	postpelvic	
5-5	37-40	15-20	4-6	9-10
7-7	38-42	6-8	0-0	24-29
7-7	35-37	3-5	0-0	22-26
8-8	37-38	4-9	7-10	18-26
7-8	40-44	16-19	8-12	18-24
6-8	40-44	25-27	6-8	22-28
7-7	37-44	17-20	8-10	22-27
9-9	58-58	19-23	13-16	25-38
9-10	60-90	19-25	13-17	55-110
9-9	54-71	18-23	12-18	17-32
7-8	20-22	1*	0	10-12
8-8	37-45	16-20	10-13	?
8-8	40-40	6-9	0	39-76
8-8	38-45	16-19	12-14	28-37

			total number of rays		
			dorsal fin	anal fin	pectoral fin
15		<i>Hilsa kelee</i>	16-19	17-23	13-16
16		<i>Laeviscutella dekimpei</i>	14-16	17-20	12-13
17		<i>Limnothrissa miodon</i>	13-18	15-19	?
18		<i>Microthrissa congica</i>	13-15	18-22	11-13
19		<i>Microthrissa minuta</i>	12-15	18-21	10-13
20		<i>Microthrissa moeruensis</i>	12-15	15-22	10-13
21		<i>Microthrissa royauxi</i>	11-14	22-27	12-15
22		<i>Microthrissa whiteheadi</i>	11-14	20-25	12-14
23		<i>Nannothrissa parva</i>	12-15	20-23	11-12
24		<i>Nannothrissa stewarti</i>	14-16	17-19	13-13
25		<i>Odaxothrissa ansorgii</i>	14-18	17-21	13-16
26		<i>Odaxothrissa losera</i>	15-18	19-24	12-16
27		<i>Odaxothrissa mento</i>	15-18	18-21	12-15
28		<i>Pellonula leonensis</i>	13-19	16-22	11-16
29		<i>Pellonula vorax</i>	15-19	16-21	12-18
30		<i>Potamothrissa acutirostris</i>	13-14	16-20	?
31		<i>Potamothrissa obtusirostris</i>	13-15	16-20	?
32		<i>Potamothrissa whiteheadi</i>	14-15	19-22	13-13
33		<i>Sardinella maderensis</i>	18-23	17-23	14-17
34		<i>Sauvagella madagascariensis</i>	13-17	17-19	11-12
35		<i>Sauvagella robusta</i>	11-15	13-17	11-11
36		<i>Sierrathrissa leonensis</i>	12-15	16-20	8-10
37		<i>Spratellomorpha bianalis</i>	14-17	14-16 + 2	12-13
38		<i>Stolothrissa tanganicae</i>	15-16	16-17	?
39		<i>Thrattidion noctivagus</i>	14-16	23-25	10-10

	scales	number of scutes		lower gill rakers
pelvic fin	lateral series	prepelvic	postpelvic	
8-8	39-44	15-17	12-14	75-175
8-8	38-38	7-8	5-6	21-26
8-8	45-48	11-15	6-11	20-40
8-8	26-35	10-15	8-11	17-24
7-8	37-43	11-12	6-8	18-22
8-8	33-40	10-12	5-8	18-20
8-8	34-41	13-16	3-7	14-17
8-8	35-39	13-16	5-9	14-18
7-8	35-42	12-15	6-8	24-31
7-8	34-35	9-10	7-9	20-23
8-8	40-45	13-17	8-11	22-33
8-8	39-50	10-14	7-10	18-29
7-8	43-46	13-18	8-10	16-19
8-8	36-45	8-15	6-10	20-35
8-8	38-48	11-16	8-11	24-37
8-8	36-42	11-13	10-12	16-18
8-8	39-45	7-10	9-12	14-16
8-9	40-40	8-10	6-9	14-17
8-8	40-50	14-20	12-15	70-166
8-8	43-45	1*	0	17-20
8-8	±37***	1*	0	15-19
6-7	37-38	1-11**	6-11	13-16
8-9	41-45	1*	0	26-31
8-8	36-46	13-14	8-9	36-42
7-8	0	4-7	3-5	10-12

The Aruwimi River (here its tributary the Lulu), a major right bank affluent of the Middle Congo, is home to several species of *Microthrissa*, *Odaxothrissa* and *Potamothrissa*. © RMCA



2. Identification key to the families

1a. numerous small denticles on bony surface of head; less than 10 dorsal-fin rays; well-developed, complete lateral line along the flank Denticipitidae

1b. no denticles on bony surface of head; more than 10 dorsal-fin rays; rudimentary lateral line canal anteriorly on the flank. 2

2a. articulation of lower jaw well behind eye; lower jaw usually slender (Figure 2-1A) Engraulidae

2b. articulation of lower jaw under or just behind eye; lower jaw usually deep (Figure 2-1B) 3

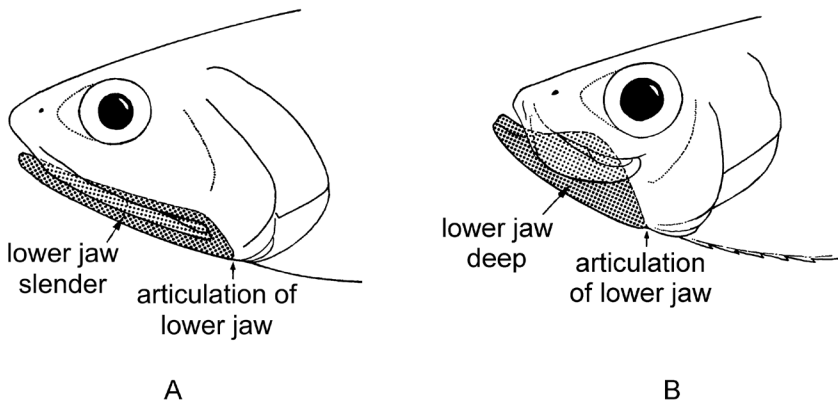


Figure 2-1. A) articulation of lower jaw well behind eye; lower jaw slender. B) articulation of lower jaw under eye; lower jaw deep (from Whitehead 1985).

3a. no scutes along belly, pelvic scute absent or reduced; 2 fanglike canine teeth in upper jaw, directed anteriorly Chirocentridae *

3b. scutes usually present along belly, pelvic scute always present; canine teeth rare, never directed anteriorly in upper jaw. 4

- 4a. long anal fin, more than 33 anal-fin rays Pristigasteridae
- 4b. short to moderate anal fin, less than 28 anal-fin rays 5

- 5a. pelvic scute W-shaped and unkeeled, no other scutes anterior and posterior of pelvic fins 6
- 5b. pelvic scute with lateral arms, scutes usually present anterior and posterior of pelvic fins Clupeidae

- 6a. numerous branchiostegal rays (11-18); premaxilla rectangular (seen from above; Figure 2-2A). Dussumieriidae *
- 6b. few branchiostegal rays (6-7); premaxilla triangular (seen from above; Figure 2-2B). Spratelloididae *

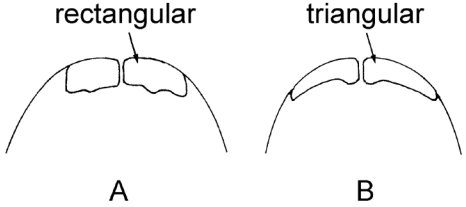


Figure 2-2. Shape of the premaxillae in A) Dussumieriidae and B) Spratelloididae (from Whitehead 1985).

3. Species descriptions

3.1. Denticipitidae

Denticipitidae are distinguished from other Clupeiformes by the presence of numerous small denticles on the bony surface of the head and a complete lateral line along the flanks (Teugels 2003a; Vreven & Teugels 2007). Other important characters include the presence of ventral scutes along the belly, the absence of a supramaxilla and a short dorsal fin with 8-9 rays.

There is only one species, *Denticeps clupeioides* Clausen, 1959, found in the coastal rivers of Benin, Nigeria and Cameroon. This species occurs in shoals that tend to keep to the middle of the stream, where the current is at its strongest (Vreven & Teugels 2007).

Genus *Denticeps* Clausen, 1959

The genus is monospecific: *Denticeps clupeioides*.

Denticeps clupeioides Clausen, 1959

Common names: Denticle herring (E), Mbanga fish (Cameroon).

Description: numerous small denticles on surface of dermal head bones; lateral line complete, with 37-40 cycloid scales; midventral scutes present, 15-20 prepelvic and 4-6 postpelvic scutes (Teugels 2003a; Vreven & Teugels 2007). Supramaxilla absent (Teugels 2003a).

Maximum length: 15.0 cm TL (Teugels 2003a).

Colour: In life: silvery with greenish tint on flanks, whitish on belly, and darker yellowish-grey on dorsum; dorsum with golden or black dorsal line running from head to caudal fin; blackish pigmented zones at bases of scales forming a reticulate pattern of vertical rhomboid fields; eyes reflect light with a conspicuous glimmer; dorsal part of iris orange, ventral part white and pupil black (Clausen 1959; Vreven & Teugels 2007). Narrow, ill-defined zone of greenish golden sheen immediately above an equally narrow but very distinct dark green longitudinal band just above lateral line, from behind operculum to base of caudal fin; dark band



Figure 3-1. *Denticeps clupeioides*. Photo (public domain) by M. Norén.

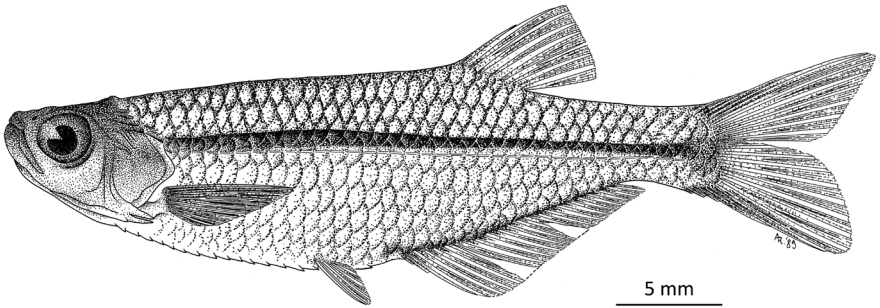


Figure 3-2. *Denticeps clupeioides*, Shagamu, S.W. Nigeria, 32.4 mm SL. Drawing by A. Reygel. © RMCA.



Figure 3-3. *Denticeps clupeioides*, Shagamu, S. W. Nigeria, RMCA 76-32-P-4915-935. © RMCA.

terminates in a greenish black Y-shaped, triangular, or diamond-shaped spot, just in front of caudal fin; width of golden zone varies with illumination and angle at which fish is viewed, sometimes seemingly expanding so as to cover and conceal blackish green band; fine black line along base of anal fin; fins colourless (Clausen 1959). Posterior part of caudal-fin base with orange hue; caudal fin yellowish orange; digestive system visible due to transparency of area below lateral line (Vreven & Teugels 2007). Preserved specimens: silvery, somewhat olivaceous dorsally; dorsum with black line running from head to caudal fin; flanks with narrow black stripe extending from gill cover to base of caudal fin, becoming broader on caudal peduncle (Teugels 2003a).

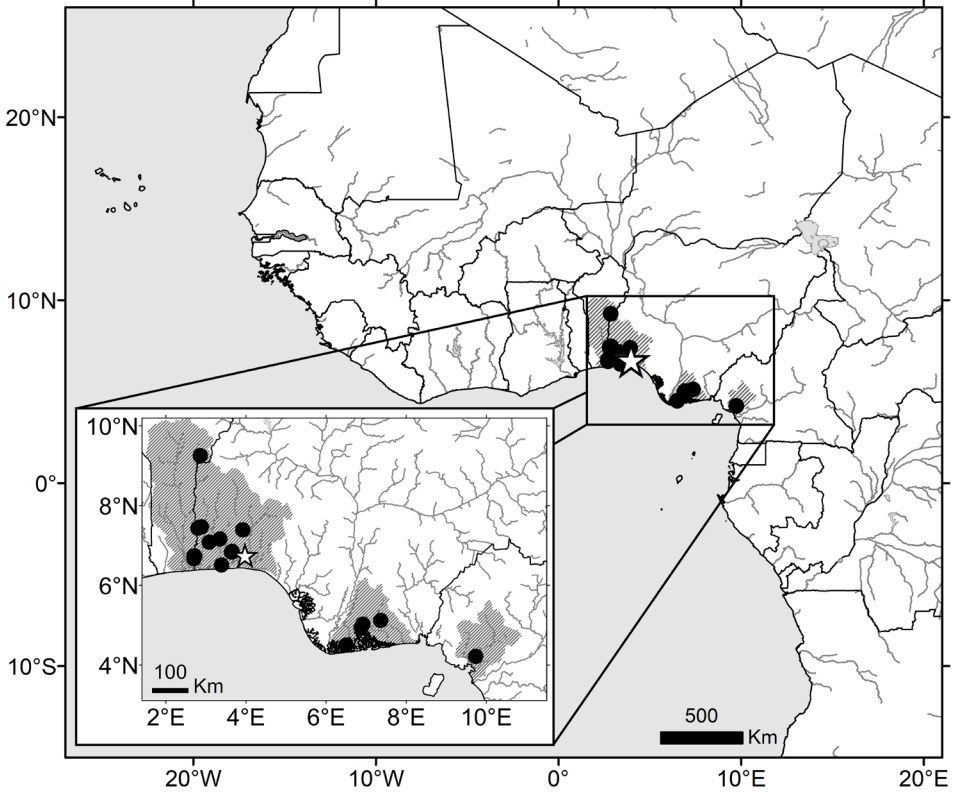


Figure 3-4. *Denticeps clupeioides*, distribution map.

Distribution: Ouémé River basin in Benin to the Niger Delta (Teugels 2003a), and the Mungo River in Cameroon (Vreven & Teugels 2007). Reports from the Cross river (Mdaihi *et al.* 2003; Offem *et al.* 2008; 2009) need confirmation as no voucher specimens are available, but its presence in the Cross is not unlikely.

3.2 Engraulidae

Engraulidae or anchovies are small to moderate-sized fishes. They are characterised by a prominent snout, projecting beyond the tip of the lower jaw, and the maxilla reaching well behind the eye. Other characters include the absence of a lateral line and, for most species, the presence of two supramaxillae (Whitehead 1974b; Whitehead & Wongratana 1986b; Whitehead *et al.* 1988). Scutes are present along the belly, either needlelike or strongly keeled, and a pelvic scute with lateral arms is always present (Whitehead 1974b; Whitehead *et al.* 1988). Typically, the dorsum is blue-green and the flanks silver, sometimes with a distinct silver stripe; fins are hyaline or faint yellow, sometimes chrome or orange (Whitehead *et al.* 1988).

There are about 165 species of anchovies (Fricke *et al.* 2020). Engraulidae are essentially marine fishes, often forming dense schools, with some species entering freshwater to feed or spawn (Whitehead *et al.* 1988). Most freshwater species occur in South America, but also in Africa four species are regularly found in freshwater and estuaries.

- 1a. no scutes along belly, except a single pelvic scute; isthmus short, urohyal exposed; anal-fin origin under or behind base of last dorsal-fin ray. . . . *Engraulis* *
- 1b. scutes present along belly; isthmus short or long; very exceptionally no scutes along belly, in which case isthmus long, urohyal not exposed and anal-fin origin before base of last dorsal-fin ray 2

- 2a. no postpelvic scutes; less than 25 anal-fin rays 3
- 2b. postpelvic scutes present; more than 25 anal-fin rays *Thryssa*

- 3a. isthmus muscle does not reach forward to posterior border of branchiostegal membrane, leaving a portion of the urohyal bone exposed (Figure 3-5A) *Encrasicolina* *
- 3b. isthmus muscle reaches forward to posterior border of branchiostegal membrane (Figure 3-5B) *Stolephorus*

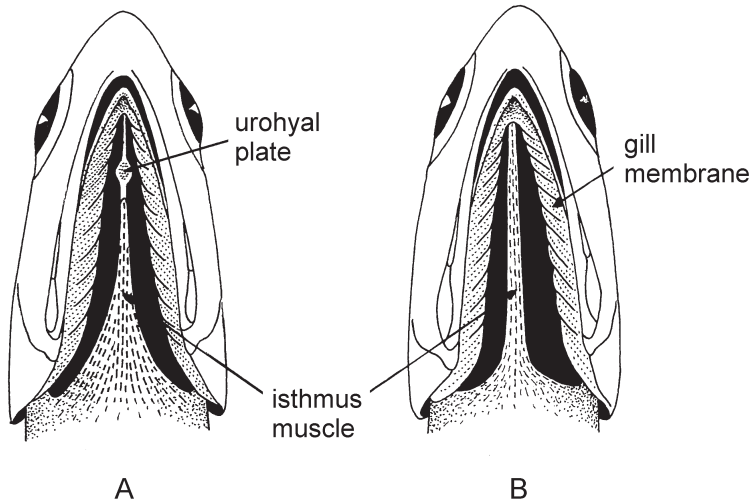


Figure 3-5. Arrangement of the isthmus muscle in A) *Encrasicholina* and B) *Stolephorus* (from Whitehead *et al.* 1988).

Genus *Stolephorus* Lacepède, 1803

The genus *Stolephorus* contains more than 20 species distributed mainly in the Indian and Pacific Oceans (Froese & Pauly 2021). Two species, *S. holodon* and *S. zephyrus*, frequently occur in estuarine inland waters in Africa, while the marine stragglers *S. belaerius* Hata, Lavoué & Motomura, 2021 and *S. insularis* Delsman, 1931 are only occasionally found in brackish waters of eastern Africa. Species of this genus have a more or less rounded belly with 1-8 sharp, needlelike prepelvic scutes, but lack post-pelvic scutes, and have an isthmus muscle that reaches forward to the hind border of the branchial membrane (Whitehead *et al.* 1988).

- 1a.** maxilla short, posterior tip slightly beyond or just reaching anterior border of preoperculum *Stolephorus belaerius* *
- 1b.** maxilla rather long, posterior tip beyond or just reaching posterior margin of preoperculum 2

- 2a. preoperculum convex; 3-5 prepelvic scutes. *Stolephorus zephyrus*
- 2b. preoperculum concave, indented near maxilla tip; 4-8 prepelvic scutes 3

- 3a. anal fin with 17-20 branched rays (Africa, southward from Kenya)
 *Stolephorus holodon*
- 3b. anal fin with 14-17 branched rays (Gulf of Aden, Red Sea)
 *Stolephorus insularis* *

Stolephorus holodon (Boulenger, 1900)

Common names: Natal anchovy (E), Anchoveta espinhosa (Mozambique), Doring-ansjovis (South Africa), Thorny anchovy (South Africa).

Description: body somewhat compressed; belly with 6-8 small, needlelike prepelvic scutes, no postpelvic scutes; maxilla tip pointed, reaching to or beyond hind border of preoperculum, which is concave and indented near maxilla tip; 24-29 lower gill rakers (Whitehead *et al.* 1988). Anal fin short, usually with 3 unbranched and 17-20 branched fin rays, its origin below about middle of dorsal-fin base (Whitehead & Wongratana 1986b; Whitehead *et al.* 1988).

Maximum length: 8.0 cm SL (Whitehead *et al.* 1988).

Colour: silvery lateral stripe along flanks (Boulenger 1900).

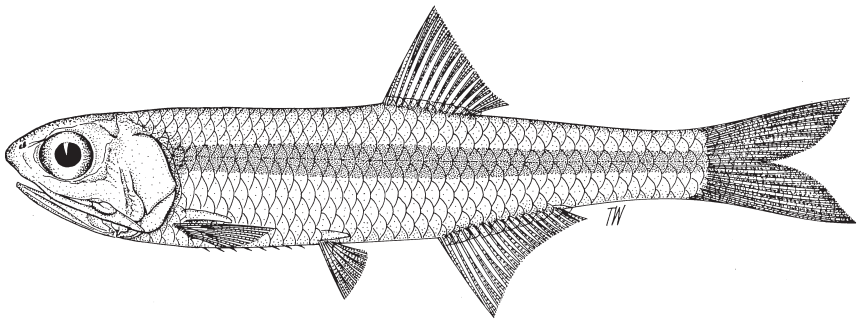


Figure 3-6. *Stolephorus holodon* (from Whitehead *et al.* 1988).

Distribution: coastal areas of East and southern Africa, from the Sabaki estuary in Kenya (SAIAB 4809 and 5305) to False Bay (West Cape, South Africa), including the estuaries of the rivers Zwartkops (just south of the Sundays River) (Whitehead & Wongratana 1986b; Whitehead *et al.* 1988), Kei (Whitehead *et al.* 1988) and Umtata (Winterbottom 1976) in South Africa. Also recorded from ‘off northern Madagascar’ (SAIAB/FC 190209). Report from Mauritius (Baissac 1990) based on a misidentification of *S. commersonii* (Fricke 1999).

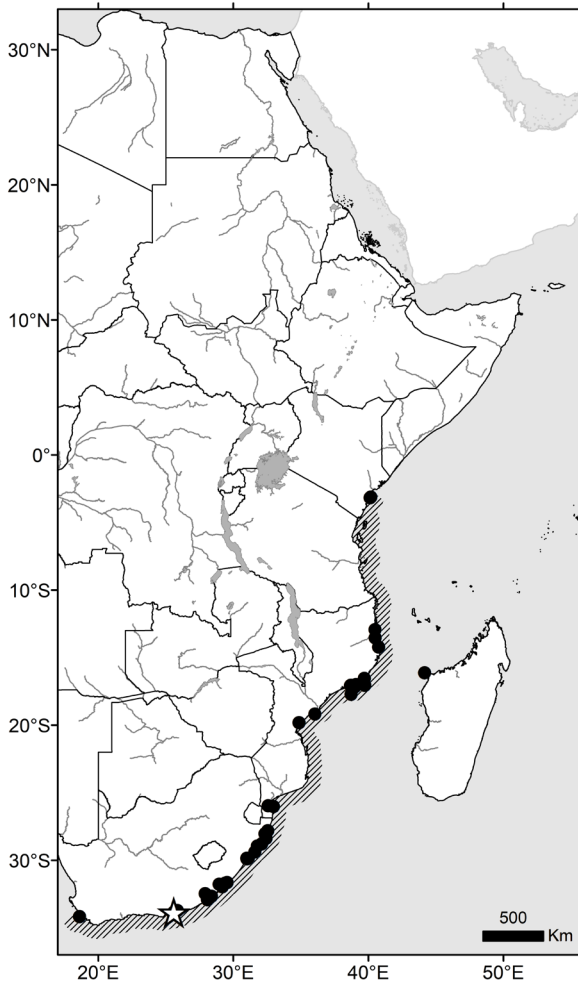


Figure 3-7.
Stolephorus holodon,
distribution map.

■ *Stolephorus zephyrus* Hata, Lavoué & Motomura, 2021

Common names: Zephyr anchovy (E).

Description: body moderately compressed; belly with 3-5 small, needlelike pre-pelvic scutes; maxilla rather long, posterior tip just reaching to or slightly beyond hind border of preoperculum, which is convex, rounded; 22-26 lower gill rakers (Losse 1968; Hata *et al.* 2021). Anal fin usually with 3 unbranched and 17-19 branched fin rays, its origin below about middle of dorsal-fin base (Hata *et al.* 2021). Two pairs of dark patches on parietal and occipital regions without a following pair of dark lines; no black spots below eye and lower-jaw tip (Hata *et al.* 2021).

Maximum length: 9.4 cm SL (Hata *et al.* 2021).

Colour: Preserved specimens: body uniformly pale, a silver and light ivory longitudinal band, sometimes lost, its width narrower than pupil diameter, extending from just behind upper opercular margin to caudal-fin base; pairs of dark patches on occipital and parietal regions without a following pair of dark lines; a few melanophores scattered on anterior parts of snout tip, but not on suborbital area; all fins pale, melanophores scattered along dorsal- and caudal-fin rays (Hata *et al.* 2021).

Distribution: eastern coast of Africa from Kenya to Tanzania, the Mayotte islands, and Madagascar, including estuaries of the Ruvu and Pangani (Losse 1968; Hata *et al.* 2021). Probably occurring southwards to about Lake St. Lucia (South Africa).



Figure 3-8. *Stolephorus zephyrus*, paratype, 62.7 mm SL, lower stream of Dembeni River, east coast of Mayotte Island, KAUM-I 142590. © Harutaka Hata.

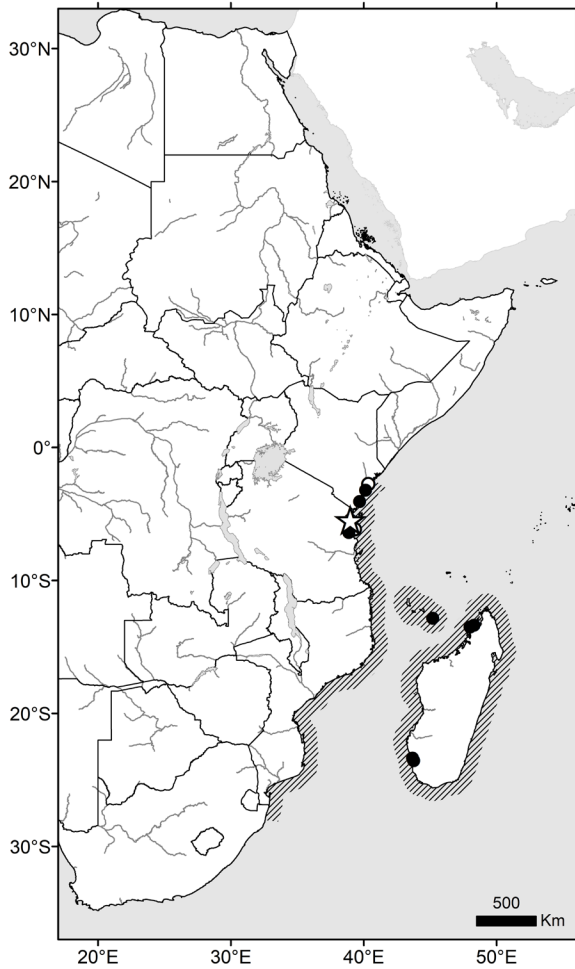


Figure 3-9.
Stolephorus zephyrus,
 distribution map.

Genus *Thryssa* Cuvier, 1829

The genus *Thryssa* contains 24 species distributed in the Indo-West Pacific region (Froese & Pauly 2021). They are found mostly inshore, along beaches and in river estuaries (Whitehead *et al.* 1988). Species of this genus have prepelvic as well as postpelvic scutes, discriminating them from other genera of Engraulidae in the area (*Engraulis*, *Stolephorus*, *Encrasicholina*) (Whitehead *et al.* 1988). Their identification is very difficult but a major separation can be made between species with a short, medium, long or very long maxilla that respectively does not extend to the gill cover, extends just beyond it, extends to the pectoral-fin base or well beyond it (Whitehead *et al.* 1988). Two species frequently enter brackish or even freshwaters in Africa: *Thryssa baelama* and *Thryssa vitrirostris*. *Thryssa setirostris* (Broussonet, 1782), a marine straggler, occurs only in small numbers in estuaries and is not dependent on these systems (Whitfield 1994; 2005).

- 1a.** 4-9 prepelvic scutes, no scutes anterior to pectoral-fin base; maxilla short, reaching to just beyond front border of preoperculum *Thryssa baelama*
- 1b.** 16-19 prepelvic scutes, scutes present anterior to pectoral-fin base (complete series of prepelvic scutes from isthmus to pelvic-fin base); maxilla long to very long, reaching beyond pectoral-fin base 2

- 2a.** maxilla very long, reaching at least to tip of pectoral fin, usually to pelvic-fin base or sometimes even to anal-fin origin; 10-12 lower gill rakers; serrae (denticles) on inner edge of gill rakers evenly distributed (Figure 3-10A) . . *Thryssa setirostris* *
- 2b.** maxilla long, reaching beyond base of first pectoral-fin ray but not to pelvic-fin base; 18-24 lower gill rakers; serrae (denticles) on inner edge of gill rakers in distinct clumps (Figure 3-10B) *Thryssa vitrirostris*

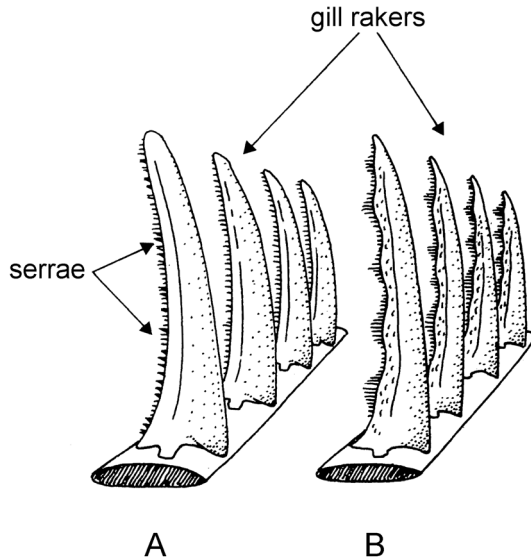


Figure 3-10. View on the serrae (denticles) on the inner side of the gill rakers in *Thryssa*: (A) evenly distributed, (B) in clumps (from Whitehead *et al.* 1988).

Thryssa baelama (Forsskål, 1775)

Common names: Baelama anchovy (E), Anchois-moustache sardine (F), Bocarte belama (S), Aida (Eritrea), Belem (Eritrea), Petite sardine (Mauritius), Sardine bâtarde (Mauritius), Ocar belama (Mozambique), Samaduul (Somalia), Dagaa (Tanzania), Dagaa-papa (Tanzania), Shembea (Tanzania).

Description: body moderately compressed; belly rounded anterior to pelvic fins, with 4-9 prepelvic and 7-10 postpelvic scutes, no prepelvic scutes anterior to pectoral-fin base; 12-18 keeled scutes; maxilla short, reaching to just beyond anterior border of preoperculum, tip pointed; 18-26 lower gill rakers; serrae (denticles) on inner edge of gill rakers evenly distributed (Figure 3-10A) (Whitehead *et al.* 1988).

Maximum length: 16.0 cm SL (Randall 2005).

Colour: Alcohol-preserved specimens: dorsal surfaces dark brown, flanks and lower part of body light brown or silvery; no silver stripe on flanks; fins hyaline (Whitehead 1965b).

Distribution: Indo-Pacific: widespread in the Indian Ocean, including the Red Sea, coasts of East Africa to Madagascar and Mauritius, Sri Lanka and Andaman Islands, but no specimens known from coast of India; and in the western central Pacific, including Indonesia, the Philippines, Papua New Guinea, northern and eastern coasts of Australia, and eastward to Tonga; no records known from the South China Sea and further north, except for one record from Ogasawara (Bonin Islands, Japan), which seems reliable (Whitehead *et al.* 1988).

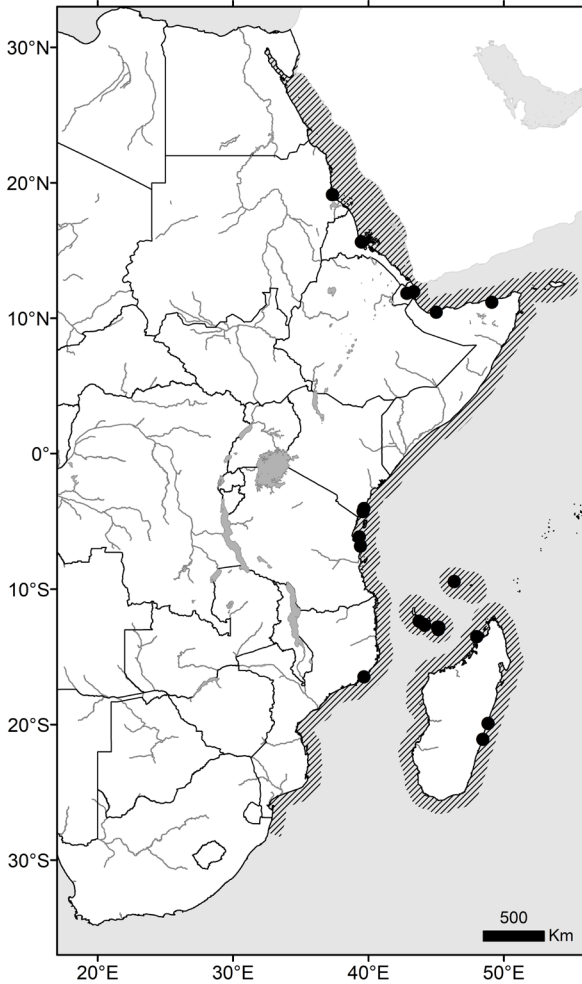


Figure 3-11.
Thryssa baelama,
distribution map.



Figure 3-12. *Thyssa baelama*, Batu Nampar, Lombok, Indonesia. Picture by J.E. Randall.

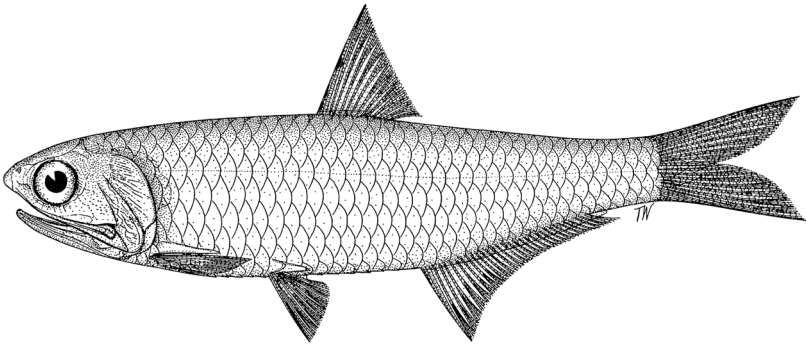


Figure 3-13. *Thyssa baelama* (from Whitehead *et al.* 1988).

Thyssa vitrirostris (Gilchrist & Thompson, 1908)

Common names: Orangemouth anchovy (E), Anchois-moustache cristal (F), Bocarte cristal (S), Renimbarivata (Madagascar), Tovey (Madagascar), Tovo (Madagascar), Malabar thryssa (Mozambique), Ocar de cristal (Mozambique), Ocares (Mozambique), Orangemouth glassnose (Mozambique, South Africa), Samaduul (Somalia), Glassnosed anchovy (South Africa), Oranjebek-glasneus (South Africa), Daga (Tanzania), Daga papa (Tanzania), Pata (Tanzania), Shembea (Tanzania).

Description: body compressed; belly with 16-19 prepelvic and 8-12 postpelvic scutes, 24-30 keeled scutes from isthmus to anus, keeled scutes present anterior to pectoral-fin base; maxilla long, reaching beyond base of first pectoral-fin ray but not to pelvic-fin base; first supramaxilla minute and oval; 18-24 lower gill rakers, serrae (denticles) on inner edge in distinct clumps in larger fishes (Figure 3-10B); anal fin with 3-4 unbranched and 31-40 branched rays; dark blotch behind upper part of gill opening; mouth and gill cavity bright orange (Whitehead *et al.* 1988; Randall 1995).

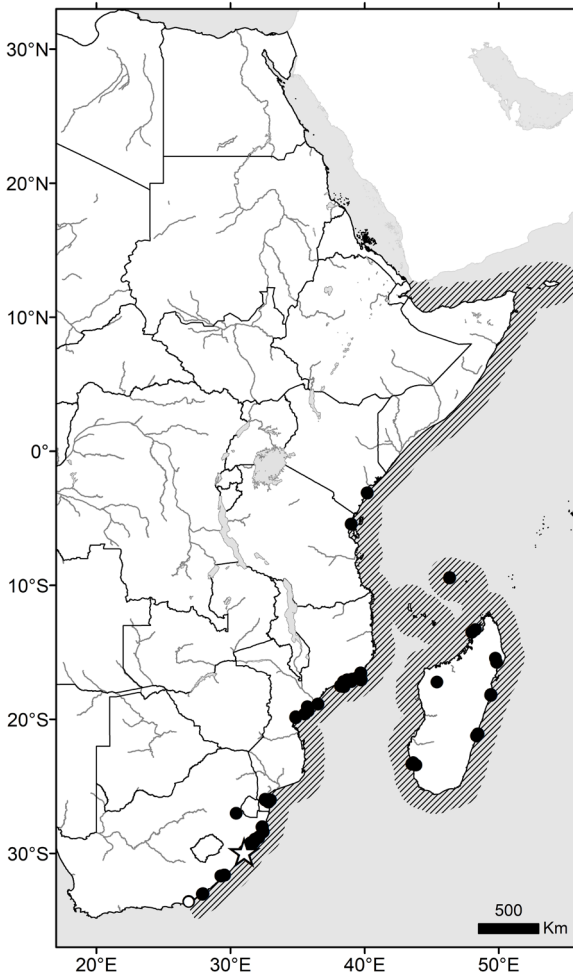


Figure 3-14.
Thyssa vitirostris,
distribution map.

Maximum length: 22.0 cm TL (Whitehead & Wongratana 1986b).

Colour: In life: overall body colour silver, but usually bluish along dorsal surface; belly white; fins translucent or dusky-yellow; inside of mouth and gill cavities conspicuously orange; dark blotch behind upper part of gill opening (Whitehead 1974b; Whitehead *et al.* 1988; van der Elst 1993; Randall 1995).

Distribution: Indian Ocean: Madagascar and coasts of Africa from Port Alfred (South Africa) northwards to the Persian Gulf, but not including the Red Sea; coasts of Pakistan and India, perhaps to Calcutta and off Myanmar, but no collection records (Whitehead 1974b; Whitehead *et al.* 1988). Present in the lower Zambezi delta in Mozambique (Bills 1999). In the Pongolo basin recorded from Driefontein, more than 200 kilometres inland (SAIAB 5324).



Figure 3-15. *Thyssa vitirostris*, Kuwait Bay, Kuwait. Picture by J.E. Randall.

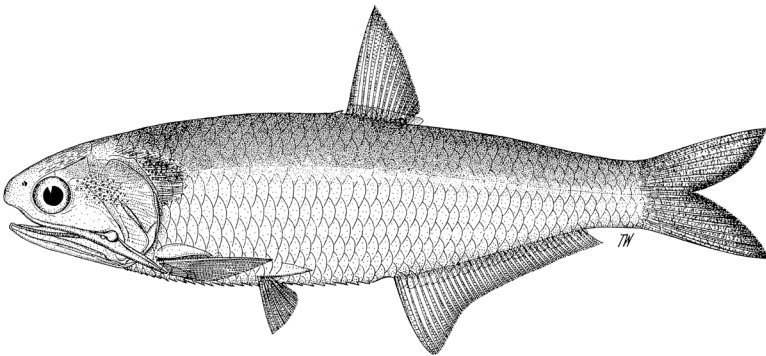


Figure 3-16. *Thyssa vitirostris* (from Whitehead & Wongratana 1984b).

3.3 Pristigasteridae

Pristigasteridae are moderately sized, relatively deep-bodied fishes with a long anal fin with more than 30 rays. The mouth is usually directed somewhat upwards, with the lower jaw projecting (Whitehead 1985). Other characters include the absence of a lateral line and the presence of two supramaxillae (Whitehead 1985).

Pristigasteridae contain about 39 species (Fricke *et al.* 2020). They are primarily marine fishes schooling in tropical and subtropical seas, with some species entering freshwater (Nelson *et al.* 2016). Two species, from two different genera, are known to penetrate the freshwaters of Africa: *Pellona ditchela* Valenciennes, 1847 in East Africa and *Ilisha africana* (Bloch, 1795) in West Africa.

A third species, *Ilisha melastoma* (Bloch & Schneider, 1801), is also reported to occur in the freshwaters of Africa in older literature, under its synonym names *Pellona ditchoa* Valenciennes, 1847 and *Pellona indica* (Swainson, 1839). However, according to Whitehead (1985) this species is confined to the eastern part of the Indian Ocean. Its presence in East Africa (Boulenger 1909), more particularly in Zanzibar (Günther 1868) and the Kingani River (Pfeffer 1896; Boulenger 1905), and its possible presence in the freshwaters of Madagascar (Pellegrin 1933), is not confirmed. These reports of *I. melastoma* should be treated as misidentifications of *Pellona ditchela*.

- 1a.** toothed hypomaxilla present; 34-42 anal-fin rays; 17-20 prepelvic and 8-10 postpelvic, sharply keeled scutes (Figure 3-17A). *Pellona*
- 1b.** no toothed hypomaxilla; 45-50 anal-fin rays; 25-27 prepelvic and 6-8 postpelvic, sharply keeled scutes (Figure 3-17B). *Ilisha*

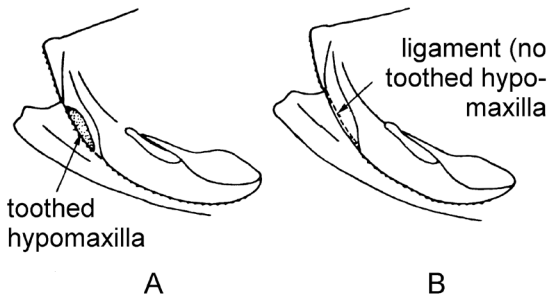


Figure 3-17. Toothed hypomaxilla A) present (*Pellona*) or B) absent (*Ilisha*) (from Whitehead 1985).

Genus *Ilisha* Richardson, 1846

The genus *Ilisha* contains 16 species (Froese & Pauly 2021) that are found in tropical and subtropical waters of the Atlantic, Indian and Pacific Oceans, with only one species in the area considered here, penetrating into almost freshwater: *Ilisha africana*. The genus is characterised by the absence of a toothed hypomaxilla between the posterior tip of the premaxilla and the blade of the maxilla, but has a soft ligament instead (Whitehead & Wongratana 1984a; Whitehead 1985).

Ilisha africana (Bloch, 1795)

Common names: West African ilisha (E), Alose rasoir (F), Sardineta Africana (S), Capasseca (Angola, Cape Verde, Guinea-Bissau), Fanhico (Angola, Cape Verde, Guinea-Bissau), Aflema (Benin), Kaflan (Benin), Kaflanvi (Benin), Kpankpadè (Benin), Litchiendjilà (Republic of Congo), Lala (Côte d'Ivoire), Nafran (Côte d'Ivoire), Péténana juaba (Côte d'Ivoire), Arenque (Equatorial Guinea), Mbèrè (Gabon), Kafila (Ghana, Togo), Kanfla (Ghana), Long-finned herring (Ghana), Tamtemire (Ghana), Lati (Guinea, Sierra Leone), Djafal (Guinea-Bissau), Bonga (Nigeria), Kankorun (Nigeria), Baa mooro (Senegal), Diarafréfo (Senegal), Indouss (Senegal), Kayette edjangone (Senegal), Rimbol (Senegal), Rimisol (Senegal), Tialimaro (Senegal), Rasoir (Togo).

Description: body relatively deep, compressed; belly with sharp and serrated keel of scutes from gill opening to anus, 25-27 prepelvic and 6-8 postpelvic, sharp scutes; eye large; mouth pointing upwards, lower jaw projecting; dorsal fin at or before midpoint of body; anal fin long, with 45-50 fin rays, its origin below dorsal-fin base; pelvic fins small; swim bladder with two short tubes extending into the muscles on either side of haemal spines (Whitehead 1981; 1985; Teugels 2003b).

Maximum length: 30.0 cm SL (Reiner 1996).

Colour: In life: dorsum grey, flanks pale grey or silver, with faint green/gold spot behind gill cover; dorsal fin yellow with dusky tip; pectoral fins with upper fin

rays yellow, otherwise colourless, as are pelvic fins; anal fin with yellow border; caudal fin yellow with upper lobe and margin dusky (Whitehead 1981). Alcohol-preserved specimens: body silvery; dark band from occiput to base of dorsal fin (Teugels 2003b).

Distribution: Atlantic coasts from northern Mauritania (Banc d'Arguin National Park) south to Benguela in Angola, including lagoons and river estuaries, which is somewhat more to the north and south compared to previous reports (see e.g. Whitehead 1985; Teugels 2003b). Found some 30 kilometres upstream in the Nyong in Cameroon (SAIAB 191498).

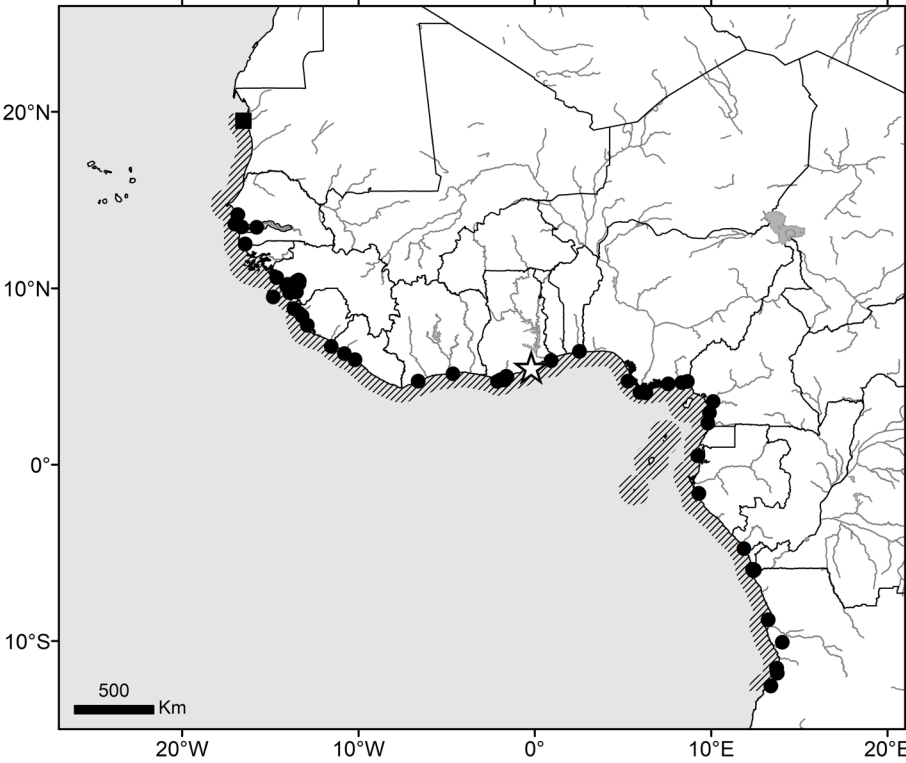


Figure 3-18. *Ilisha africana*, distribution map.

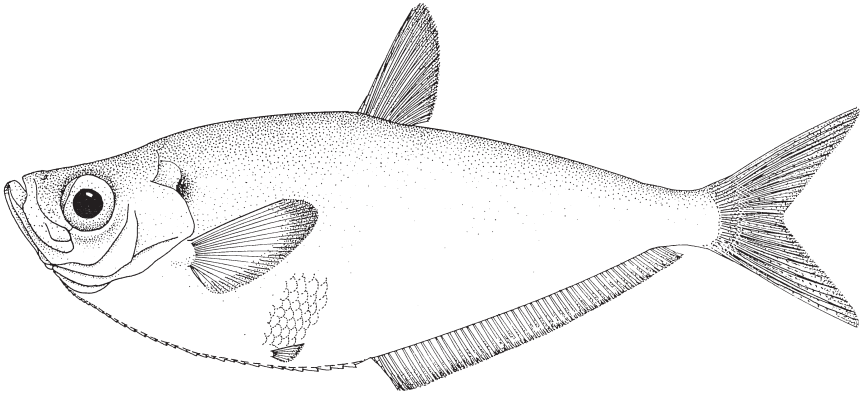


Figure 3-19. *Ilisha africana* (from Whitehead 1985).



Figure 3-20. *Ilisha africana*, 23 miles west-northwest from Banana, DRC, RMCA 94962-94965. © RMCA.

Genus *Pellona* Valenciennes, 1847

The genus *Pellona* contains six species (Froese & Pauly 2021) and is known from the freshwaters and Atlantic coastal waters of South America and from the Indo-West Pacific Ocean (Whitehead 1985). Only one species is known to enter estuaries and freshwaters in Africa: *Pellona ditchela*. The genus is characterised by the presence of a toothed hypomaxilla between the posterior tip of the premaxilla and the blade of the maxilla (Whitehead 1985).

Pellona ditchela Valenciennes, 1847

Common names: Indian pellona (E), Alose-écaille indienne (F), Sardineta indica (S), Simu (Kenya), Simu koko (Kenya), Bemaso (Madagascar), Sorindra (Madagascar), Saradinya (Mozambique), Sardinha (Mozambique), Sardinha do Indico (Mozambique), Aarijoog (Somalia), Indiese pellona (South Africa), Dagua (Tanzania), Dagua-papa (Tanzania).

Description: body moderately deep, compressed; belly with strongly keeled scutes, 17-20 prepelvic and 8-10 postpelvic scutes, adding up to a total of 25-29 scutes (Talwar & Kacker 1984; Whitehead 1985). Eye large; lower jaw projecting; upper jaw with a toothed hypomaxillary bone between hind tip of premaxilla and lower bulge of maxilla blade; 22-27 lower gill rakers; dorsal-fin origin near midpoint of body; 34-42 anal-fin rays; scales with upper and lower vertical striae slightly overlapping at centre of scales (Figure 3-21) (Whitehead 1985).

Maximum length: 16.0 cm SL (Whitehead 1985).

Colour: In life: dorsum blue-brown, flanks silvery; fins hyaline (Talwar & Kacker 1984; Whitehead & Wongratana 1986a).

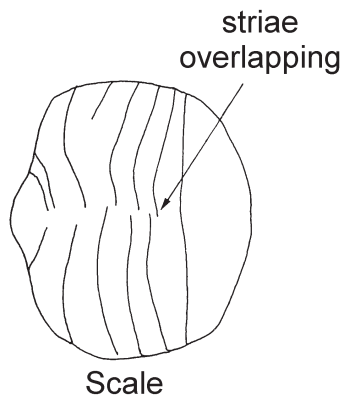


Figure 3-21. Upper and lower striae slightly overlapping at centre of scales in *Pellona ditchela* (from Whitehead 1985).



Figure 3-22. *Pellona ditchela*, Pakistan. Picture by Hamid Badar Osmany.

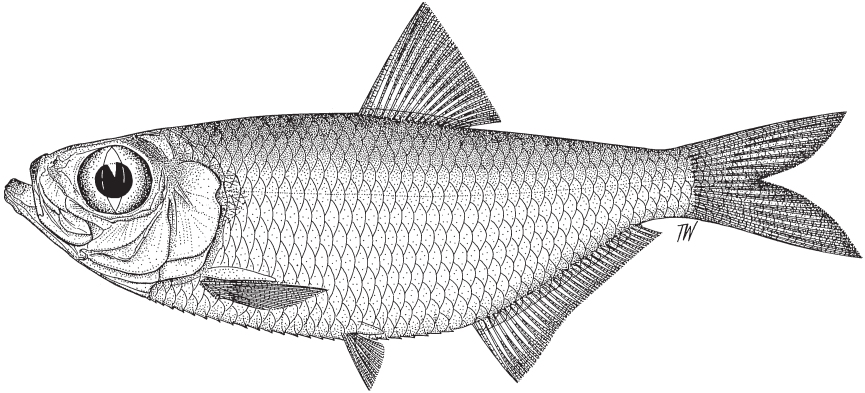


Figure 3-23. *Pellona ditchela* (from Whitehead 1985).

Distribution: Indo-West Pacific: in the Indian Ocean from the east coast of Africa northwards from about Durban (South Africa) to the Gulf of Oman, Madagascar, the coasts of India and the Andaman Sea, and south to western Australia (Poll *et al.* 1984; Talwar & Kacker 1984; Whitehead 1985). Also in the South China Sea and Indonesia to northern Australia and Papua New Guinea (Whitehead 1985).

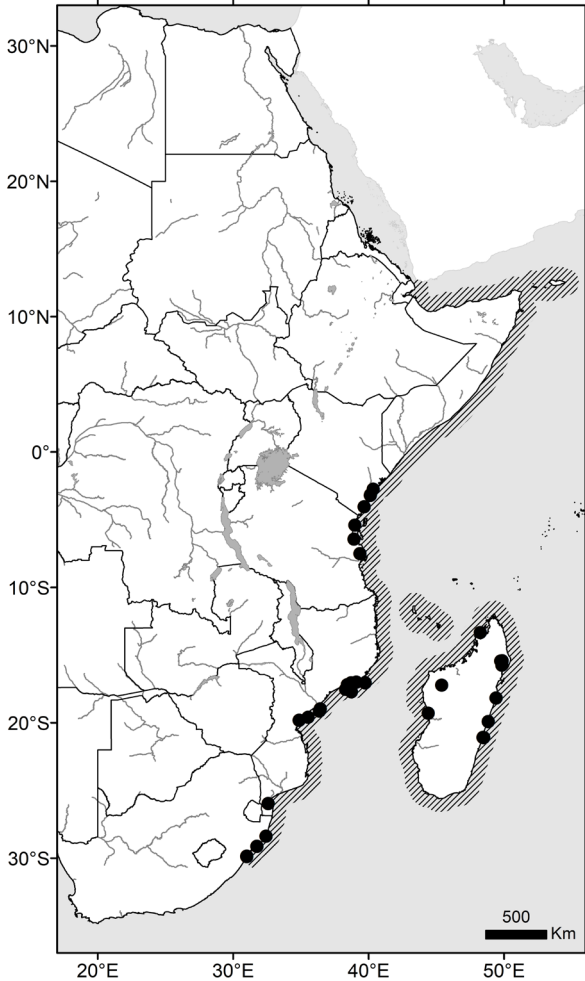


Figure 3-24.
Pellona ditchela,
distribution map.

3.4. Clupeidae

Clupeidae are small to moderately sized fishes with much variation in body shape and depth, from rounded to compressed (Whitehead 1985; Whitehead & Wongratana 1986a). The mouth is usually terminal or somewhat superior, and the maxilla is reaching a vertical through or just behind the eye. The anal fin is short to moderate and has less than 30 rays. Scales are cycloid and shed rather easily, and the lateral line is absent (Whitehead & Wongratana 1986a). Abdominal scutes are usually present, restricted to one pelvic scute only in some species (Nelson *et al.* 2016).

Clupeidae are primarily marine fishes with a very wide distribution, mostly tropical, with about 211 species (Nelson *et al.* 2016; Fricke *et al.* 2020). Most species form schools and can be found near the surface in coastal waters (Nelson *et al.* 2016). The family is primarily marine, but also includes some freshwater and anadromous species (Nelson *et al.* 2016). A total of 32 species can be found in the estuarine and freshwaters of Africa (excluding marine stragglers). Three genera can be recognised by an upper jaw with a distinct median notch: *Alosa* (with 3 species) and the monotypic genera *Ethmalosa* and *Hilsa*. Other genera have a rounded upper jaw. Some of these genera are monotypic (*Congothrissa*, *Gilchristella*, *Laeviscutella*, *Limnothrissa*, *Sierrathrissa*, *Spratellomorpha*, *Stolothrissa*, *Thrattidion*) or are only represented by a single species in the area considered here (*Herklotsichthys*, *Sardinella*).

- 1a. upper jaw with median notch (upper jaw with cleft when seen from front) (Figure 3-25A) 2
- 1b. upper jaw without median notch (upper jaw rounded when seen from front) (Figure 3-25B) 4

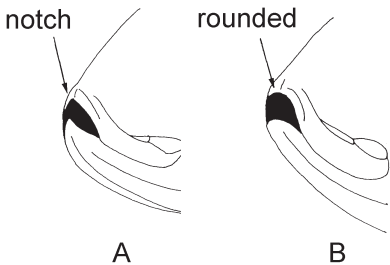


Figure 3-25.
 A) upper jaw with median notch.
 B) upper jaw without median notch (from Whitehead 1985).

- 2a. upper gill rakers of first gill arch overlapping with lower gill rakers at angle of arch; pelvic fin with 1 unbranched and 8-9 branched rays; more than 50 scales in lateral series *Alosa*
- 2b. upper gill rakers of first gill arch not overlapping with lower gill rakers at angle of arch; pelvic fin with 1 unbranched and 7 branched rays; less than 50 scales in lateral series 3
- 3a. upper gill rakers bent sharply upwards, V-shaped *Ethmalosa*
- 3b. upper gill rakers distinctly curled outwards. *Hilsa*
- 4a. anterior and posterior supramaxillae present (Figure 3-26A). 5
- 4b. no anterior supramaxilla (Figure 3-26B) 10

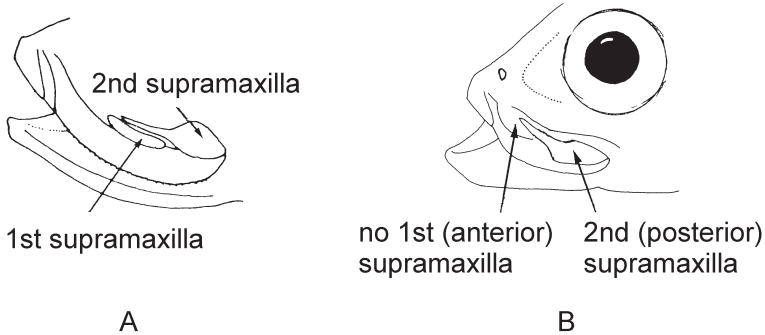


Figure 3-26. A) anterior and posterior supramaxilla present. B) no anterior supramaxilla (from Whitehead 1985).

- 5a. operculum with bony striae radiating downward (Figure 3-27) 6
- 5b. operculum smooth, without radiating bony striae 7

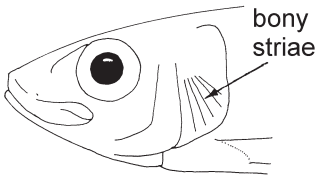


Figure 3-27. Downward radiating bony striae on operculum (from Whitehead 1985).

- 6a. lower gill rakers not shortened at angle of first gill arch (Figure 3-28A) *Sardina* *
- 6b. lower gill rakers shortened at angle of first gill arch (Figure 3-28B). . *Sardinops* *

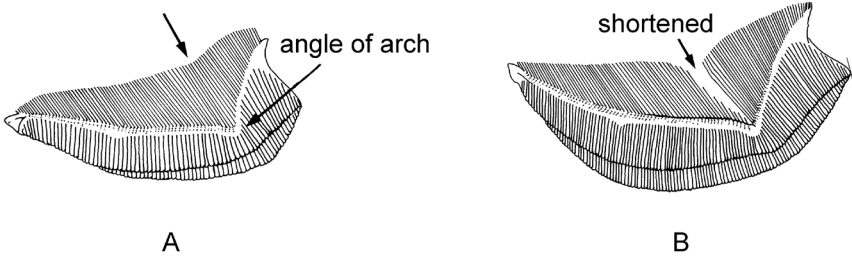


Figure 3-28. A) lower gill rakers not shortened at angle of first gill arch (*Sardina*). B) lower gill rakers shortened at angle of first gill arch (*Sardinops*) (from Whitehead 1985).

- 7a. presence of two fleshy outgrowths on posterior margin of gill opening (Figure 3-29) 8
- 7b. posterior margin of gill opening smoothly rounded *Sprattus* *

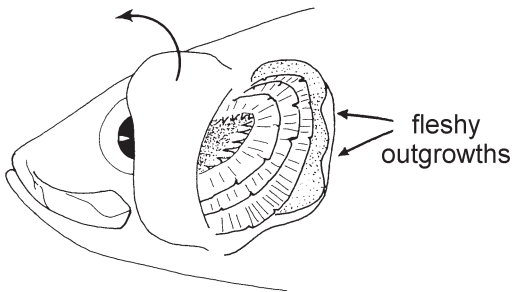


Figure 3-29. Fleshy outgrowths on the posterior margin of the gill opening (from Whitehead 1985).

8a. posterior supramaxilla asymmetrical, lower part larger than upper part (Figure 3-30A); 3-7 frontoparietal striae on top of head (Figure 3-31). . *Herklotsichthys*

8b. posterior supramaxilla symmetrical, lower part as long as upper part (Figure 3-30B); 7-14 frontoparietal striae on top of head (Figure 3-31) 9

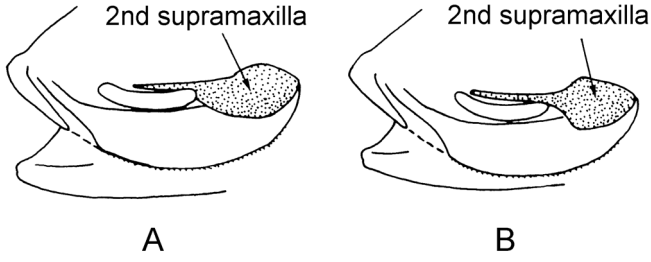


Figure 3-30. Posterior supramaxilla A) asymmetrical (*Herklotsichthys*); B) symmetrical (from Whitehead 1985).

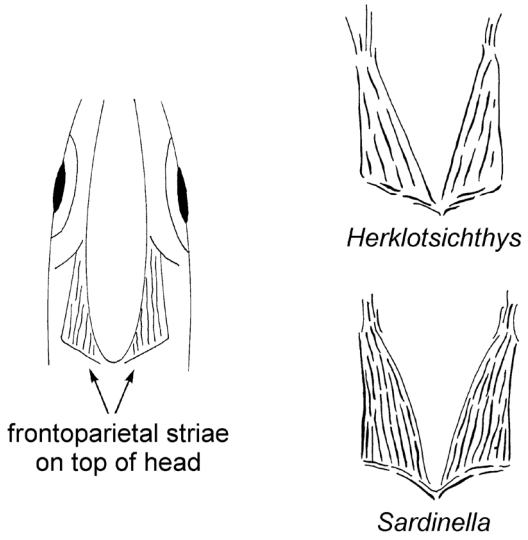


Figure 3-31. Frontoparietal striae (from Whitehead 1985).

- 9a. predorsal scales paired and overlapping in midline (Figure 3-32A) . . . *Sardinella*
- 9b. predorsal scales forming a well-defined single median row (Figure 3-32B)
 *Amblygaster* *

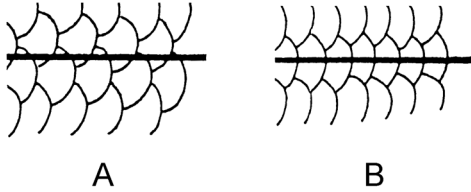


Figure 3-32. A) predorsal scales paired and overlapping in midline.
 B) predorsal scales forming a well defined single median row (from Whitehead 1985).

- 10a. posterior supramaxilla absent 11
- 10b. posterior supramaxilla present. 12

- 11a. prepelvic and postpelvic scutes with lateral arms present; 23-25 anal fin rays; scales largely absent. *Thrattidion*
- 11b. prepelvic and postpelvic scutes absent, only pelvic scute with bifurcated lateral arms; 15-17 anal fin rays; 20-22 scales in lateral series *Congothrissa*

- 12a. belly rounded, without or with indistinct, non-keeled prepelvic scutes (Figure 33-3A) 13
- 12b. belly sharp, with distinct and keeled prepelvic scutes (Figure 3-33B) . . . 17

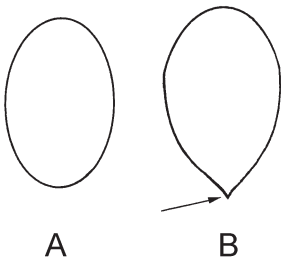


Figure 3-33. A) belly rounded, without or with indistinct, non-keeled prepelvic scutes.
 B) belly sharp, with distinct and keeled prepelvic scutes (from Whitehead 1985).

- 13a. prepelvic and postpelvic scutes absent, only one pelvic scute present with slender lateral arms 14
- 13b. prepelvic and/or postpelvic scutes present, minute or hidden by scales. . . 15

- 14a. anal fin with last 2 rays forming a distinct little finlet, separated from main anal fin; 26-31 lower gill rakers on first gill arch *Spratellomorpha*
- 14b. last 2 anal rays not separated from others; 15-20 lower gill rakers on first gill arch *Sauvagella*

- 15a. 0-10 prepelvic scutes without lateral arms in front of pelvic scute with lateral arms (Figure 3-34A); pelvic fin with 1 unbranched and 5-6 branched rays, its insertion well before dorsal-fin base *Sierrathrissa*
- 15b. 6-9 prepelvic scutes with lateral arms (Figure 3-34B); pelvic fin with 1 unbranched and 7 branched rays, its insertion below or just before dorsal-fin base. . 16

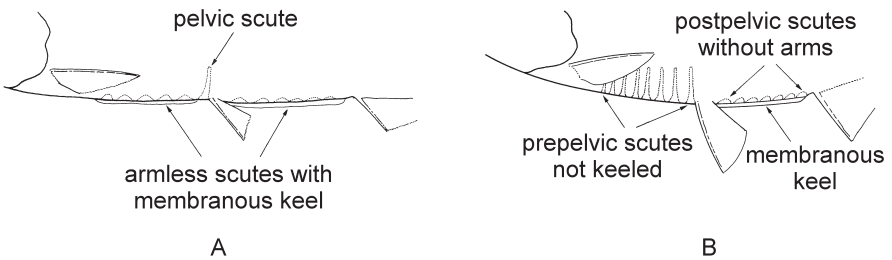


Figure 3-34. A) prepelvic scutes without lateral arms (*Sierrathrissa*).
 B) pelvic scutes with lateral arms (from Whitehead 1985).

- 16a. no postpelvic scutes; 39-76 lower gill rakers on first gill arch . . *Gilchristella*
- 16b. 5-6 keeled postpelvic scutes without lateral arms; 21-26 lower gill rakers on first gill arch. *Laeviscutella*

- 17a. premaxilla with strong canine teeth (Figure 3-35). *Odaxothrissa*
- 17b. premaxilla toothless or with small teeth, sometimes well-developed but never caninelike 18

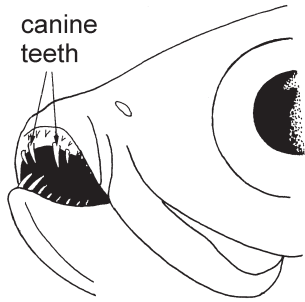


Figure 3-35. Premaxilla with strong canine teeth (*Odaxothrissa*) (from Whitehead 1985).

- 18a. maxillary blade deep, its depth no more than 3 times in its length, upper edge without ridge; posterior supramaxilla diamond shaped (Figure 3-36A) 19
- 18b. maxillary blade long and slender, its depth more than 3 times in its length, upper edge with ridge flared outwards; posterior supramaxilla small and spatulate (Figure 3-36B) 20

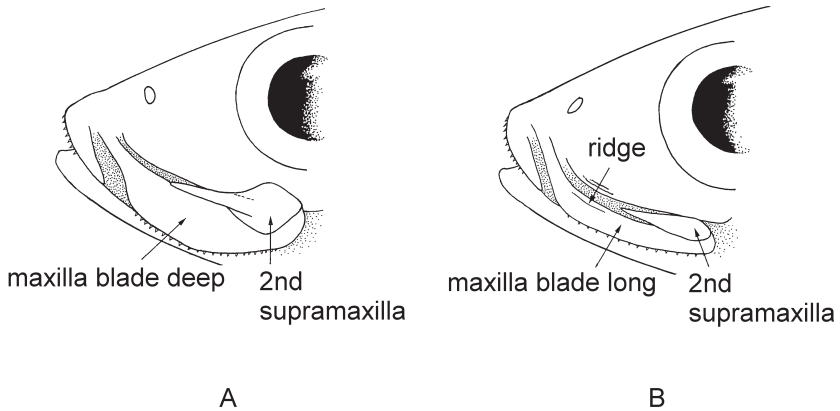


Figure 3-36. A) maxillary blade deep; posterior supramaxilla diamond shaped. B) maxillary blade long and slender, its upper edge with a ridge flared outwards; posterior supramaxilla small and spatulate (from Whitehead 1985).

- 19a. dentary and premaxilla toothless *Nannothrissa*
- 19b. dentary and premaxilla with relatively well-developed teeth *Pellonula*

- 20a. maxillary blade only slightly longer than its shaft. 21
- 20b. maxillary blade long, more than 2 times length of its shaft 22

- 21a. lower jaw deep, with small teeth limited to anterior part (Figure 3-37A);
maxilla with small conical teeth *Microthrissa*
- 21b. lower jaw slender, with small teeth on anterior and posterior part, dentition
sawlike (Figure 3-37B); maxilla toothless *Potamothrissa*

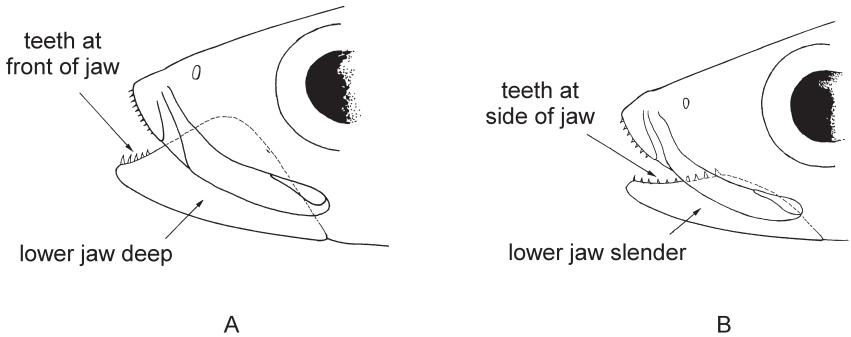


Figure 3-37. A) lower jaw deep, with small teeth limited to anterior part (*Microthrissa*). B) lower jaw slender, with small teeth on anterior and posterior part, dentition sawlike (*Potamothrissa*) (from Whitehead 1985).

- 22a. maxilla blade very long, more than 4 times length of its shaft; toothed lower edge of maxilla reaching tip of premaxilla (Figure 3-38A). *Limnothrissa*
- 22b. maxilla blade long, slightly more than 2 times length of its shaft; toothed lower edge of maxilla not reaching tip of premaxilla (Figure 3-38B) *Stolothrissa*

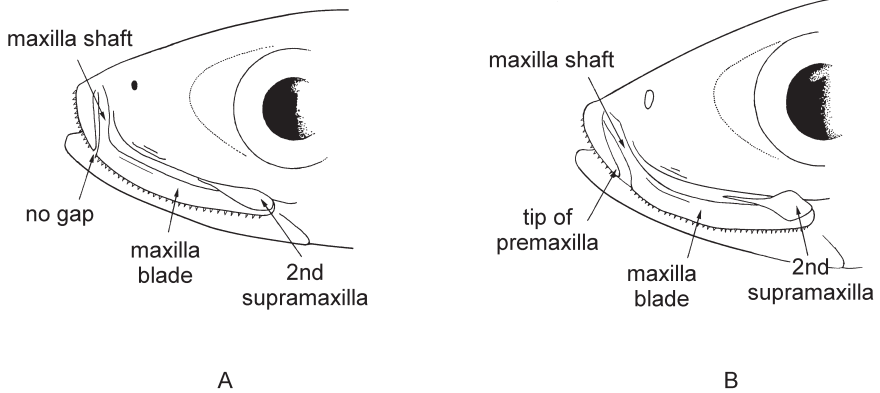


Figure 3-38. A) toothed lower edge of maxilla reaching tip of premaxilla (*Limnothrissa*). B) toothed lower edge of maxilla not reaching tip of premaxilla (*Stolothrissa*) (from Whitehead 1985).

Genus *Alosa* Linck, 1790

The genus *Alosa* contains 24 species (Froese & Pauly 2021) and can be found in the North and Central Atlantic Ocean, the Mediterranean Sea, the Black Sea, the Caspian Sea, and associated rivers and lakes (Whitehead 1985). Most species are anadromous or form landlocked populations and are very sensitive to environmental impacts resulting from impoundment, water pollution and overfishing (Kottelat & Freyhof 2007). The upper jaw has a median notch and the long upper gill rakers overlap with the lower gill rakers at the angle of the gill arch. These characters can be used to distinguish *Alosa* from similar genera of Clupeidae (Whitehead 1985). However, the taxonomy of *Alosa* is confusing and more study is required (Baglinière *et al.* 2003; Kottelat & Freyhof 2007). Due to the large overlap in morphological characters and in colour pattern, and because of hybridization, it is difficult to separate the various species, resulting in instabilities in nomenclature and confusion in the distribution of the species. Here we follow the taxonomic decisions of Kottelat (1997) and Kottelat & Freyhof (2007) and present the morphological characters they reported.

- 1a. more than 85 gill rakers on first gill arch; 60-90 scales in lateral series *Alosa alosa*
- 1b. less than 85 gill rakers on first gill arch; 54-71 scales in lateral series 2
- 2a. 40-60 slender gill rakers on first gill arch *Alosa algeriensis*
- 2b. 31-50, rarely up to 60, thick gill rakers on first gill arch *Alosa fallax*

■ *Alosa algeriensis* Regan, 1916

Common names: North African shad (Algeria), Sábalo rifeño (Morocco).

Description: dorsal profile convex; gill rakers slender, 25-38 on lower part of first gill arch, 40-60 in total; palatine and vomer lacking teeth (Kartas 1991; Kottelat 1997; Kottelat & Freyhof 2007).

Maximum length: 43.5 cm SL (male); 50.0 cm SL (female) (Kartas 1991).

Colour: (based on the illustration of a fresh specimen in Kottelat & Freyhof 2007) In life: body silvery with dorsal side dark blue-grey; a single black blotch behind gill opening, followed by some faint blotches; caudal fin yellowish with black posterior margin.

Distribution: Africa: along the North African coasts of the Mediterranean Sea, from the Rif Peninsula in Morocco to northern Tunisia, entering permanent rivers in Algeria and Tunisia (Kartas 1991; Kottelat & Freyhof 2007). A landlocked population exists in Lake Ichkeul, Tunisia (Kottelat & Freyhof 2007). Europe: restricted to western Sardinia in Italy (Kottelat & Freyhof 2007).



Figure 3-39. *Alosa algeriensis*, Oued Soummam, Algeria. Picture by Mahmoud Bacha.

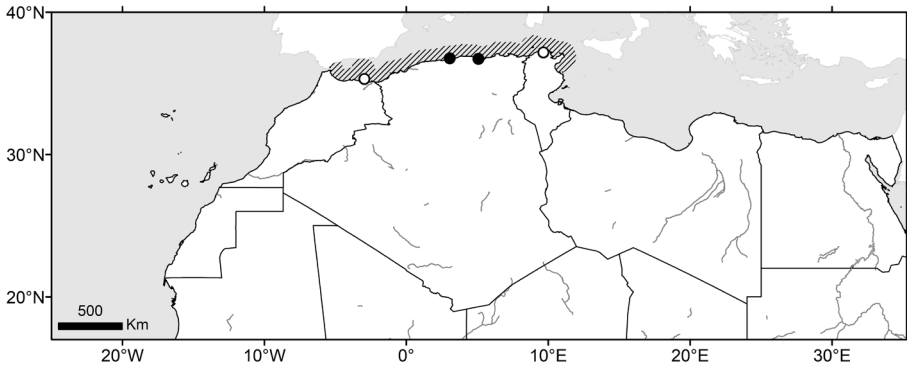


Figure 3-40. *Alosa algeriensis*, distribution map.

Alosa alosa (Linnaeus, 1758)

Common names: Allis shad (E), Alose vraie (F), Sábalo común (S), Grande alose (Morocco).

Description: no teeth on palatine and vomer; gill rakers long, slender and numerous, 55-110 on lower part of first gill arch, 90-155 in total, distinctly longer than branchial filaments in individuals longer than 250 mm SL (Whitehead 1985; Quignard & Douchement 1991a; Kottelat & Freyhof 2007). Scales irregularly arranged on flank (Kottelat & Freyhof 2007). Usually a single dark spot posterior to gill opening, sometimes absent, occasionally followed by several small blotches (Kottelat & Freyhof 2007).

Maximum length: 69.0 cm TL (male; Quignard & Douchement 1991a); 83.0 cm TL (female; Aprahamian *et al.* 2003).

Colour: In life: dark blue or blue-green dorsum, becoming greenish brown or golden on flanks; flanks and ventral side silvery (Baglinière *et al.* 2003). A single dusky spot behind gill opening, sometimes absent, and occasionally followed by several small spots (Aprahamian *et al.* 2003; Kottelat & Freyhof 2007).

Distribution: Eastern Atlantic and Mediterranean Sea: Baltic, North and western Mediterranean Seas, Atlantic coast of Great Britain, Ireland, France, Spain, Portugal and Morocco from where adults ascend rivers, migrating far upstream to spawn; landlocked populations occur in some man-made lakes in Morocco and Portugal (Kottelat & Freyhof 2007). Southern distribution possibly extends to northern Mauritania (Whitehead 1985). A dried specimen from Alexandria (Egypt;

NRM 37964) is registered as this species; gill rakers could not be verified in this specimen, but it does seem to have an irregular scale pattern. However, this is far outside the distribution range and needs verification.

Note: *Alosa vulgaris* is a synonym of *Alosa alosa* (Whitehead 1967a; Kottelat 1997). However, the identity of the paralectotypes from Algeria of this species (MNHN 3133 and 3134) is ambiguous. The first specimen is listed as *Alosa alosa* in the MHNH database, the second lot with two specimens as *Alosa fallax*, in accordance with the identifications by Bertin (1940) and Whitehead (1967a). These need to be verified. According to Kottelat & Freyhof (2007), only one species is supposed to occur along the coast of Algeria, which is *A. algeriensis*.



Figure 3-41. *Alosa alosa*. Picture from www.noordzeeloket.nl

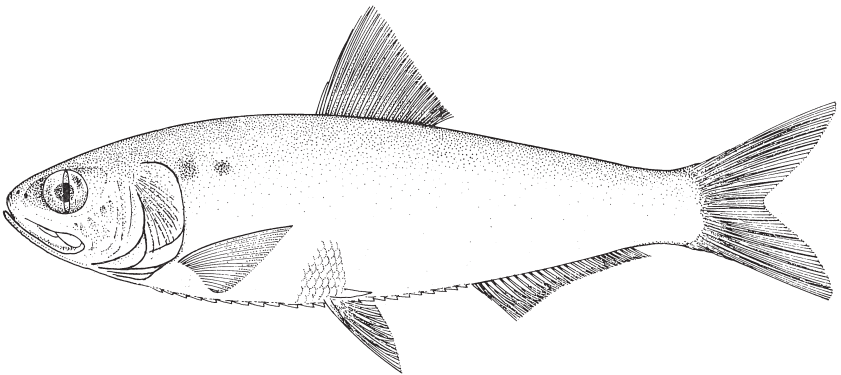


Figure 3-42. *Alosa alosa* (from Whitehead 1985).

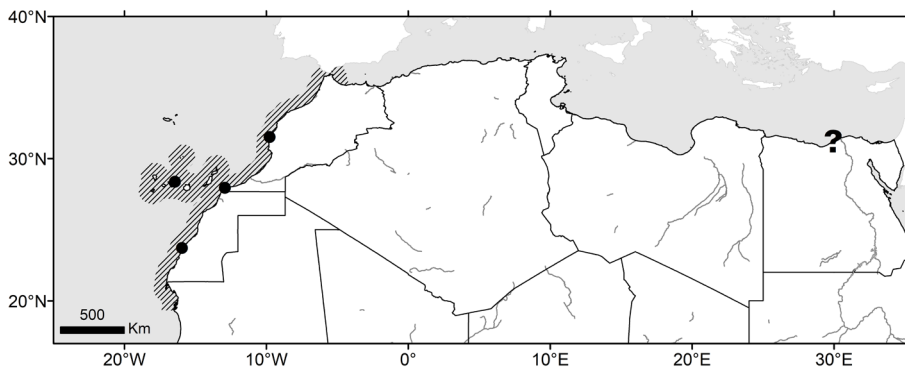


Figure 3-43. *Alosa alosa*, distribution map.

Alosa fallax (Lacepède, 1803)

Common names: Twaite shad (E), Alose feinte (F), Saboga (S).

Description: no teeth on palatine and vomer; gill rakers fairly short and stout, 17-32 on lower part of first gill arch, 31-50 in total (rarely up to 60), about as long as gill filaments; scales regularly arranged on flank (Quignard & Douchement 1991b, 1991c; Kottelat & Freyhof 2007). Usually a series of 4-8 black blotches behind gill opening, but sometimes only a single blotch is visible (Whitehead 1985; Kottelat & Freyhof 2007).

Maximum length: 60.0 cm SL (Quignard & Douchement 1991c).

Colour: In life: flanks and ventral side silvery, deep blue dorsally; usually a series of 4-8 black blotches behind gill opening, sometimes a single blotch (Whitehead 1985; Aprahamian *et al.* 2003; Kottelat & Freyhof 2007).

Distribution: Eastern Atlantic and Mediterranean Sea: southern shore of Baltic, North Sea northward to Bergen, Atlantic coasts from Scotland and Ireland to Morocco, northern Mediterranean (and Nile) and rarely in northern Black Sea, occasionally east to Crimea, from where adults ascend rivers, migrating a short distance upstream to spawn; ascended Drin to Lake Ohrid; earlier ascended the Rhône River for 600 km (Kottelat & Freyhof 2007).

Note: Several subspecies have been recognised based on the number of gill rakers and geographical location (Quignard & Douchement 1991b). Some have since been given species-status (including *Alosa algeriensis*), others are regarded as synonyms of *Alosa fallax* (including *A. fallax nilotica*) (Kottelat 1997; Kottelat & Freyhof 2007).



Figure 3-44. *Alosa fallax*, photograph taken on board RV *Belgica* at Westdiep, North Sea. Picture by H. Hillewaert (CC-BY-SA 4.0).

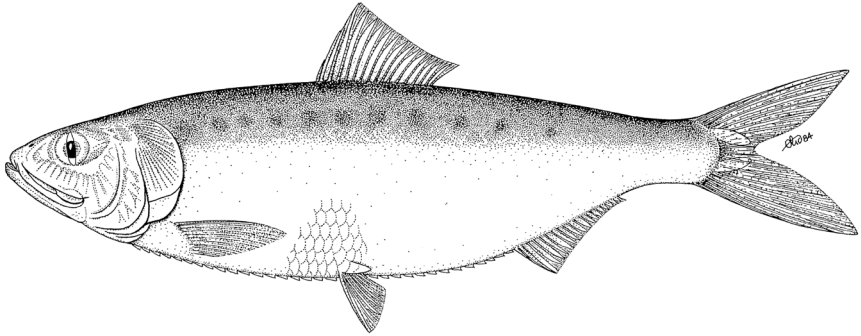


Figure 3-45. *Alosa fallax* (from Whitehead 1985).

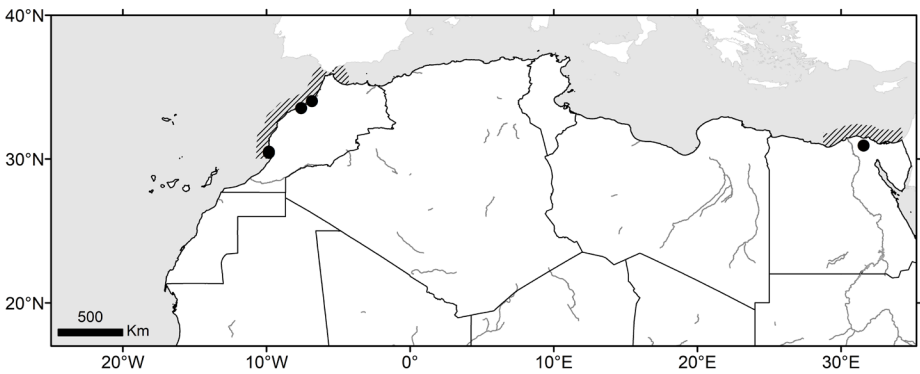


Figure 3-46. *Alosa fallax*, distribution map.

Genus *Congothrissa* Poll, 1964

The single species in this genus, *Congothrissa gossei*, occurs in schools with other clupeid species, but the smoothly rounded belly, the absence of spiny postpelvic scutes and the lack of a second (= posterior) supramaxilla make it unmistakable (Whitehead 1985).

Congothrissa gossei Poll, 1964

Common names: Smoothbelly pellowline (E).

Description: small and fairly slender, body depth around 22-24% SL; belly rounded, smooth, prepelvic and postpelvic scutes absent, but pelvic scute present and with lateral arm tips bifurcated; jaws about equal, with fine teeth; no posterior supramaxilla; 10-12 lower gill rakers; pelvic-fin insertion just behind dorsal-fin origin (Whitehead 1985). Scales large, 20-22 in lateral series (Poll 1974; Whitehead 1985).

Maximum length: 3.5 cm SL (Whitehead 1985).

Colour: In life: body probably silvery (Poll 1964). Preserved specimens: body pale yellow; dark brown/black chromatophores present on dorsal surface of head; usually a band of dark brown/black chromatophores in middle of flanks, especially on caudal peduncle (Poll 1964).

Distribution: only known from the Middle Congo River near Kisangani (DRC) and the Ubangi River (upstream of Bangui in the Central African Republic) (Poll 1974; Whitehead 1985).

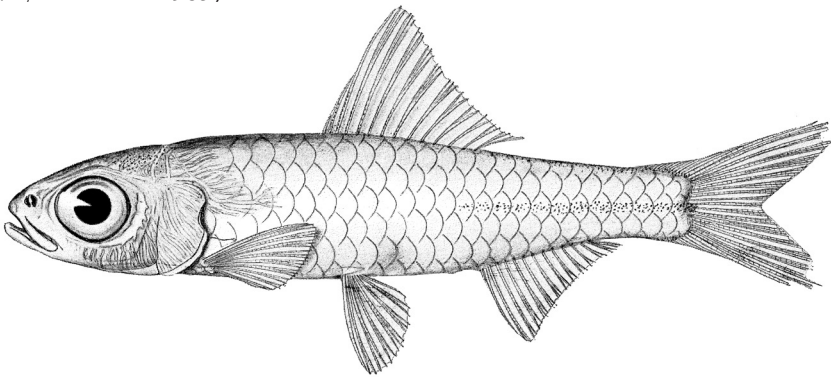


Figure 3-47. *Congothrissa gossei*, drawing based on paratypes from Yaekela, near Yangambi, DRC (from Poll 1964).



Figure 3-48 . *Congothrissa gosseï*, paratype, Yaekela, Congo River, DRC, RMCA 102019-022. © RMCA.

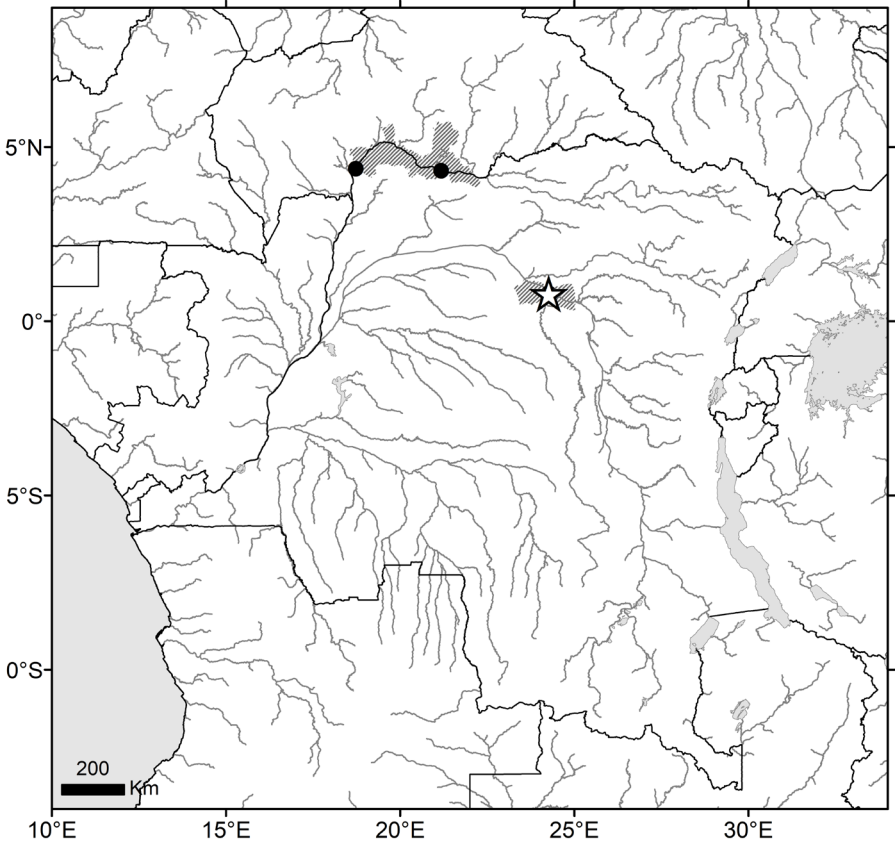


Figure 3-49 . *Congothrissa gosseï*, distribution map.

Genus *Ethmalosa* Regan, 1917

The single species of this genus, *Ethmalosa fimbriata*, has a fairly deep and compressed body, an upper jaw with a distinct median notch and upper gill rakers of the first gill arch that are strongly bent, V-shaped and not overlapping the lower gill rakers at the angle of the gill arch (Whitehead 1985).

Ethmalosa fimbriata (Bowdich, 1825)

Common names: Bonga shad (E), Ethmalose d’Afrique (F), Sábalo africano (S), Bonga (Angola, Equatorial Guinea, Guinea, Guinea-Bissau, Liberia, Nigeria, Sierra Leone), Galucha (Angola, Cape Verde, Guinea-Bissau), Quilucha (Angola, Cape Verde), Aywé (Benin), Folé (Benin), Kanflanvi (Benin), Tiaka (Benin), Wékuko (Benin), Cachumbeta (Cape Verde), Sável-africano (Cape Verde), Liandji (Republic of the Congo), Mandji (Republic of the Congo), Aywo (Côte d’Ivoire), Ehoube (Côte d’Ivoire), Kpraakpre (Côte d’Ivoire), Kprekpre (Côte d’Ivoire), Sardina (Equatorial Guinea), Mbéré (Gabon), Mvélé (Gabon), Ossako Mbèrè (Gabon), Sardine des estuaires (Gabon), Tialo (Gambia), Agbodzo (Ghana), Eflo (Ghana), Fia (Ghana), Fole (Ghana), Kokole (Ghana), Kokore (Ghana), Kwamokyi (Ghana), Bonga seri (Guinea), Djafal (Guinea-Bissau), Awatt (Mauritania, Senegal), Ethmalose (Mauritania, Senegal, Togo), Igir bicham (Mauritania), Machoello mario (Mauritania), Obeu (Mauritania, Senegal), Sardinelle jaune (Mauritania), Sardinha carça (São Tomé e Príncipe), Chalo (Senegal), Cobo (Senegal), Diata (Senegal), Fassou coba (Senegal), Idath (Senegal), Issal (Senegal), Kafelej (Senegal), Kobo (Senegal), Kóóóó (Senegal), Obo (Senegal), Ööbë (Senegal), Tiatj (Senegal), Tindal tchatch (Senegal), Awe-fu (Sierra Leone), Bongo (Sierra Leone), Bonji (Sierra Leone), Folevi (Togo).

Description: body fairly deep and compressed; scutes present along belly; upper jaw with distinct notch, into which tip of lower jaw fits; lower gill rakers long, fine and numerous, about 3 times as long as gill filaments, upper gill rakers bent sharply upward and V-shaped; pelvic fin with 1 unbranched and 7 branched rays; caudal-fin tips long and pointed (Whitehead 1985). Faint dark spot behind gill cover, sometimes followed by others; dorsal-fin tip black; caudal fin deep chrome yellow; golden tints on body (Whitehead 1985; Gourène & Teugels 2003).

Maximum length: 46.0 cm TL (Daget & Iltis 1965).

Colour: In life: dorsum blue/green, flanks silvery, with a faint oval spot behind upper part of gill cover; golden areas on upper part of head; dorsal-fin base and anterior dorsal-fin rays dark, rest of fin yellow; anal fin yellowish/hyaline; caudal fin deep chrome yellow, but upper edge and hind margin grey (Whitehead 1981). Alcohol-preserved specimens: silvery, with dorsum brownish to greenish; rounded black spot behind upper part of operculum, sometimes followed by one or more, less visible, spots aligned in a longitudinal series (Whitehead 1985; Gourène & Teugels 2003; Teugels 2007).

Distribution: Eastern central Atlantic Ocean: from Dakhla in Western Sahara southward to Lobito Bay (just north of Benguela) in Angola (Whitehead 1985, 1990; Gourène & Teugels 2003; Teugels 2007), occasionally entering freshwater (Poll *et al.* 1984). Reports from Cape Verde Islands are based on an erroneous type locality for *Clupea fimbriata* by Bowdich (1825), which was later rectified as ‘most likely Gambia’ (Whitehead 1967b, 1985).

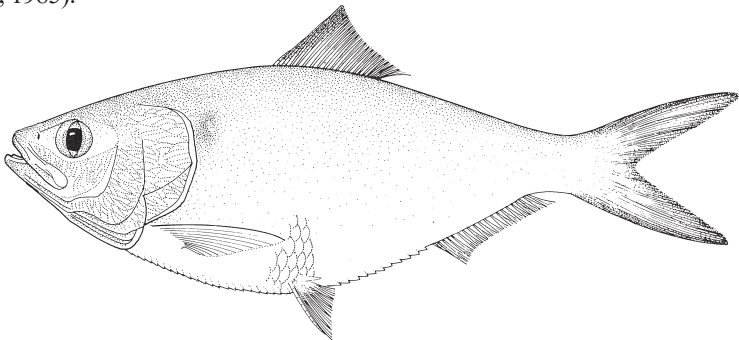


Figure 3-50. *Ethmalosa fimbriata* (from Whitehead 1985).



Figure 3-51. *Ethmalosa fimbriata*, Ganvie, Lake Nokoué, Benin, RMCA 73-1-P-212-213. © RMCA.

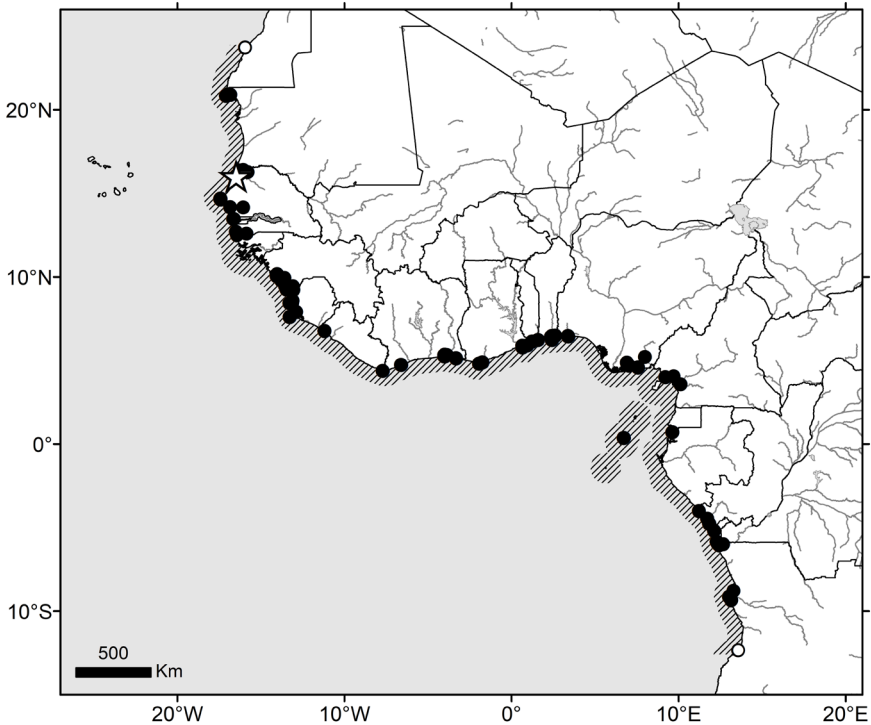


Figure 3-52. *Ethmalosa fimbriata*, distribution map.

Genus *Gilchristella* Fowler, 1935

The single species of this genus, *Gilchristella aestuaria*, is known from southern Africa and resembles *Spratelloides* and *Sauvagella* species, which occur in Madagascar (*Spratelloides bianalis* possibly also in Kenya) and also lack post-pelvic scutes. *Gilchristella* however can be distinguished from these by the presence of prepelvic scutes, non-keeled but with lateral arms (Whitehead 1985).

Gilchristella aestuaria (Gilchrist, 1913)

Common names: Gilchrist's round herring (E), Estuarine round-herring (South Africa), Rivier-rondeharing (South Africa), Whitebait (South Africa), Witaas (South Africa).

Description: body rather compressed, belly rounded; 6-9 thin, unkeeled prepelvic scutes followed by an equally thin pelvic scute, all with slender ascending arms;

no postpelvic scutes; snout pointed; lower jaw a little prominent, with a single row of fine teeth in each jaw; posterior supramaxilla paddle-shaped; 39-76 lower gill rakers on first branchial arch; posterior face of third epibranchial with small gill rakers (Whitehead 1985). Pelvic fin with 1 unbranched and 7 branched fin rays, under or slightly in front of dorsal-fin origin (Whitehead 1985; Skelton 2001).

Maximum length: 9.0 cm SL (Skelton 2001).

Colour: In life: silvery, dorsal and lateral parts of head and body thickly sprinkled with black dots; brilliant silver lateral stripe on posterior part of flank; dorsum dark (Barnard 1925; Whitehead & Wongratana 1986a). Alcohol-preserved specimens: uniformly light brown with faint midlateral silvery band; individual bases of dorsal and anal rays black (Whitehead 1963).

Distribution: Incomati River mouth (Mozambique, SAIAB 45257) southwards along the east coast of South Africa and on the west coast as far north as the mouth of the Orange River (Poll *et al.* 1984; Whitehead 1985; Whitehead & Wongratana 1986a). Reports from Madagascar are based on confusion with *Sauvagella madagascariensis*; report from India (Blaber 1997) dubious (Stiassny 2002). Currently a single species is recognised, but at least two forms, possibly different species, are known (Skelton 2001).

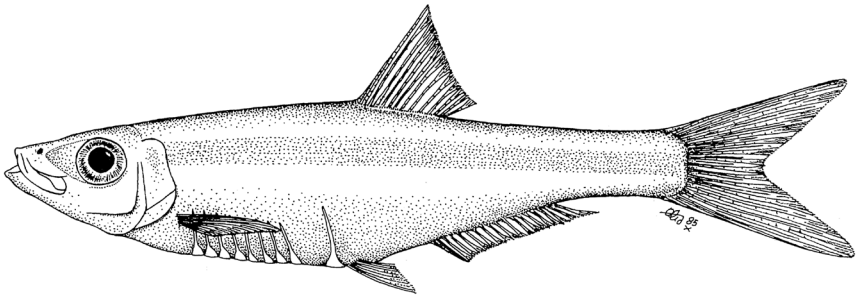


Figure 3-53. *Gilchristella aestuaria* (from Whitehead 1985).



Figure 3-54. *Gilchristella aestuaria*, Knysna and Swartvlei, South Africa, RMCA 89-12-P-459-521. © RMCA.

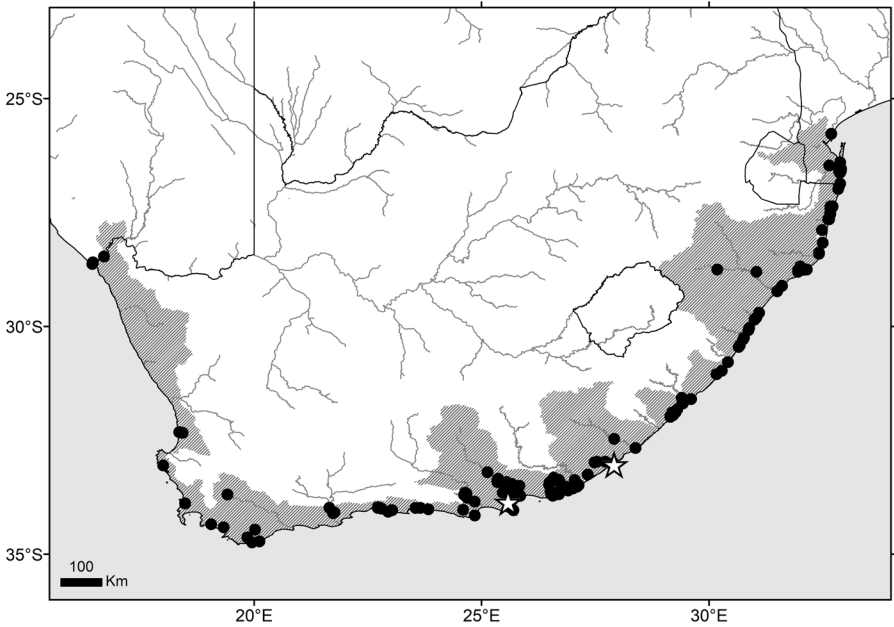


Figure 3-55. *Gilchristella aestuaria*, distribution map.

Genus *Herklotsichthys* Whitley, 1951

The genus *Herklotsichthys* contains 12 species (Froese & Pauly 2021) and is characterised by the presence of an anterior and posterior supramaxilla, with the lower part of the posterior supramaxilla larger than the upper part, the smooth operculum without bony striae, the presence of two fleshy outgrowths on the posterior margin of the gill opening and 3-7 frontoparietal striae on top of the head (Whitehead 1974a; 1985). Species of *Herklotsichthys* are marine pelagic and schooling fishes only found in the Indo-Pacific region, mainly in tropical and subtropical waters (Whitehead 1985; Whitehead & Wongratana 1986a), occasionally penetrating the southern Atlantic Ocean in South Africa. One species enters estuaries and sometimes freshwaters in Africa: *Herklotsichthys quadrimaculatus*.

***Herklotsichthys quadrimaculatus* (Rüppell, 1837)**

Common names: Bluestripe herring (E), Hareng à bande bleue (F), Arenque banda azul (S), Gozila (Comoros), Mchile (Comoros), Ampiny (Madagascar), Besisika (Madagascar), Besisike-pepe (Madagascar), Geba (Madagascar), Marotaolana (Madagascar), Morotaolana (Madagascar), Pepe (Madagascar), Sardine blanche (Mauritius), Sardine goemon (Mauritius), Sardine gros yeux (Mauritius), Sardinha banda azul (Mozambique), Sardine queue blanc (Réunion), Sardin ordiner (Seychelles), Bloulintharing (South Africa), Blueline herring (South Africa), Daga-papa (Tanzania).

Description: body slender, its depth 18-30% SL; sharp belly with 16-19 prepelvic and 12-14 postpelvic keeled scutes (Whitehead 1985; Whitehead & Wongratana 1986a). Elongate winglike scales present, almost hidden beneath the normal paired predorsal scales (Whitehead & Wongratana 1984a; Whitehead 1985). Flank silvery with electric blue line preceded by two orange spots (Whitehead 1985).

Maximum length: 25.0 cm SL (Kuitert & Tonzuka 2001).

Colour: In life: back blue-green without spots; flank silvery with two orange spots behind gill opening and a blue midlateral band (Whitehead & Wongratana 1984a, 1986a).

Distribution: Indo-Pacific: widespread in the Indian Ocean and western Pacific, including the entire eastern coast of Africa, Madagascar and Mauritius eastward to Japan, eastern Australia and Samoa; introduced in Hawaii, apparently by accident, and now abundant (Whitehead 1985). On the western coast of southern Africa occurring northwards up to Lamberts Bay (Western Cape, South Africa).



Figure 3-56. *Herklotsichthys quadrimaculatus*. Picture by BEDO (Thailand) (CC-BY-SA 4.0).

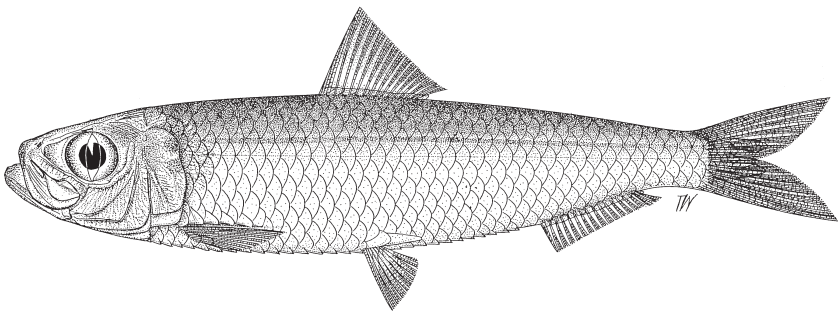


Figure 3-57. *Herklotsichthys quadrimaculatus* (from Whitehead 1985).

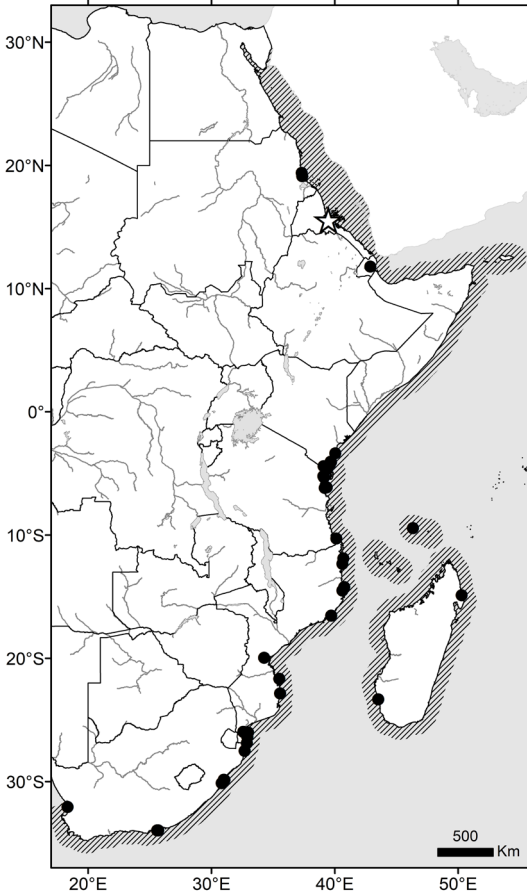


Figure 3-58.
Herklotsichthys quadrimaculatus,
 distribution map.

Genus *Hilsa* Regan, 1917

The single species of this genus, *Hilsa kelee*, is characterised by an upper jaw with a median notch, by the upper gill rakers that are distinctly curled outwards (not upwards and V-shaped), not overlapping the lower gill rakers at the angle of the first branchial arch, and by the numerous frontoparietal striae on top of the head (Whitehead 1985).

Hilsa kelee (Cuvier, 1829)

Common names: Kelee shad (E), Alose palli (F), Sábalo chandano (S), Pandepili (Comoros), Ampina (Madagascar), Karapapaka (Madagascar), Magumba (Mozambique), Malola (Mozambique), Saradinya (Mozambique), Aarijoog (Somalia), Kelee-haring (South Africa), Daga (Tanzania), Mbarata (Tanzania), Pata (Tanzania), Pawali (Tanzania).

Description: body fairly deep and compressed; belly with distinct keel of scutes; top of head with numerous frontoparietal striae; upper jaw with median notch; about 75-175 gill rakers, on inner arches distinctly curled; outer row of gill filaments on first arch not more than half length of gill rakers; a series of small triangular scales above posterior part of pectoral-fin base; black spot behind gill cover, usually followed by up to 10 spots along flank (Whitehead 1985; Whitehead & Wongratana 1986a).

Maximum length: 35.0 cm TL (Heemstra 1995).

Colour: In life: back blue-green, flank silvery with black spot behind gill opening and up to 10 similar spots dorso-laterally along flank (Whitehead & Wongratana 1984a; Whitehead 1985; van der Elst 1993).

Distribution: Indo-West Pacific: probably all coasts of the Indian Ocean, from the Gulf of Oman and the Gulf of Aden south to Krysna (South Africa) and Madagascar, across the Bay of Bengal, Gulf of Thailand, Java Sea and north to Hong Kong and east to Papua New Guinea and possibly further, entering estuaries and able to tolerate quite low salinities (7ppt) (Whitehead 1985). Also present in the Red Sea from Sudan (SMF 28172, identification verified on photographs), though never reported from that area (see e.g. Golani & Fricke 2018).

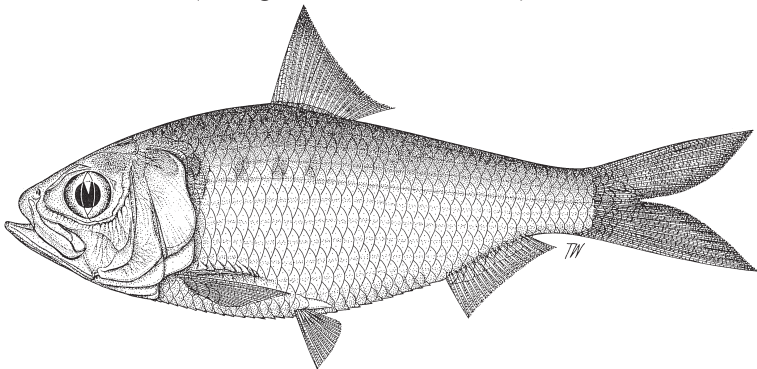


Figure 3-59. *Hilsa kelee* (from Whitehead 1985).



Figure 3-60. *Hilsa kelee*, Karachi, Pakistan, 19 cm SL. Picture by Hamid Badar Osmany (CC-BY).

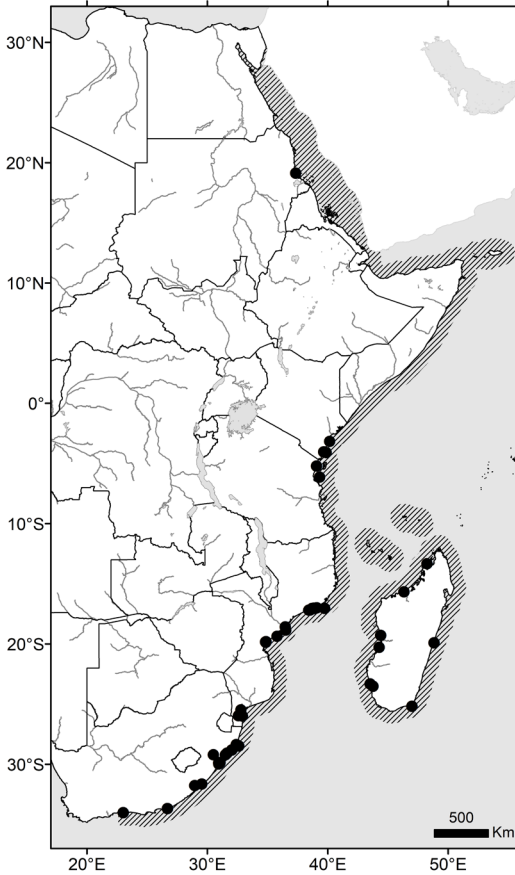


Figure 3-61. *Hilsa kelee*, distribution map.

Genus *Laeviscutella* Poll, Whitehead & Hopson, 1965

The single species of this genus, *Laeviscutella dekimpei*, is characterised by the presence of non-keeled prepelvic scutes with lateral arms, postpelvic scutes without arms and a pelvic fin inserted more or less below the dorsal-fin origin (Whitehead 1985). In all other West African pellowulines with scutes, the postpelvic scutes have lateral arms, except in *Sierrathrissa*, in which prepelvic scutes also lack arms and the pelvic fin is inserted well anterior to the dorsal-fin origin (Whitehead 1985; Teugels 2007).

***Laeviscutella dekimpei* Poll, Whitehead & Hopson, 1965**

Common names: Roundbelly pellowuline (E), Isoun (Nigeria), Ntita (Nigeria), Salanpore (Nigeria), Taga rana (Nigeria), Worongi (Nigeria).

Description: relatively small, somewhat elongate species, with slightly rounded belly; body depth 22-25% SL; 7-8 prepelvic scutes with lateral arms but without keels and hidden by scales; postpelvic scutes without arms, but supporting a low membranous keel; 21-26 lower gill rakers (Whitehead 1985; Gourène & Teugels 2003; Teugels 2007). Teeth present on premaxilla, maxilla, dentary, vomer and tongue (Gourène & Teugels 2003; Teugels 2007).

Note: One of the characters mentioned by Gourène & Teugels (2003) and Teugels (2007) is ‘dorsal fin inserted more or less above the insertion of the pectoral fin’. This should read as ‘dorsal fin inserted more or less above the insertion of the pelvic fin’ as can be observed in the illustrations.

Maximum length: 4.6 cm SL (Teugels 2007).

Colour: Alcohol-preserved specimens: generally pale yellow to yellowish-grey (Gourène & Teugels 2003; Teugels 2007), with pale trace of midlateral stripe from gill opening to caudal base, slightly wider and more distinct along posterior half of body (Poll *et al.* 1965). Dorsally a median double series of small melanophores, becoming larger and more dense on either side of dorsal fin and post-dorsally; a series of small melanophores extending midlaterally from under second half of dorsal fin to caudal base, becoming denser and larger posteriorly;

a melanophore at the base of each anal ray; bases of outer caudal rays dotted with melanophores, and a dark line separating caudal peduncle and caudal fin; melanophores dotted on premaxilla, shaft of maxilla and on dentary; fins colourless (Poll *et al.* 1965).

Distribution: lower parts of rivers and lagoons in western Africa (Whitehead 1985), in the Casamance River and from the Volta basin to the Niger delta (Gourène & Teugels 2003), in the lower Ogowe River in Gabon and the Loémé River in the Republic of the Congo (Teugels 2007).

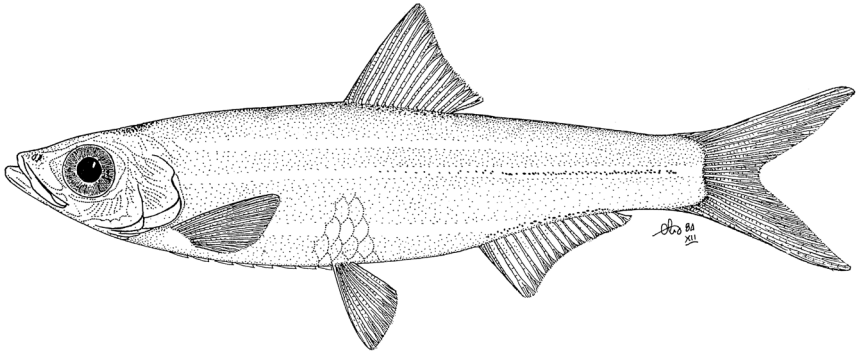


Figure 3-62. *Laeviscutella dekimpei*, holotype, 41.0 mm SL, Dawenia Dam, near Tema, Ghana, NHMUK 1965.2.10.1 (from Poll *et al.* 1965).



Figure 3-63. *Laeviscutella dekimpei*, paratype, Dawenia Dam, near Tema, coast of Ghana, RMCA 142828-837. © RMCA.

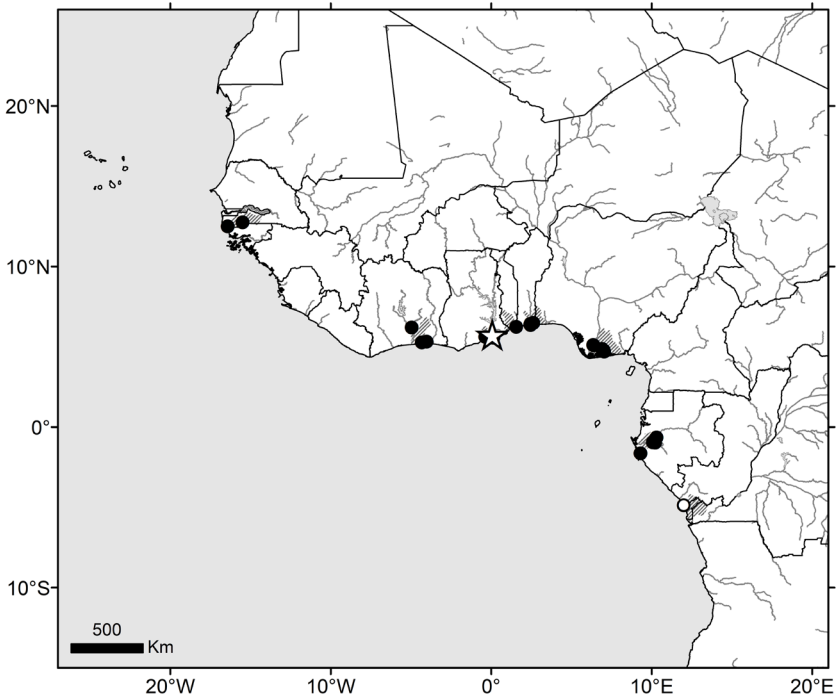


Figure 3-64. *Laeviscutella dekimpei*, distribution map.

Genus *Limnothrissa* Regan, 1917

The single species of this genus, *Limnothrissa miodon*, resembles *Stolothrissa tanganicae*, the second endemic clupeid of Lake Tanganyika, but is slightly deeper-bodied, has a larger eye, a longer maxilla blade (more than 4 times the length of its shaft, its depth more than 3 times in its length) with a ridge flared outwards on its upper edge and reaching forward to the posterior tip of the premaxilla, and a less symmetrical, paddle-shaped posterior supramaxilla with the lower part larger than the upper (Whitehead 1985).

Limnothrissa miodon (Boulenger, 1906)

Common names: Lake Tanganyika sardine (E), Lumpu (Burundi, DRC), Ndagala (Burundi), Dagaa (DRC, Tanzania), Lumbu (DRC, Tanzania), Ndakala (DRC), Agahuza (Rwanda), Indagara (Rwanda), Isambaza (Rwanda), Karumba (Rwanda), Yorogo (Rwanda), Kapenta (South Africa, Zambia), Tanganikameer-sardyn (South Africa), Tanjanikameer sardyn (South Africa), Ndagaa (Tanzania), Chisamba (Zambia), Lumbo (Zambia), Nsembe (Zambia), Tanganyikan anchoveta (Zambia).

Description: body fairly slender, depth about 22-24% SL; prepelvic scutes not strongly keeled, beginning behind base of last pectoral-fin ray; maxilla blade over 4 times as long as its shaft, its lower toothed edge continued forward to meet hind tip of premaxilla; posterior supramaxilla asymmetrical with lower half largest; eye diameter about equal to postorbital length; 20-40 long and slender lower gill rakers; distinct silver stripe along flank (Boulenger 1909; Whitehead 1985; Gourène & Teugels 1993).

Maximum length: 17.0 cm SL (Poll 1953).

Colour: In life: olive above, silvery below, with a blue indistinct lateral band; dorsal and caudal greyish, other fins white (Boulenger 1906).

Distribution: endemic to Lake Tanganyika (Gourène & Teugels 1994; Snoeks *et al.* 2012), but introduced into several other water bodies, including Lake Kivu and the reservoirs Itezhi-Tezhi and Kariba, from where it spread downstream to the Cahora Bassa reservoir (Skelton 2001; Thys van den Audenaerde 1994, Snoeks *et al.* 2012).

Note: Reported as *Microthrissa stappersii* from Lake Mweru but this is based on an erroneous type locality (Gourène & Teugels 1993).

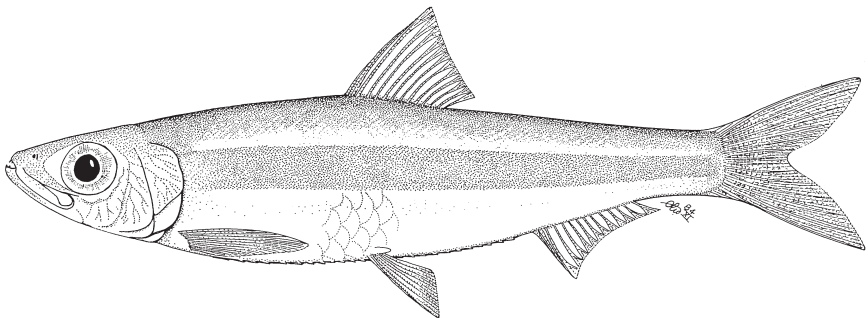


Figure 3-65. *Limnothrissa miodon* (from Whitehead 1985).



Figure 3-66. *Limnothrissa miodon*, Ulwile Island, northern shore, Lake Tanganyika, Tanzania, RMCA 92-081-P-0292. © RMCA.

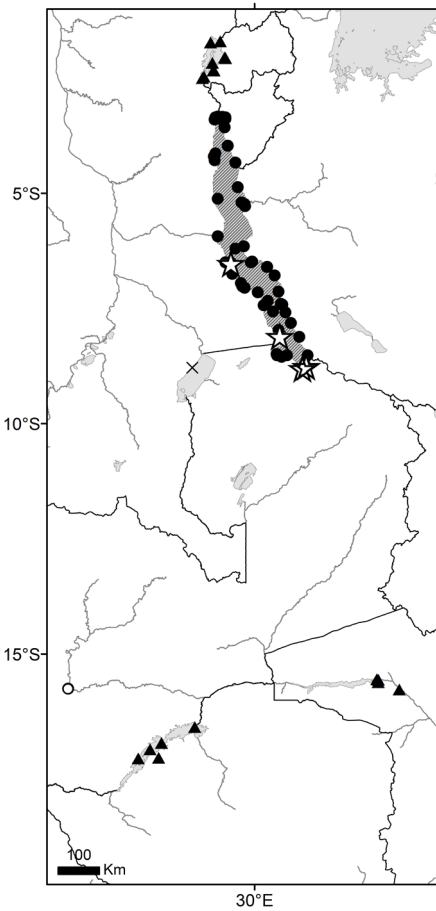


Figure 3-67. *Limnothrissa miodon*, distribution map.

Genus *Microthrissa* Boulenger, 1902

The genus *Microthrissa* contains five species (Gourène & Teugels 1989; Froese & Pauly 2021), all occurring in freshwater and endemic to the Congo basin (Whitehead 1985). The genus can be identified by the distinct and keeled prepelvic scutes, the deep lower jaw without teeth on the posterior part, the premaxilla without strong canine teeth, the maxilla with small conical teeth, the long and slender maxillary blade, only slightly longer than its shaft but with a ridge flared outwards on its upper edge, and the small and spatulate posterior supramaxilla (Whitehead 1985).

- 1a. no scutes in front of pectoral-fin base. 2
- 1b. 1 or more scutes in front of pectoral-fin base. 4

- 2a. scutes beginning just behind pectoral-fin base (first prepelvic scute always located behind base of last pectoral-fin ray); 33-40 scales in lateral series; premaxilla with 11-24 conical teeth. *Microthrissa moeruensis*
- 2b. scutes beginning under pectoral-fin base (first prepelvic scute always located before base of last pectoral-fin ray); 26-43 scales in lateral series; premaxilla with 12-42 conical teeth 3

- 3a. 26-35 scales in lateral series; premaxilla with 24-42 conical teeth
. *Microthrissa congica*
- 3b. 37-43 scales in lateral series; premaxilla with 12-30 conical teeth
. *Microthrissa minuta*
(specimens < ca. 35 mm SL)

- 4a. premaxilla with 32-40 small, inward pointing teeth . *Microthrissa whiteheadi*
- 4b. premaxilla with 12-30 small, inward or outward pointing teeth 5

- 5a. premaxilla with inward pointing teeth; 18-21 anal-fin rays; 18-22 lower gill rakers on first gill arch; 11-12 prepelvic scutes, first 1-2 scutes without ascending arms
. *Microthrissa minuta*
(specimens > ca. 35 mm SL)

5b. premaxilla with outward pointing teeth; 22-27 anal-fin rays; 14-17 lower gill rakers on first gill arch; 13-16 prepelvic scutes, first 3-4 scutes without ascending arms
..... *Microthrissa royauxi*

Microthrissa congica (Regan, 1917)

Common names: Bigscale pellonuline (E), Central Zaire pellonuline (E), Ifofole (DRC), Lifole (DRC).

Description: body slender, depth about 20-24% SL; scutes strongly keeled, no scutes in front of pectoral-fin base, first prepelvic scute always located before base of last pectoral-fin ray, 10-15 prepelvic and 8-11 postpelvic scutes; lower jaw not or slightly projecting, included in upper when mouth closed, with small teeth limited to anterior part; premaxillae with a single row of 24-42 small conical teeth directed inwards; maxilla slender, its blade more than 3 times as long as deep, upper edge quite strongly ridged; posterior supramaxilla slender, spatulate, with distinct anterior shaft, shaft longer than blade; 17-24 lower gill rakers (Whitehead 1985; Gourène & Teugels 1989). 26-35 scales in lateral series; 18-22 anal-fin rays (Gourène & Teugels 1989).

Maximum length: 7.0 cm SL (Poll 1974).

Colour: Preserved specimens: body yellow greyish, ventral region and middle of flanks lighter coloured; tip of snout and occiput, and middle part of flanks dotted with melanophores (Gourène & Teugels 1989) forming a narrow lateral band on posterior half of body (Regan 1917).

Distribution: widely distributed in the Congo River basin (Gourène & Teugels 1989; 1994), from the Lower Congo River near its estuary up to the upper Lualaba River but excluding the Luapula-Mweru region (Whitehead 1985). Present in major tributaries of the Congo including the lower courses of the Kasai system and the Sangha, Ruki and Ubangi drainages.

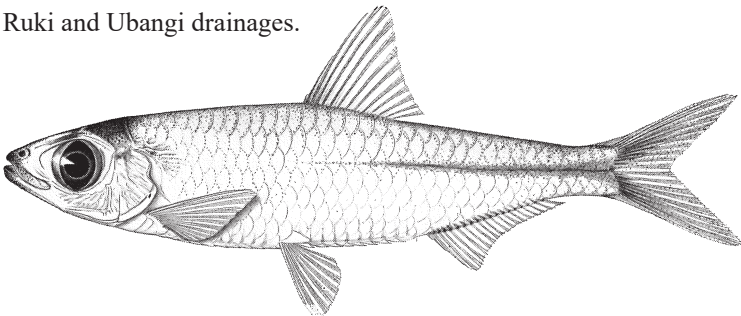


Figure 3-68. *Microthrissa congica*, holotype of *Poecilothrissa centralis*, 50 mm SL, Coquilhatville (now Mbandaka), DRC, RMCA 88319 (from Poll 1974).



Figure 3-69. *Microthrissa congica*, station 4, Stanley Pool, close to the N'Sele River, RMCA 116694-116704. © RMCA.

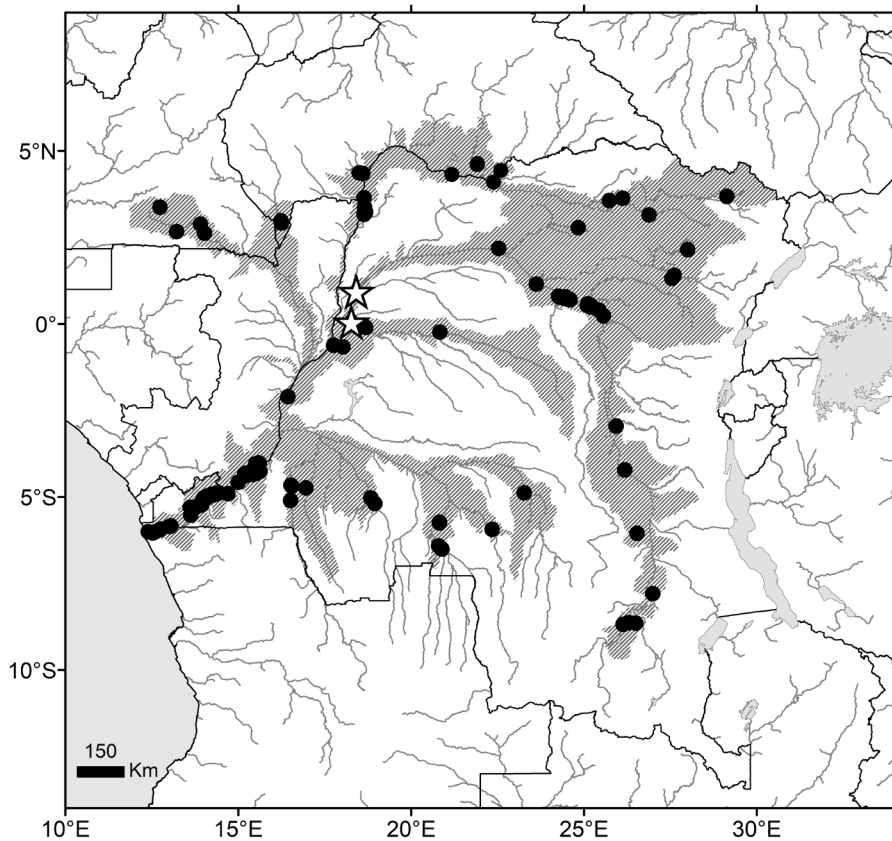


Figure 3-70. *Microthrissa congica*, distribution map.

Microthrissa minuta Poll, 1974

Common names: Dungu sprat (E).

Description: body moderately deep, depth about 22-30% SL; scutes strongly keeled, 1-2 before base of first pectoral-fin ray, 11-12 prepelvic and 6-8 postpelvic scutes; snout pointed; lower jaw not or slightly projecting, included in upper when mouth closed, with small teeth limited to anterior part; premaxilla with 12-30 small conical teeth directed inwards; maxilla blade slender, more than 3 times as long as deep, upper edge with a ridge flared outward; posterior supramaxilla small, spatulate, shaft as long as blade; 18-22 lower gill rakers (Poll 1974; Whitehead 1985; Gourène & Teugels 1989). 37-43 scales in lateral series; 18-21 anal-fin rays (Gourène & Teugels 1989). Specimens smaller than ca. 35 mm SL have no real prepectoral scutes, rather the first scute is situated under the pectoral fin but always before the base of the last pectoral-fin ray. These small specimens can be distinguished from *M. congica* by the higher number of scales in lateral series (37-43 vs. 26-35 in *M. congica*) (Gourène & Teugels 1989).

Maximum length: 4.3 cm SL (Gourène & Teugels 1989).

Colour: Preserved specimens: yellow greyish or silvery, occiput blackish due to numerous melanophores; weakly visible trace of melanophores on caudal peduncle ending in small black spot at base of lower lobe of caudal fin (Poll 1974; Gourène & Teugels 1989).

Distribution: known from disjunct populations in the Lower Congo River and in the Uélé drainage (Dungu River and its tributary the Garamba) (Whitehead 1985; Gourène & Teugels 1989). Also collected in a protected inlet of Pool Malebo and in the Sangha River (Middle Congo River basin) (AMNH collection). In the Upper Congo basin reported as *Microthrissa* cf. *minuta* from the mouth of the Niemba River (Lukuga River tributary, outflow of Lake Tanganyika) (Kullander & Roberts 2012).



Figure 3-71. *Microthrissa minuta*, paratype, Garamba River, DRC, RMCA 188616-633. © RMCA.

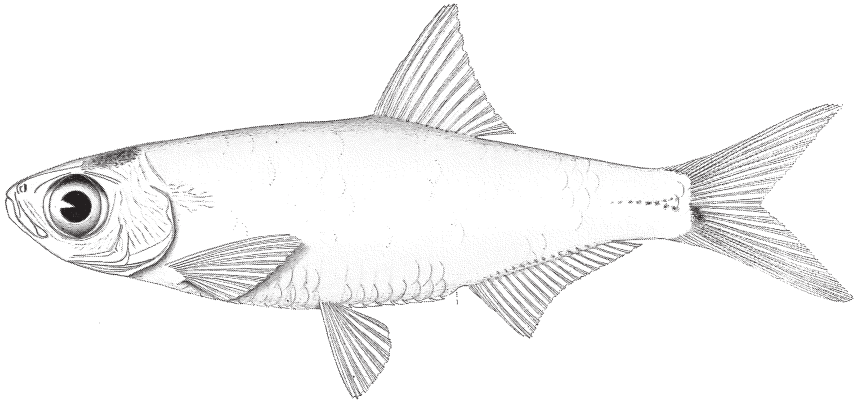


Figure 3-72. *Microthrissa minuta*, holotype, 30.5 mm SL, Garamba River, DRC, RMCA 188615 (from Poll 1974).

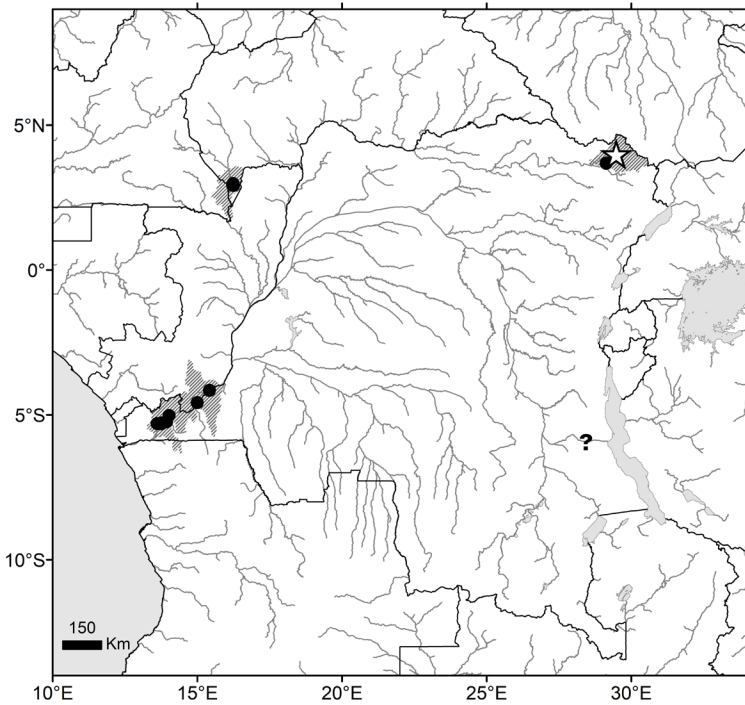


Figure 3-73. *Microthrissa minuta*, distribution map.

Microthrissa moeruensis (Poll, 1948)

Common names: Lake Mweru sprat (E), Kasepa (Zambia).

Description: body slender, depth about 20-25% SL; scutes strongly keeled, starting just behind base of last pectoral-fin ray, about 10-12 prepelvic and 5-8 postpelvic scutes; snout slightly pointed; lower jaw not or slightly projecting, with small teeth limited to anterior part; premaxillae with a single row of 11-24 small conical teeth directed inwards; maxilla slender, its blade a little more than 3 times longer than deep, upper edge a little ridged; posterior supramaxilla slender, spatulate, with distinct anterior shaft, shaft longer than blade; 18-20 lower gill rakers (Whitehead 1985; Gourène & Teugels 1989). 33-40 scales in lateral series; 15-22 anal-fin rays (Poll 1974; Gourène & Teugels 1989).

Maximum length: 4.1 cm SL (Jackson 1961).

Colour: Preserved specimens: body yellowish-brown, lighter on ventral side; flanks more or less silvery (Poll 1948). A paler lateral band, often covered with a series of melanophores in its posterior part; snout, chin and occiput also covered with melanophores; no black spot on base of lower lobe of caudal fin (Gourène & Teugels 1989).

Distribution: endemic to the Lake Mweru system (Whitehead 1985; Gourène & Teugels 1994), including Mweru Wantipa and the lower Luapula River.

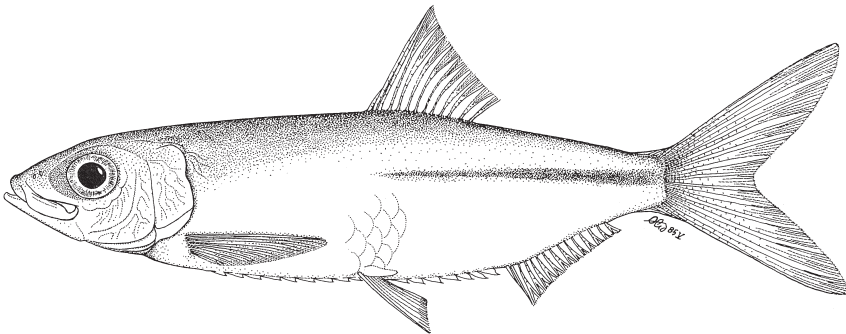


Figure 3-74. *Microthrissa moeruensis* (from Whitehead 1985).



Figure 3-75. *Microthrissa moeruensis*, KashiLu, 5 km upstream from mouth, Luapula River, Zambia, RMCA 94-019-P-2022-2080. © RMCA.

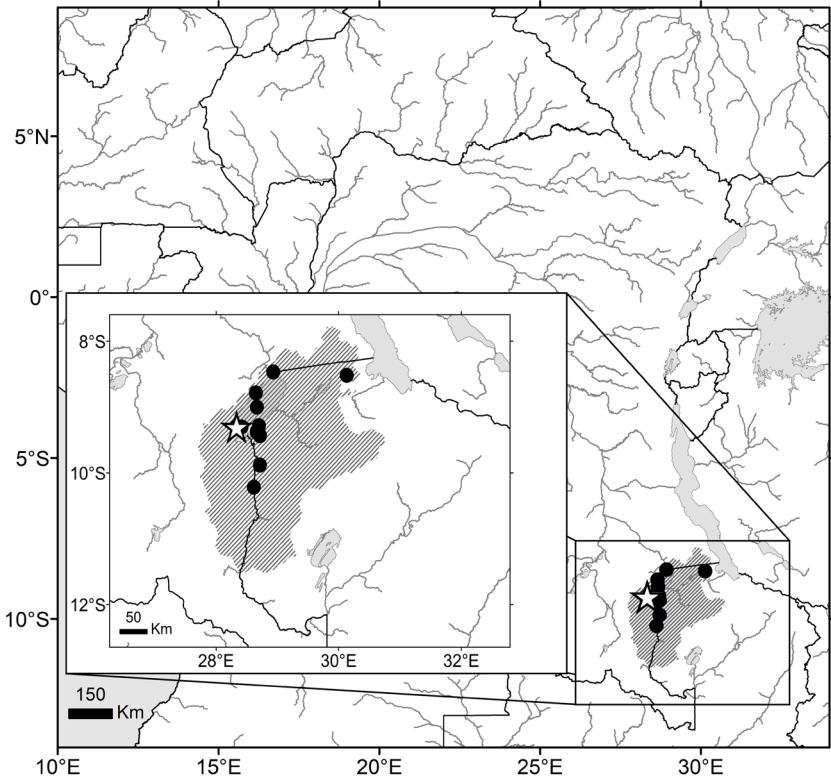


Figure 3-76. *Microthrissa moeruensis*, distribution map.

Microthrissa royauxi Boulenger, 1902

Common names: Royal sprat (E), Lifambalamba (DRC), Ndakala (DRC).

Description: body relatively deep, depth about 30-37% SL; scutes strongly keeled, 1-3 anterior to base of first pectoral-fin ray, 13-16 prepelvic and 3-7 postpelvic scutes; snout fairly pointed; lower jaw not or slightly projecting, included in upper when mouth closed, with small teeth limited to anterior part; premaxilla with medial notch and 16-26 small conical teeth directed outwards; maxilla blade slender, more than 3 times as long as deep, upper edge with a ridge flared outward; posterior supramaxilla small, spatulate, shaft as long as or longer than blade; 14-17 lower gill rakers (Whitehead 1985; Gourène & Teugels 1989). 34-41 scales in lateral series; 22-27 anal-fin rays (Gourène & Teugels 1989).

Maximum length: 9.9 cm TL (Poll *et al.* 1984).

Colour: Preserved specimens: brownish or yellow greyish, with a rather indistinct silvery lateral band (Boulenger 1909; Gourène & Teugels 1989).

Distribution: widespread in the Congo River basin, from the Lower Congo River up to Lake Mulenda in the Upemba region in the Democratic Republic of the Congo. Absent from the Luapula-Mweru. Recent collections have expanded the reported distribution by Gourène & Teugels (1989) to the Lower Congo (their Lower Congo specimens were actually from Pool Malebo), to the left bank affluents of the Middle Congo such as the Kasai, and to the Upper Congo.

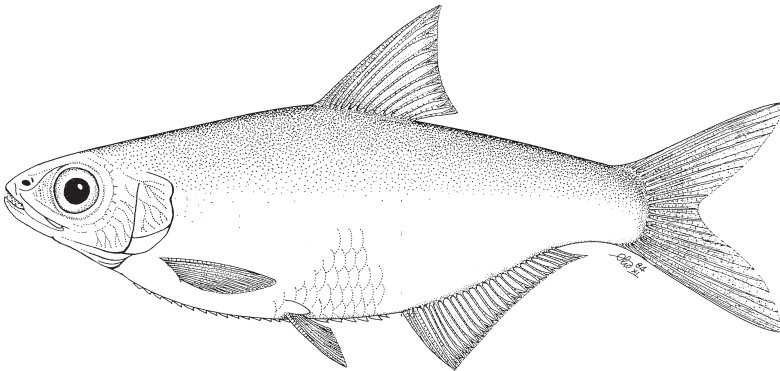


Figure 3-77. *Microthrissa royauxi* (from Whitehead 1985).



Figure 3-78. *Microthrissa royauxi*, Pool Malebo, Yankau, DRC, RMCA 73-22-P-139. © RMCA.

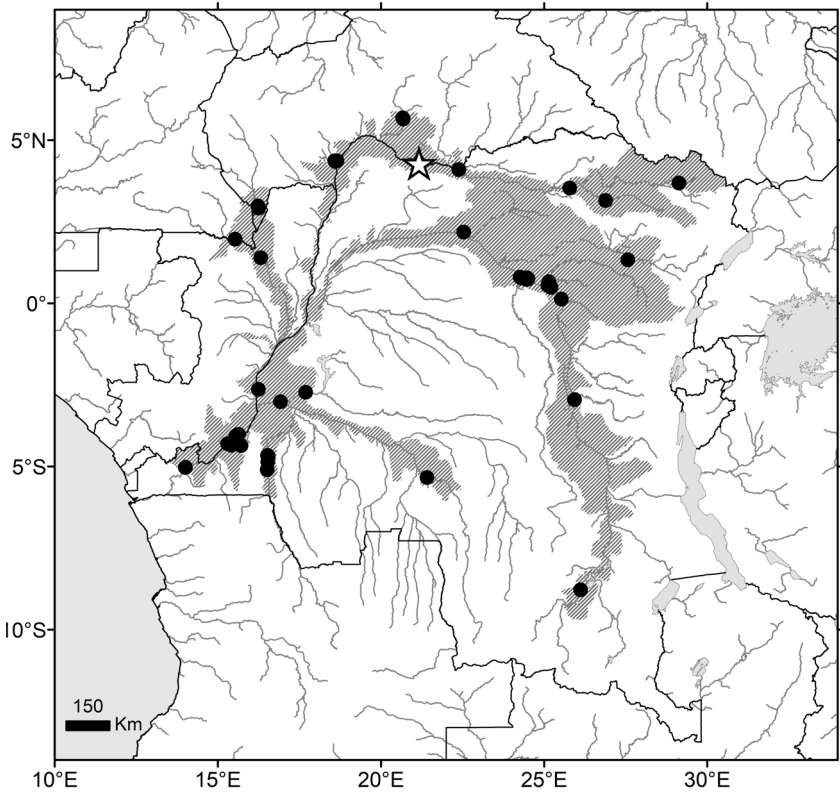


Figure 3-79. *Microthrissa royauxi*, distribution map.

Microthrissa whiteheadi Gourène & Teugels, 1988

Common names: Whitehead's sprat (E).

Description: body moderately deep, depth about 28-37% SL; scutes keeled, 1-2 before base of first pectoral-fin ray, 13-16 prepelvic and 5-9 postpelvic scutes; snout rounded; lower jaw not or slightly projecting, with small teeth limited to anterior part; premaxilla lacking a medial notch and with 32-40 small conical teeth directed inwards; maxilla blade slender, more than 5 times as long as deep, lower edge bordered with minute conical teeth; posterior supramaxilla about as long as maxilla blade, its shaft as long as its blade; 14-18 lower gill rakers; 35-39 scales in lateral series; 20-25 anal-fin rays (Gourène & Teugels 1988; 1989).

Maximum length: 5.7 cm SL (Gourène & Teugels 1988).

Colour: Preserved specimens: brownish-yellow, with eye, midlateral part of flanks and ventral region often silvery; flanks with a silvery longitudinal band, with a high concentration of melanophores on caudal part; base of each caudal lobe blackish (Gourène & Teugels 1988; 1989).

Distribution: Middle and Upper Congo River system up to the upper Lualaba, but absent from the Luapula-Mweru (Gourène & Teugels 1988; 1989). Mainly found in larger rivers including the Sangha, the Ubangi and its tributary Uélé, the Lulua (Kasai drainage), the confluence of the Lindi and Tshopo and from the Lualaba up to the Upemba region.

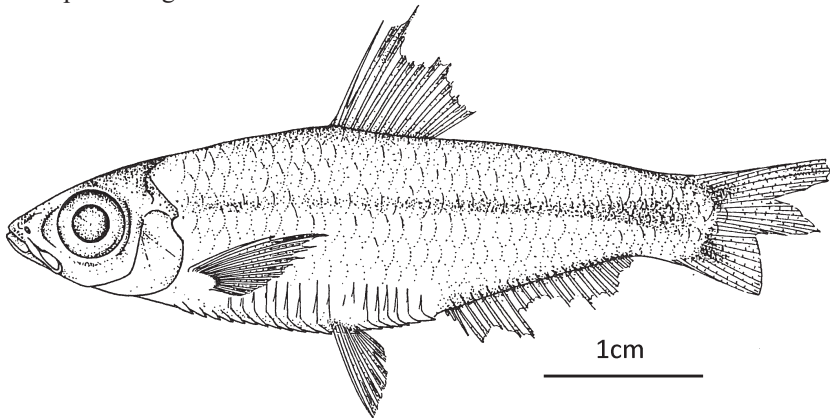


Figure 3-80. *Microthrissa whiteheadi*, holotype, 42.3 mm SL, Nyonga, DRC, RMCA 23240 (from Gourène & Teugels 1988).



Figure 3-81. *Microthrissa whiteheadi*, holotype, 42.3 mm SL, Nyonga, DRC, RMCA 23240. © RMCA.

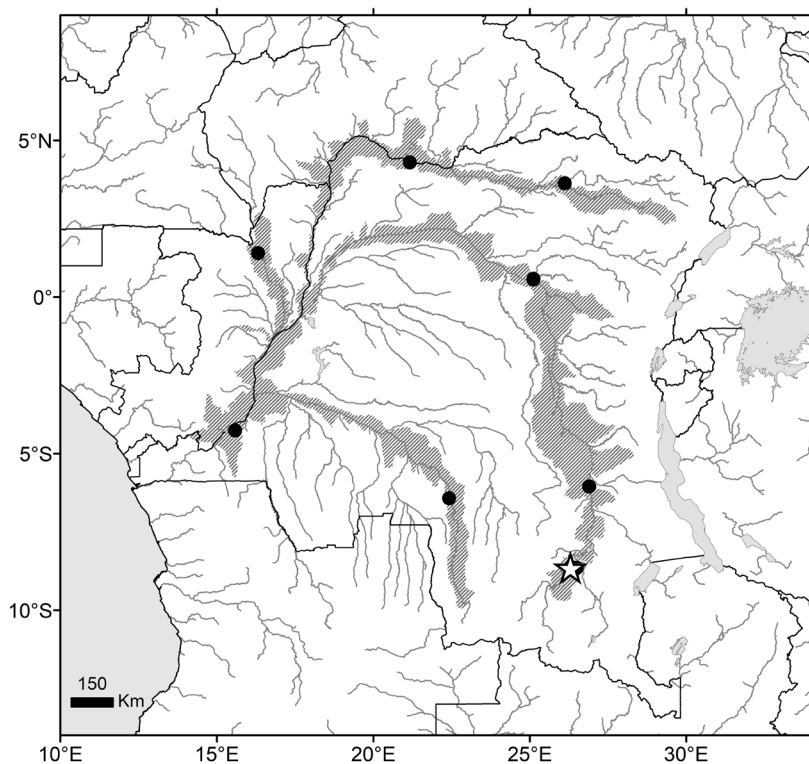


Figure 3-82. *Microthrissa whiteheadi*, distribution map.

Genus *Nannothrissa* Poll, 1965

The genus *Nannothrissa* contains two species (Froese & Pauly 2021). Both are found in freshwater and are endemic to the Congo River basin (Whitehead 1985). The maximum length of these dwarf species is 42 mm SL. The genus is characterised by the distinct and keeled prepelvic scutes, the deep maxillary blade without ridge, the diamond-shaped posterior supramaxilla and the toothless dentary and premaxilla (Whitehead 1985).

1a. 20-23 anal-fin rays; 24-31 lower gill rakers on first gill arch; 12-15 prepelvic scutes; 35-42 scales in lateral series *Nannothrissa parva*

1b. 17-19 anal-fin rays; 20-23 lower gill rakers on first gill arch; 9-10 prepelvic scutes; 34-35 scales in lateral series. *Nannothrissa stewarti*

Nannothrissa parva (Regan, 1917)

Common names: Lake Tumba dwarf sprat (E), Isandja (DRC), Mempesu (DRC).

Description: body slender, depth about 20% SL; scutes beginning at isthmus or just behind, very strongly keeled, 12-15 prepelvic and 6-8 postpelvic scutes; lower jaw projecting and toothless; no teeth on premaxilla or maxilla; posterior supramaxilla as deep as maxilla blade and with long, slender anterior shaft; 24-31 lower gill rakers; pelvic fin with 1 unbranched and 6-7 branched rays, inserted just before dorsal-fin origin; 20-23 anal-fin rays; 35-42 scales in lateral series (Regan 1917; Whitehead 1985).

Maximum length: 4.2 cm SL (Whitehead 1985).

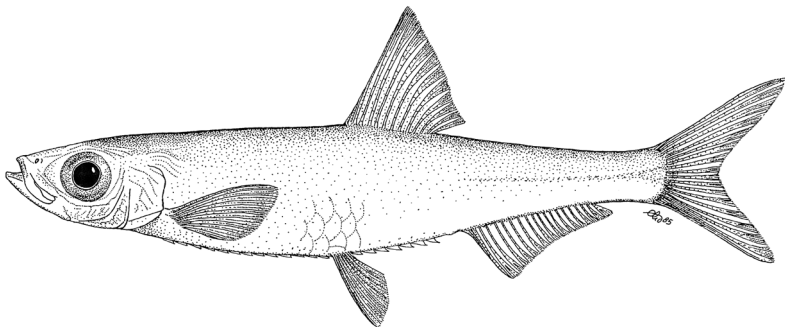


Figure 3-83. *Nannothrissa parva* (from Whitehead 1985).



Figure 3-84. *Nannothrissa parva*, Gumugu, Ubangi River, DRC, RMCA 166251-258. © RMCA.

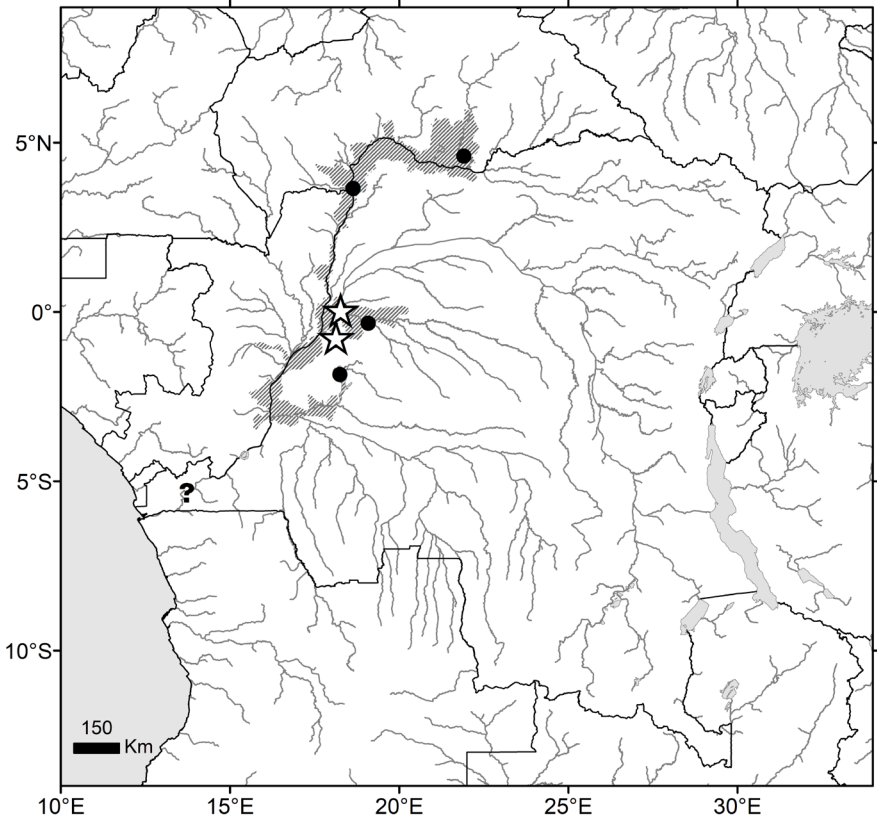


Figure 3-85. *Nannothrissa parva*, distribution map.

Colour: In life: more or less transparent, entirely silvery with pearly blue-green and pink reflections; dorsal region slightly darker; top of head, tip of snout and chin black; eye black; ventral scutes and base of unpaired fins black; pelvic and anal fins transparent; pectoral and dorsal fins slightly darkened; lobes of caudal fin black; faint black band on caudal peduncle, widening towards base of latter, clearly visible in preserved specimens (Matthes 1964).

Distribution: Middle Congo River basin, in Lakes Tumba and Mai-Ndombe and the rivers Ruki and Ubangi (Matthes 1964; Gosse 1968; Poll 1974; Gourène & Teugels 1994; Micha *et al.* 2020). Reported from near Kinganga in the Lower Congo River by Roberts & Stewart (1976), but not on the list of Lower Congo species of Lowenstein *et al.* (2011).

Nannothrissa stewarti Poll & Roberts, 1976

Common names: Mai-Ndombe dwarf sprat (E).

Description: body slender or moderate, depth about 25% SL; scutes a little behind isthmus, very strongly keeled, 9-10 prepelvic and 7-9 postpelvic scutes; lower jaw very slightly projecting, toothless; no teeth on premaxilla or maxilla; posterior supramaxilla as deep as maxilla blade and with long slender anterior shaft; 20-23 lower gill rakers; pelvic fin with 1 unbranched and 6-7 branched rays, inserted just below dorsal-fin origin; 17-19 anal-fin rays; 34-35 scales in lateral series (Poll & Roberts 1976; Whitehead 1985).

Maximum length: reported as 2.3 cm SL by Whitehead (1985); interestingly specimens of just over 7 cm SL were recently reported by Micha *et al.* (2020).

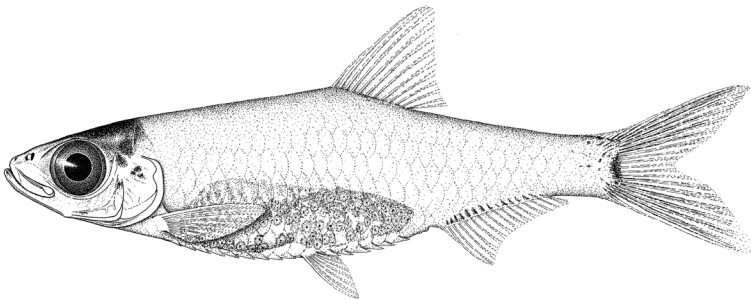


Figure 3-86. *Nannothrissa stewarti*, holotype, 22.5 mm SL, Lake Mai Ndombe or Inongo, near Ipeke, DRC, RMCA 75-50-P-1 (from Poll & Roberts 1976).



Figure 3-87. *Nannothrissa stewarti*, paratype, Lake Mai Ndombe, near Ipeke, DRC, RMCA 75-50-P-2-3. © RMCA.

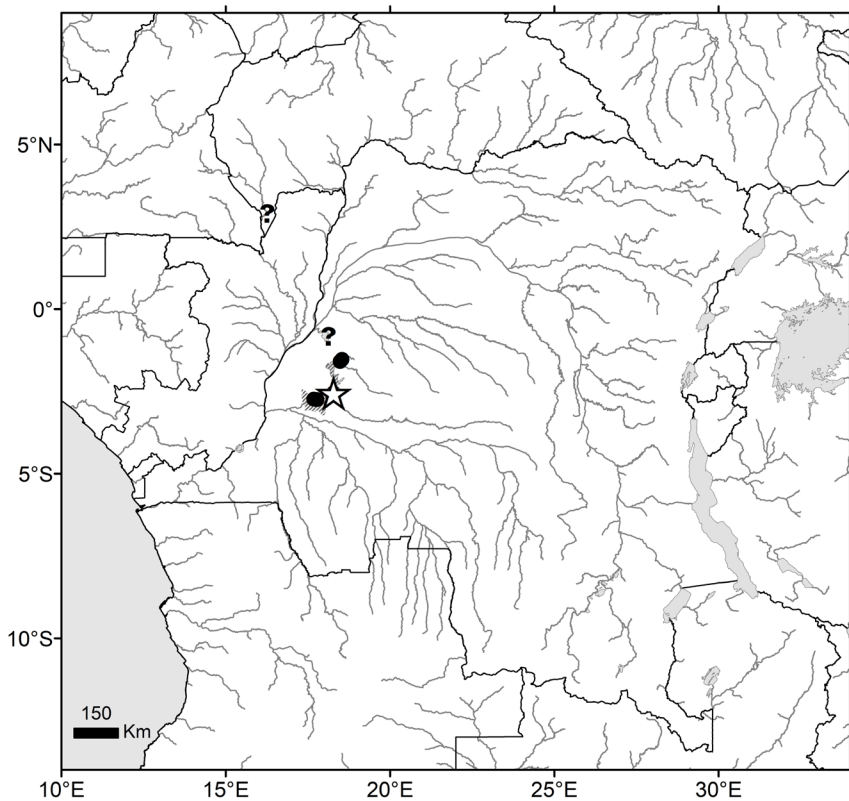


Figure 3-88. *Nannothrissa stewarti*, distribution map.

Colour: In life: characterised by pronounced bluish reflection on entire body (Poll & Roberts 1976). Preserved specimens: silvery, with faint black spot at base of caudal fin, a series of small black dots at origin of anal rays, blackish occiput and some small spots on opercular region (Poll & Roberts 1976).

Distribution: endemic to Lake Mai-Ndombe in the DRC (Poll & Roberts 1976; Gourène & Teugels 1994). Records from the Sangha River (AMNH collection) and Lake Tumba (AMNH collection, identified as *Nannothrissa* cf. *stewarti*) need confirmation.

Genus *Odaxothrissa* Boulenger, 1899

The genus *Odaxothrissa* contains three species (Gourène & Teugels 1991a; Froese & Pauly 2021) that can be found in rivers and lagoons in western Africa, from Senegal to Angola (Whitehead 1985). A fourth species of *Odaxothrissa* was reported from the Ebrié Lagoon in Côte d’Ivoire as *Cynothrissa* sp. by Daget & Iltis (1965) and Whitehead (1985), but this undescribed species was shown to be conspecific with *Odaxothrissa ansorgii* (Gourène & Teugels 1991a). The genus can be recognised by the keeled pre-pelvic scutes, the presence of strong canine teeth in the lower and upper jaws and by the lower gill rakers that are usually shorter than the corresponding gill filaments in adults (Whitehead 1985; Gourène & Teugels 1991a).

1a. no prepectoral scutes; premaxilla with 1-3 large canine teeth on each side, half-way along normal outer series (Figure 3-89A) *Odaxothrissa losera*

1b. prepectoral scutes present; premaxilla with 2-4 large canine teeth on each side, behind normal outer series of small teeth (Figure 3-89B) 2

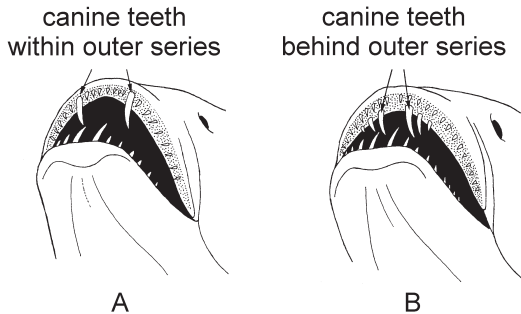


Figure 3-89. Canine teeth A) within or B) behind outer series of small teeth (from Whitehead 1985).

2a. 22-33 lower gill rakers on first gill arch; first prepectoral scute longer and more developed than subsequent scutes that lack ascending arms . *Odaxothrissa ansorgii*

2b. 16-19 lower gill rakers on first gill arch; first prepectoral scute as long as or smaller than subsequent scutes that lack ascending arms. . . *Odaxothrissa mento*

 ***Odaxothrissa ansorgii*** Boulenger, 1910

Common names: Ansorge fangtooth pellowline (E), Mabemba (Angola), Issiga (Gabon).

Description: body moderate, often deep, its depth 25% SL or more; 13-17 pre-pelvic and 8-11 postpelvic scutes, 1-2 prepectoral scutes, first prepectoral scute longer and more developed than following scutes without ascending arms; lower jaw strongly projecting, with strong canine teeth at symphysis; premaxilla with 2-4 strong backward-pointing canine teeth on each side behind outer row of premaxillary teeth; 22-33 lower gill rakers, shorter than corresponding gill filaments; 17-21 anal-fin rays; silver stripe along flank (Whitehead 1985; Gourène & Teugels 1991a; Teugels 2007).

Maximum length: 13.0 cm SL (Whitehead 1985).

Colour: In life: upper half of body, dorsal fin and base of caudal fin pale olive-green; lower half and other fins white; broad silvery band along each side (Boulenger 1910). Preserved specimens: generally light yellowish-grey, or yellowish-brown; gill cover, longitudinal stripe and ventral region much lighter (Gourène & Teugels 1991a, 2003; Teugels 2007).

Distribution: western Africa, from the lower Senegal River to the Cuanza in Angola (Whitehead 1985, Gourène & Teugels 1994; Skelton 2019), including lagoons in Côte d'Ivoire, the Niger Delta, the Ogowe, lower Kouilou and Lower Congo (Gourène & Teugels 1991a, 2003; Teugels 2007). Reports from upstream of Pool Malebo in the Congo River basin (Likouala-aux-herbes River, AMNH collection, and Lake Mai-Ndombe, RMCA collection) need confirmation.

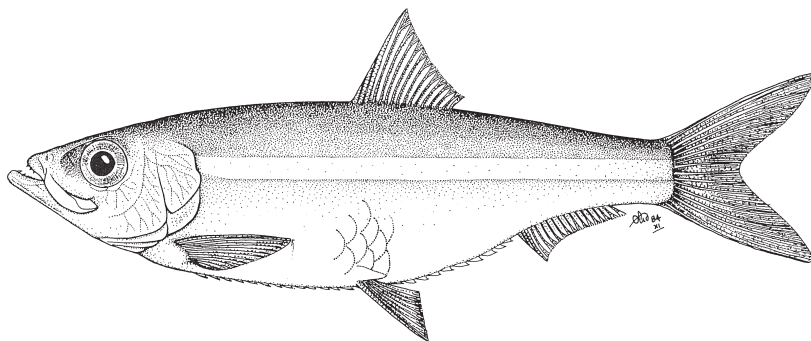


Figure 3-90. *Odaxothrissa ansorgii* (from Whitehead 1985).

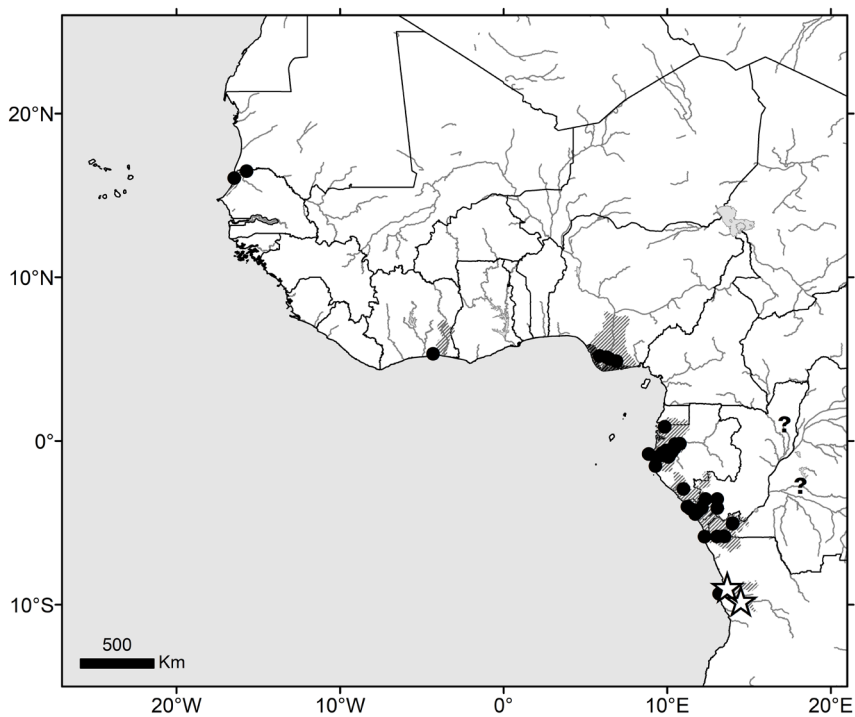


Figure 3-91. *Odaxothrissa ansorgii*, distribution map.



Figure 3-92. *Odaxothrissa ansorgii*, Pelican River, Ogove River basin, Gabon, RMCA 2000-048-P-1279. © RMCA.

Odaxothrissa losera Boulenger, 1899

Common names: Losera fangtooth pellowline (E), Losera (Republic of the Congo), Luhelele (Republic of the Congo), Itetembu (DRC), Litembu (DRC).

Description: body slender or moderately deep, its depth about 22-29% SL; 10-14 prepelvic and 7-10 postpelvic scutes, no prepectoral scutes, first scute beginning slightly before or behind base of last pectoral-fin ray and identical as following scutes without ascending arms; lower jaw strongly projecting, with strong canine teeth at symphysis; premaxilla with one large backward-pointing canine tooth on each side, about halfway along normal premaxillary series, rarely 1-2 smaller ones beside or a little behind it; 18-29 lower gill rakers, shorter than corresponding gill filaments, anterior ones reduced to stumps in large adults; 19-24 anal-fin rays; silver stripe along flank (Whitehead 1985; Gourène & Teugels 1991a).

Maximum length: 14.4 cm SL (Gourène & Teugels 1991a).

Colour: In life: upper part olive-brown, lower part whitish; ventral side of head pinkish; a more or less distinct silvery lateral band; fins olive; iris silver (Boulenger 1899; 1909). Preserved specimens: general colouration ranging from light yellow-brown to grey yellow-brown, with operculum, ventral region and middle of flanks lighter (Gourène & Teugels 1991a).

Distribution: widely distributed in the Congo River basin (Gourène & Teugels 1991a), from its mouth to the Upemba region in the Upper Congo basin, including the Sangha and Ubangi (Roberts & Stewart 1976; Banister & Bailey 1979; Whitehead 1985), but largely absent from the Kasai drainage and not recorded from the Luapula-Mweru.

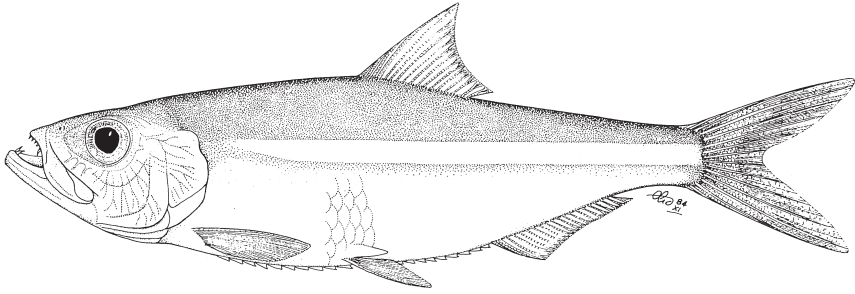


Figure 3-93. *Odaxothrissa losera* (from Whitehead 1985).

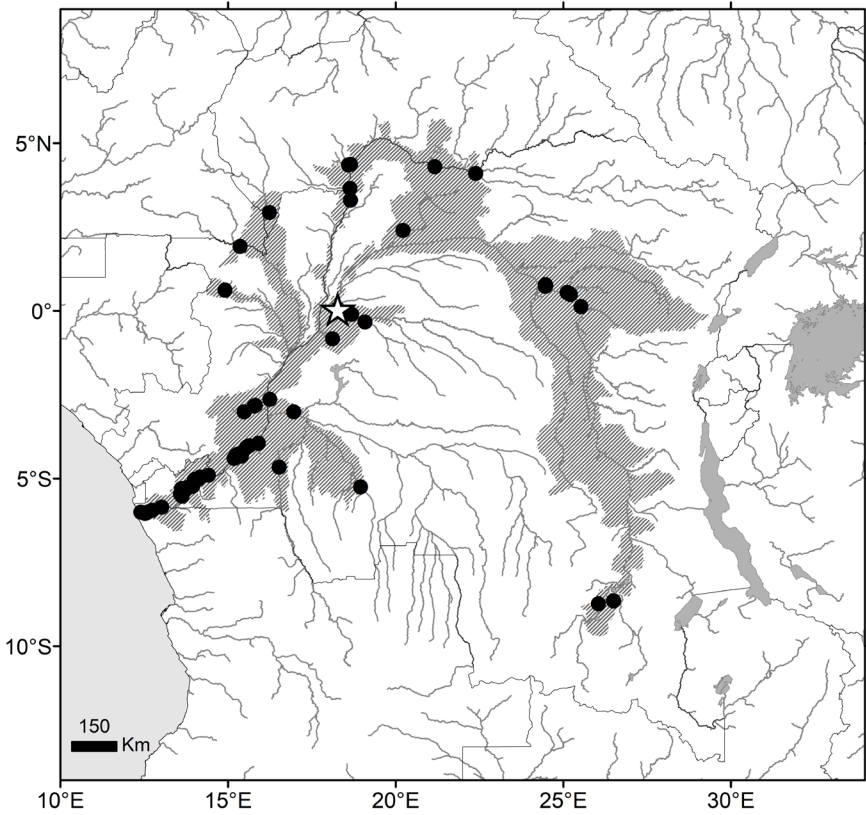


Figure 3-94. *Odaxothrissa losera*, distribution map.



Figure 3-95. *Odaxothrissa losera*, Landjia, Ubangi River, Central African Republic, RMCA 82-13-P-1590. © RMCA.

Odaxothrissa mento (Regan, 1917)

Common names: Nigerian fangtooth pellowuline (E), Deyi (Ghana), Sardine (Ghana), Agadagba (Nigeria), Ntita (Nigeria), Salanpore (Nigeria), Taga rana (Nigeria), Worongi (Nigeria).

Description: body moderately deep to deep, its depth 25% SL or more; 13-18 prepelvic and 8-10 postpelvic scutes, 1-2 scutes before pectoral-fin origin, first prepectoral scute as long as, or smaller than, following scutes without ascending arms; lower jaw strongly projecting, with strong canine teeth at symphysis; premaxilla with 2-4 strong backward-pointing canine teeth on each side behind outer row of premaxillary teeth; 16-19 lower gill rakers, shorter than corresponding gill filaments; 18-21 anal-fin rays; silver stripe along flank (Whitehead 1985; Gourène & Teugels 1991a; Teugels 2007).

Maximum length: 14.0 cm SL (Reynolds 1969).

Colour: Preserved specimens same colour as *Odaxothrissa ansorgii* (Gourène & Teugels 2003; Teugels 2007): general colour light yellow-brown to grey yellow-brown; operculum, longitudinal stripe and ventral region silvery coloured or much lighter (Gourène & Teugels 1991a).

Distribution: Volta basin and lower parts of the Niger (Whitehead 1985; Gourène & Teugels 1991a), including the Benue River (Gourène & Teugels 2003). Also present in the Cross and the Wouri River in Cameroon (Whitehead 1985; Teugels 2007).

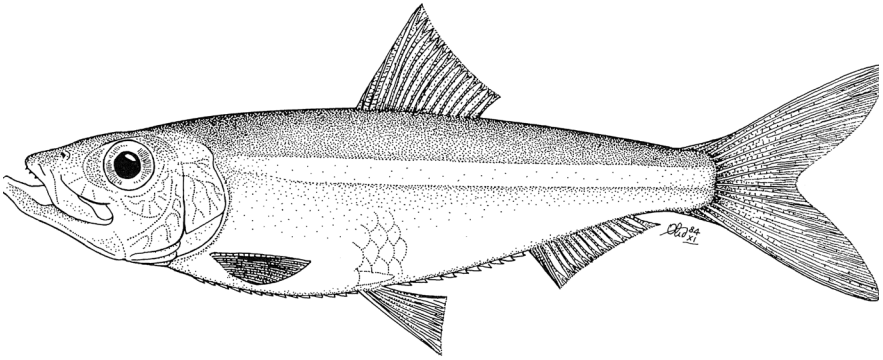


Figure 3-96. *Odaxothrissa mento* (from Whitehead 1985).

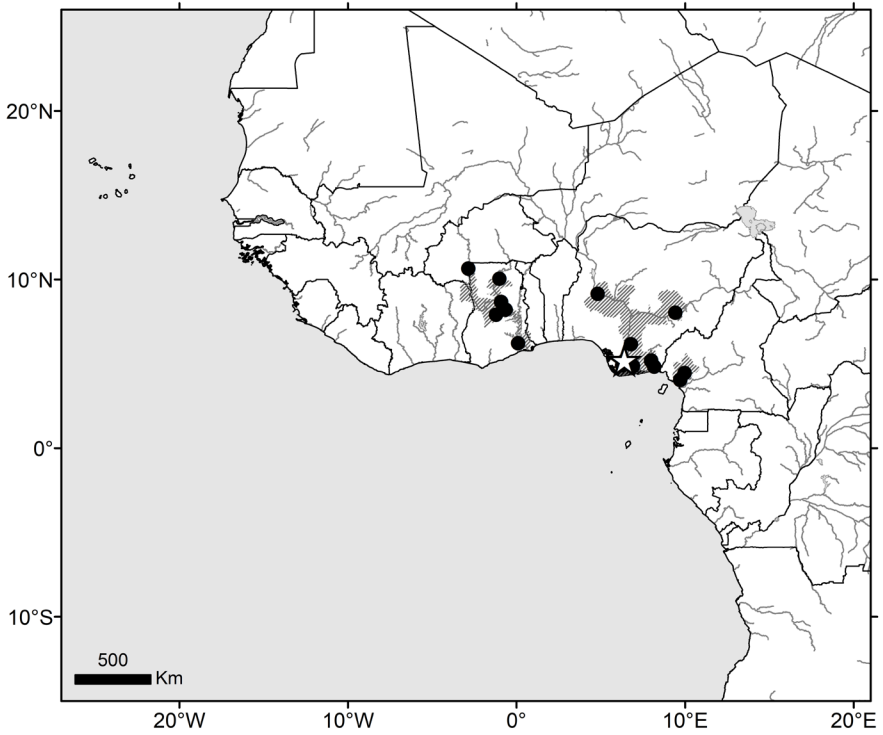


Figure 3-97. *Odaxothrissa mento*, distribution map.



Figure 3-98. *Odaxothrissa mento*, Yeji, Lake Volta, Ghana, RMCA 91-103-P-0001-0003. © RMCA.

Genus *Pellonula* Günther, 1868

The genus *Pellonula* contains two species (Gourène & Teugels 1991b; Froese & Pauly 2021). They are found in rivers in western Africa, from Senegal to Angola, sometimes entering brackish water of estuaries and lagoons (Whitehead 1985; Gourène & Teugels 1991b). Species of *Pellonula* have a deep maxillary blade without ridge on the upper edge, a diamond-shaped posterior supramaxilla, a premaxilla (and dentary) with relatively well-developed but not large canine teeth and lower gill rakers that are equal to or longer than the corresponding gill filaments; juveniles of *Pellonula* are sometimes mistaken for *Sierrathrissa leonensis*, but *Pellonula* has keeled scutes with lateral arms, pelvic fins with 1 unbranched and 7 branched rays and a pelvic fin inserted more or less below the dorsal-fin origin (Whitehead 1985).

1a. no scutes in front of base of first pectoral-fin ray; first prepelvic scute, without ascending arms, as long as subsequent scutes without ascending arms; premaxilla with small inward pointing teeth (Figure 3-99A). *Pellonula leonensis*

1b. one or more scutes in front of base of first pectoral-fin ray; first prepelvic scute, without ascending arms, longer and more developed than subsequent scutes without ascending arms; premaxilla with well-developed outward pointing teeth (Figure 3-99B) *Pellonula vorax*

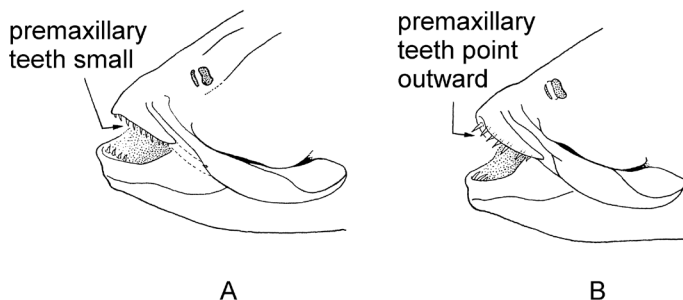


Figure 3-99. Premaxillary teeth A) pointing inward in *P. leonensis* and B) pointing outward in *Pellonula vorax* (from Whitehead 1985).

Pellonula leonensis Boulenger, 1916

Common names: Smalltoothed pellonula (E), Spratelle de Guinée (F), Sardinita guineana (S), Nzombimbi (Gabon), Osendjélè (Gabon), Sardine (Ghana), Totivi (Ghana), Espadilha-da-Guiné (Guinea-Bissau), Banabanagi (Nigeria), Isoun (Nigeria), Ntita (Nigeria), Salanpore (Nigeria), Taga rana (Nigeria), Waranga (Nigeria), Worongi (Nigeria).

Description: body slender to moderately deep, its depth 17-30% SL; scutes starting behind base of first pectoral-fin ray, 8-15 prepelvic and 6-10 postpelvic scutes, and a total of 17-23 scutes; first prepelvic scute, without ascending arms, as long as subsequent scutes without ascending arms; lower jaw very slightly projecting, teeth at symphysis only slightly enlarged; premaxillary teeth small and inward pointing, only the tips usually apparent, no strongly marked indentation at centre of jaw; 20-35 lower gill rakers, equal to or longer than corresponding gill filaments; silver stripe along flank (Whitehead 1985; Gourène & Teugels 1991b; Teugels 2007).

Maximum length: 12.1 cm TL (Daget & Iltis 1965).

Colour: Preserved specimens very similar in colour to *Pellonula vorax* (Gourène & Teugels 2003; Teugels 2007): variable ground colour, from yellow-brown to yellow-grey; operculum, ventral region and flanks usually lighter (Gourène & Teugels 1991b). Silver stripe along flank (Boulenger 1916; Whitehead 1985).

Distribution: lagoons, lakes, lower and upper courses of rivers of West Africa (Gourène & Teugels 1991b; 2003) and Lower Guinea (Gourène & Teugels 1991b; Teugels 2007), from the Senegal to the Congo River, including upper reaches of the Niger and Benue (Whitehead 1985; Gourène & Teugels 2003) and the Lake Chad basin (Gourène & Teugels 2003). In the Congo restricted to the lower basin. Specimens from the Léfini River (Middle Congo basin in the Republic of the Congo) (Ibala Zamba 2010) do not belong to this genus and have tentatively been reidentified as *Potamothrissa* sp.

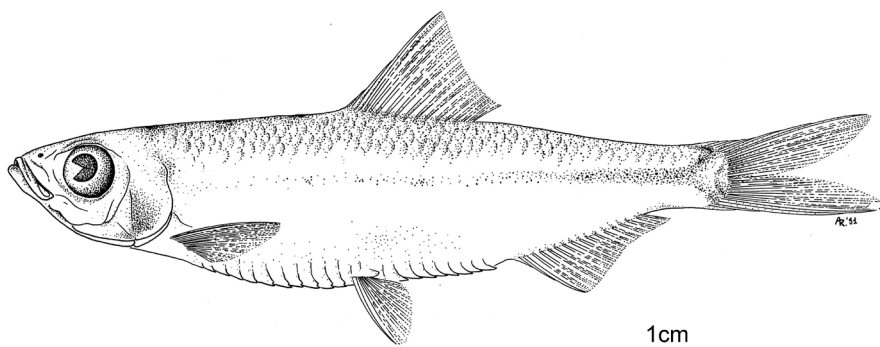


Figure 3-100. *Pellonula leonensis*. Drawing by A. Reygel. © RMCA.



Figure 3-101. *Pellonula leonensis*, Noubi River at Noubi, Republic of Congo, RMCA 2004-046-P-1461-1470. © RMCA.

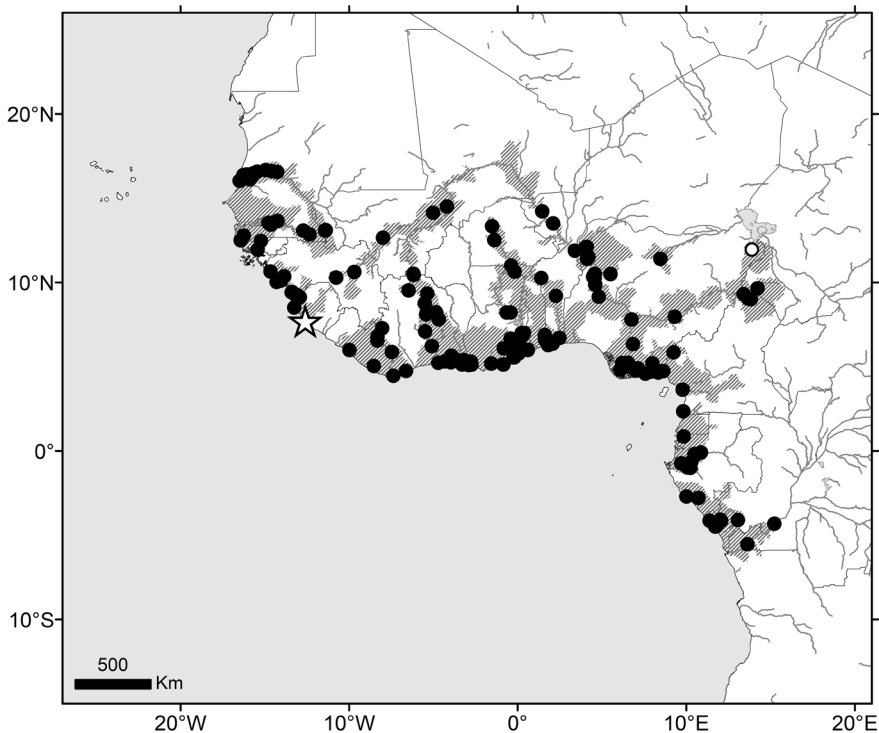


Figure 3-102. *Pellonula leonensis*, distribution map.

Pellonula vorax Günther, 1868

Common names: Bigtoothed pellonula (E), Gbodo (Benin), Honoumassaè (Benin), Mbia (Côte d'Ivoire), Isiga (Gabon), Nzombimbi (Gabon), Osendjele (Gabon), Sardine (Gabon, Senegal), Amoni (Ghana), Isoun (Nigeria), Ntita (Nigeria), Salanpore (Nigeria), Taga rana (Nigeria), Worongi (Nigeria), Njasaan (Senegal), Pellonale (Senegal), Samba amul kawar (Senegal), Sprat (Senegal).

Description: body moderate or fairly deep, its depth 23-30% SL; 1 or more scutes beginning in front of base of first pectoral-fin ray, with 11-16 prepelvic and 8-11 postpelvic scutes, and a total of 20-25 scutes; first prepelvic scute, without ascending arms, longer and more developed than subsequent scutes without

ascending arms; lower jaw slightly projecting, teeth at symphysis large in large specimens; premaxillary teeth well-developed, fairly straight and outward pointing, an indented toothless gap at centre of jaw; 24-37 lower gill rakers, equal to or longer than corresponding gill filaments; silver stripe along flank (Whitehead 1985; Gourène & Teugels 1991b; Teugels 2007).

Maximum length: 12.0 cm SL (Whitehead 1985).

Colour: Preserved specimens: ground colour variable, yellow-brown to yellow-grey; operculum, ventral region and flanks usually lighter (Gourène & Teugels 1991b, 2003; Teugels 2007). Silver stripe along flank (Whitehead 1985).

Distribution: lagoons and lower parts of rivers in western Africa, from Guinea-Bissau to Angola (Lévêque *et al.* 1989; Gourène & Teugels 1991b, 2003; Teugels 2007). Usually not observed far upstream in rivers (Gourène & Teugels 1991b). Report from the Middle Niger (Jebba; NHMUK 1899.8.23.63-65) needs confirmation. Specimens from the Léfini River (Middle Congo basin in the Republic of the Congo) (Ibala Zamba 2010) do not belong to this genus and have tentatively been reidentified as *Potamothrissa* sp.

Note: The type locality of the syntypes of the synonym *Pellonula stanleyana*, Stanley Falls in the Democratic Republic of the Congo (Regan 1917), seems to be erroneous and should be 'Cette Cama [= Sette Cama]' in Gabon (Whitehead 1985; Gourène & Teugels 1991b).

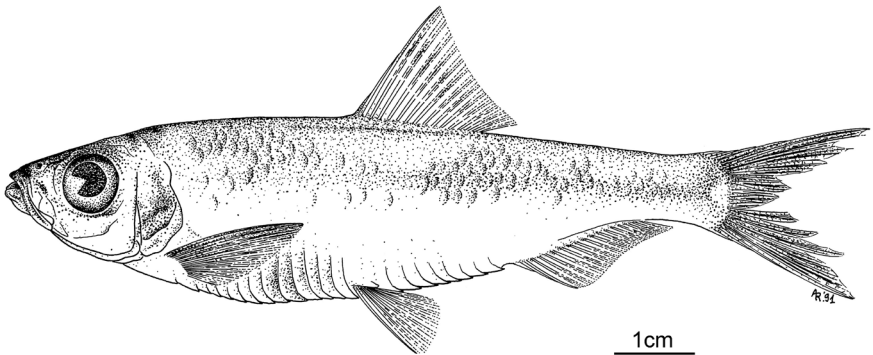


Figure 3-103. *Pellonula vorax*. Drawing by A. Reygel. © RMCA.



Figure 3-104. *Pellonula vorax*, Nkomi lagoon, St. Anne jetty, Ogove River basin, Gabon, RMCA 2000-048-P-1170-1190. © RMCA.

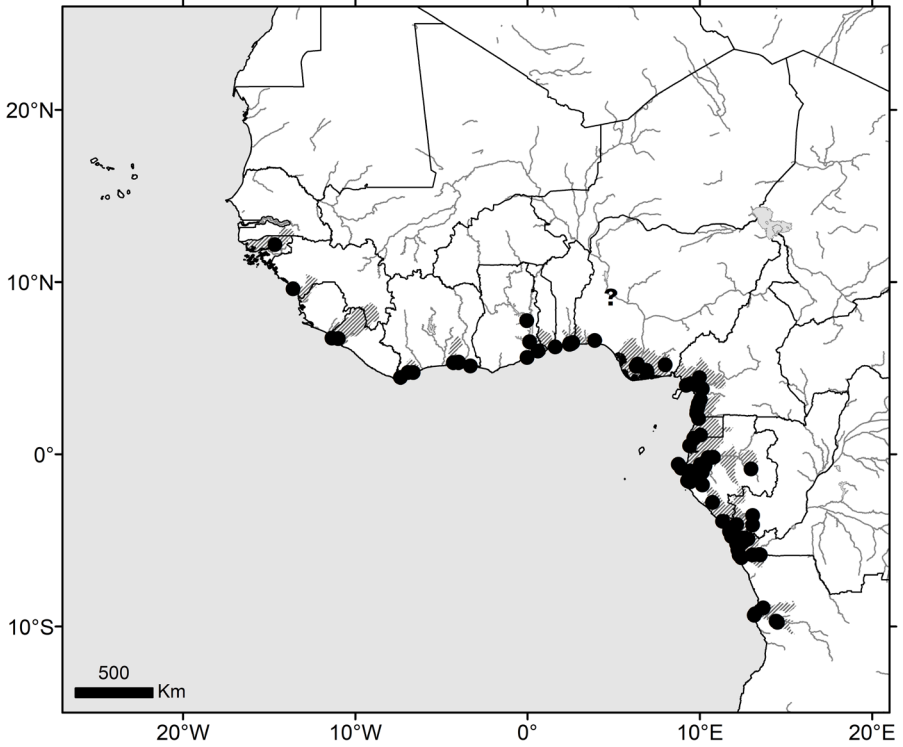


Figure 3-105. *Pellonula vorax*, distribution map.

Genus *Potamothrissa* Regan, 1917

The genus *Potamothrissa* contains three species (Froese & Pauly 2021), endemic to the Congo basin (Whitehead 1985). They are characterised by a slender lower jaw with moderately sized teeth along its length (from its symphysis to the back), which is highly unusual in clupeid fishes, giving the dentition a sawlike appearance; similar but smaller teeth (on a deep lower jaw) occur in *Limnothrissa* (Whitehead 1985).

- 1a. snout acutely pointed; 11-13 prepelvic scutes, first scute situated under or just before base of first pectoral-fin ray *Potamothrissa acutirostris*
- 1b. snout bluntly rounded; 7-10 prepelvic scutes, first scute situated under or behind base of last pectoral-fin ray 2

- 2a. small dermal denticles on snout and border of mouth; 6-9 postpelvic scutes; posterior supramaxilla minute, virtually without anterior shaft.
. *Potamothrissa whiteheadi*
- 2b. no dermal denticles on snout and border of mouth; 9-12 postpelvic scutes; posterior supramaxilla small, shaft about as long as blade *Potamothrissa obtusirostris*

***Potamothrissa acutirostris* (Boulenger, 1899)**

Common names: Sharpnosed sawtooth pellonuline (E), Lifambalamba (DRC), Chisense (Zambia).

Description: body slender, depth 19-27% SL; prepelvic scutes fairly strongly keeled, beginning under or just before pectoral-fin base, 11-13 prepelvic and 10-12 postpelvic scutes; snout pointed; lower jaw not projecting, included in upper when mouth closed, deepest at midpoint of jaw, with small teeth along length of lower jaw, dentition sawlike; premaxilla with peglike teeth, those near midline pointing forward; maxilla very slender, toothless, its blade over 3 times as long as deep, upper edge ridged; posterior supramaxilla very small, spatulate, shaft about as long as blade; 16-18 lower gill rakers (Whitehead 1985). No dermal denticles on snout and border of mouth (Poll 1974).

Maximum length: 7.0 cm SL (Whitehead 1985).

Colour: In life: olive dorsally, whitish ventrally, with silvery lateral band; sometimes a large steel blue spot on gill cover and scapular region, and another at base of caudal fin; iris silvery, with yellow circle around pupil, which is elongated vertically (Boulenger 1899; 1909). Preserved specimens: black spot on operculum and scapular region (Boulenger 1899).

Distribution: widespread in the Congo basin (Whitehead 1985; Gourène & Teugels 1994), including the Sangha, Ubangi, Ruki and lower courses of the Kasai system (Gosse 1968; Poll 1974). Reported to be present in Lake Mweru (Poll 1933; De Kimpe 1964; Bell-Cross 1965), but no preserved specimens are available. Absent from the upper courses of the Kasai system and the Lualaba upstream of Ankoro.

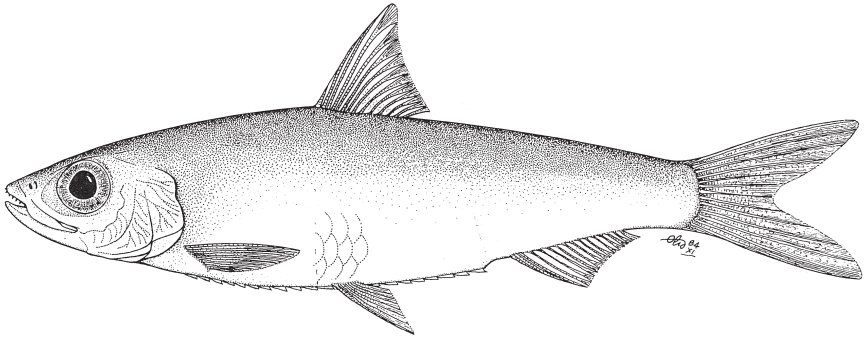


Figure 3-106. *Potamothrissa acutirostris*
(from Whitehead 1985).



Figure 3-107. *Potamothrissa acutirostris*, in front of Bokewaka,
Congo River, DRC, RMCA 120365-366. © RMCA.

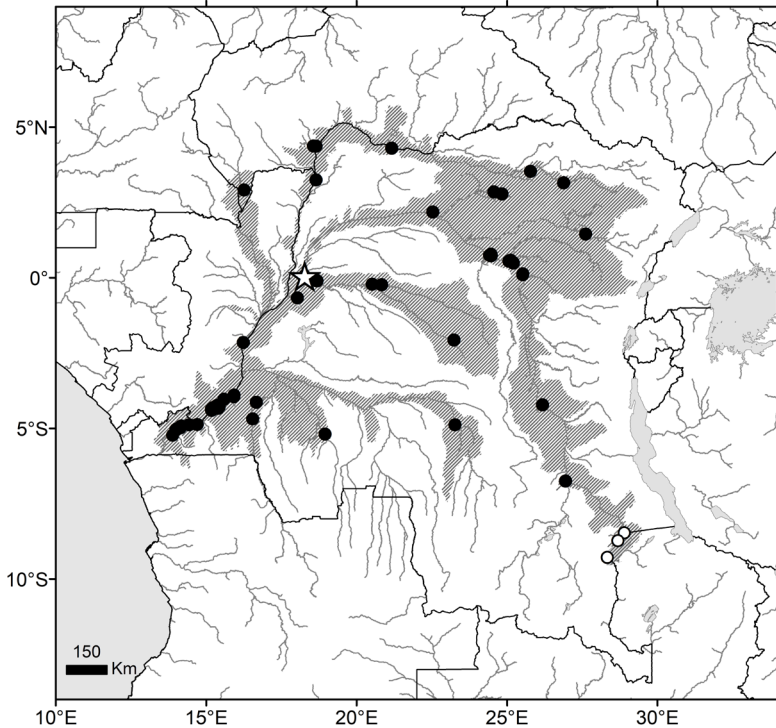


Figure 3-108. *Potamothrissa acutirostris*, distribution map.

■ *Potamothrissa obtusirostris* (Boulenger, 1909)

Common names: Blunt-nosed sawtooth pellonuline (E), Isandja (DRC), Ititili (DRC), Lotili (DRC).

Description: body slender, depth 18-27% SL; prepelvic scutes not strongly keeled, beginning under or behind base of last pectoral-fin ray, 7-10 prepelvic and 9-12 postpelvic scutes; belly rounded; snout bluntly rounded; lower jaw not projecting, exactly meeting tip of upper when mouth closed, deepest at midpoint of jaw, with small teeth along length of lower jaw, dentition sawlike; premaxilla with small teeth not pointing forward; maxilla very slender, toothless, its blade over 3 times as long as deep, upper edge ridged; posterior supramaxilla very small, spatulate, shaft

about as long as blade; 14-16 lower gill rakers; silver stripe on flank, narrower anteriorly; no dermal denticles on snout or edge of mouth (Whitehead 1985; Gourène & Teugels 1994).

Maximum length: 6.0 cm SL (Whitehead 1985).

Colour: Preserved specimens: body yellowish, head silvery (Boulenger 1909). Broad, silvery lateral band on flank, narrower anteriorly (Boulenger 1909; Whitehead 1985).

Distribution: widespread in the Congo basin (Poll 1974; Gourène & Teugels 1994), including the Ubangi (Gosse 1968; Poll 1974) and Ruki drainages (Matthes 1964; Monsembula Iyaba & Stiassny 2013) and lower courses of the Kasai system. Not recorded from the upper courses of the Kasai system, the Lualaba upstream of Ankoro and the Luapula-Mweru.

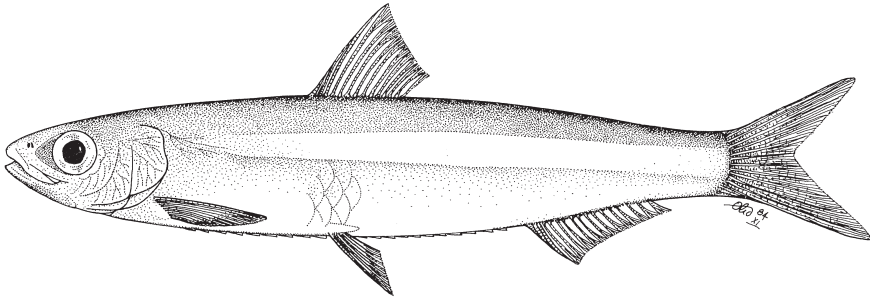


Figure 3-109. *Potamothrissa obtusirostris* (from Whitehead 1985).



Figure 3-110. *Potamothrissa obtusirostris*, Oso River, about 334 kilometres on Lubutu-Bukavu road, DRC, RMCA 89-43P-271-276. © RMCA.

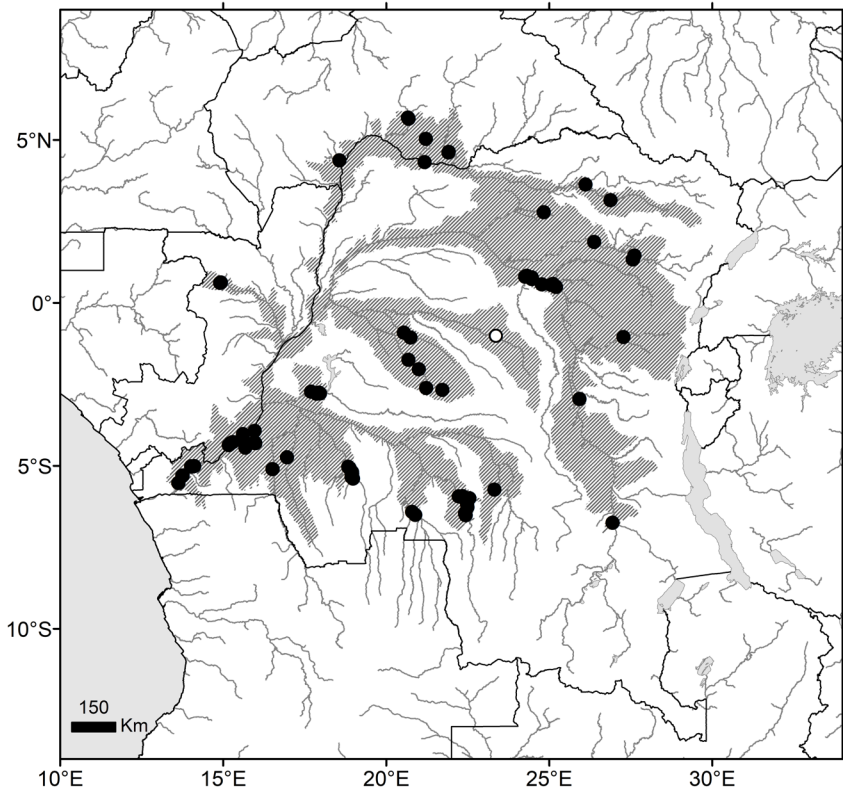


Figure 3-111. *Potamothrissa obtusirostris*, distribution map.

***Potamothrissa whiteheadi* Poll, 1974**

Common names: Whitehead's sawtooth pellowline (E).

Description: body slender, depth 22-25% SL; prepelvic scutes not strongly keeled, beginning under or behind base of last pectoral-fin ray, 8-10 prepelvic and 6-9 post-pelvic scutes; belly rounded; snout bluntly rounded; lower jaw not projecting, exactly meeting tip of upper jaw when mouth closed, deepest at midpoint of jaw, with small teeth along length of jaw, dentition sawlike; premaxilla with small teeth not pointing forward; maxilla very slender, toothless, its blade over 3 times as long as deep, upper edge ridged; posterior supramaxilla minute, virtually without anterior

shaft; 14-17 lower gill rakers; silver stripe along flank, narrower anteriorly (Whitehead 1985; Gourène & Teugels 1994). Snout and edges of mouth with small horny denticles on skin of maxillary (Poll 1974; Whitehead 1985).

Maximum length: 4.7 cm SL (Whitehead 1985).

Colour: Preserved specimens: silvery, especially a lateral band with an underlying pigmented band, narrower anteriorly, more marked on the dorsum; weak pigmentation at base of caudal fin and on both lobes; snout and occiput weakly pigmented (Poll 1974; Whitehead 1985).

Distribution: only known from the Hombo River (Lowa River tributary, Upper Congo basin, DRC) (Poll 1974; Whitehead 1985; Gourène & Teugels 1994). Report from the Lindi-Tshopo by Decru *et al.* (2017) erroneous, based on an error in genus name and referring to *Microthrissa whiteheadi* (Decru, pers. comm.).

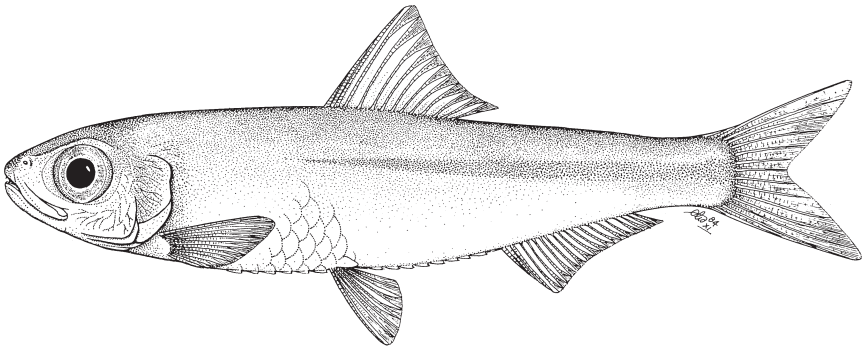


Figure 3-112. *Potamothrissa whiteheadi* (from Whitehead 1985).



Figure 3-113. *Potamothrissa whiteheadi*, paratype, Hombo River, affluent of Luhoho River, DRC, RMCA 188673-682. © RMCA.

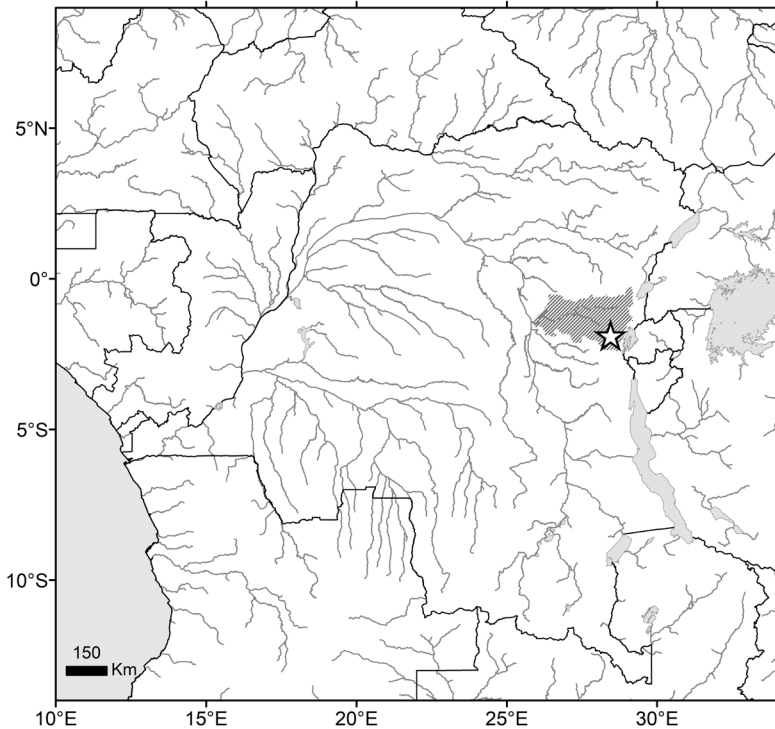


Figure 3-114. *Potamothrissa whiteheadi*, distribution map.

Genus *Sardinella* Valenciennes, 1847

The genus *Sardinella* contains 22 species (Froese & Pauly 2021) and is characterised by the presence of an anterior and posterior supramaxilla, with the lower part of the posterior supramaxilla as long as the upper part, a smooth operculum without bony striae, the presence of two fleshy outgrowths on the posterior margin of the gill opening, 7-14 frontoparietal striae on top of the head and the overlap of the paired predorsal scales in the midline (Whitehead 1974a; 1985). Species of the genus *Sardinella* are marine, pelagic and schooling. They occur on both sides of the Atlantic Ocean, in the Mediterranean Sea and in the tropical and subtropical parts of the Indo-West Pacific

region (Whitehead 1985; Whitehead & Wongratana 1986a). One species, *Sardinella maderensis*, enters estuaries along the Mediterranean and East Atlantic African coast south to Angola, while three others are classified here as marine stragglers. Two of these, *S. aurita* and *S. rouxi*, also occur along the Atlantic coast of western Africa (Gourène & Teugels 2003), while the third, *S. melanura*, is found in the Indian Ocean along the coasts of eastern Africa and Madagascar (Whitehead 1985).

1a. pelvic fin with 1 unbranched and 8 branched rays; black spot on posterior part of operculum *Sardinella aurita* *

1b. pelvic fin with 1 unbranched and 7 branched rays; no black spot on posterior part of operculum, sometimes faint gold or black area just behind operculum. 2

2a. 30-40 gill rakers on lower limb of first gill arch; caudal fin pale yellow with distal margin dusky *Sardinella rouxi* *

2b. 38-166 gill rakers on lower limb of first gill arch; caudal fin with black tips . . . 3

3a. 70-166 gill rakers on lower limb of first gill arch; black spot at base of anterior dorsal-fin rays (western Africa, Atlantic Ocean) *Sardinella maderensis*

3b. 38-74 gill rakers on lower limb of first gill arch; no black spot at base of anterior dorsal-fin rays (eastern Africa, Indo-West Pacific Ocean). . *Sardinella melanura* *

Sardinella maderensis (Lowe, 1838)

Common names: Madeiran sardinella (E), Grande allache (F), Machuelo (S), Latcha (Algeria), Salaga (Algeria), Sarakin (Algeria), Palheta (Angola), Sardinela (Angola, Guinea-Bissau), Sardinha (Angola, Cape Verde, São Tomé e Príncipe), Sardinha-arinca (Angola), Sardinha-palheta (Angola, Guinea-Bissau), Manhounvi (Benin), Maoun (Benin), Arenque (Cape Verde), Sardinela da Madeira (Cape Verde), Sardinha da Madeira (Cape Verde), Makouala (Republic of the Congo), Agouwa (Côte d’Ivoire), Djandjerema (Côte d’Ivoire), Egreka kragpe (Côte

d'Ivoire), Gran (Côte d'Ivoire), Ofo (Côte d'Ivoire), Oofo (Côte d'Ivoire), Sardin madiera (Egypt), Sardina mifattara (Egypt), Adruku (Ghana), Antebo (Ghana), Bonga séri (Guinea), Sardinela-da-Madeira (Guinea-Bissau), Machoello (Mauritania), Sardinelle plate (Mauritania), Tayit (Mauritania), Téryit (Mauritania), Yabotass (Mauritania, Senegal), Madeiran sardinelle (Namibia, South Africa), Madeira-sardinelle (Namibia, South Africa), Eba (Senegal), Itass (Senegal), Yabóy tas (Senegal), Yayeboyo (Senegal), Yèssou yaboï (Senegal), Herring (Sierra Leone), Adroukou (Togo), Deyi (Togo), Hareng (Togo), Manvi (Togo), Mâvi (Togo).

Description: body elongate but variable in depth; belly fairly sharply keeled; 14-20 prepelvic and 12-15 postpelvic scutes, 31-34 in total; 70-166 lower gill rakers, increasing with growth; upper pectoral-fin rays white on outer side, membrane black (Whitehead 1985; Whitehead & Wongratana 1986a; Gourène & Teugels 2003). Pelvic fin with 1 unbranched and 7 branched rays; faint golden or blackish area just behind gill opening; caudal fin grey, its tips almost black; black spot at base of anterior dorsal-fin rays (Whitehead 1981, 1985; Gourène & Teugels 2003).

Maximum length: 30.0 cm SL (Whitehead 1985).

Colour: Preserved specimens: body silvery (Gourène & Teugels 2003; Teugels 2007). Upper pectoral-fin rays externally white, membranes black; caudal fin greyish with black tipped lobes; no postopercular spot, but golden or sometimes blackish area just behind gill opening (Gourène & Teugels 2003; Teugels 2007).

Distribution: southern and eastern parts of the Mediterranean Sea, also penetrating the Suez Canal (Whitehead 1985; Quignard & Tomasini 2000), and eastern Atlantic Ocean, from Gibraltar southward to Angola; a single recorded specimen from Walvis Bay in Namibia (Whitehead 1985; 1990; Gourène & Teugels 2003; Teugels 2007).



Figure 3-115. *Sardinella maderensis*. Picture by Etrusko25.

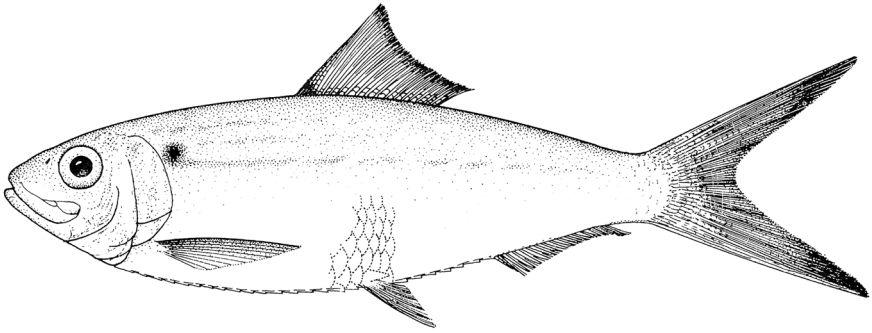


Figure 3-116. *Sardinella maderensis* (from Whitehead 1985).

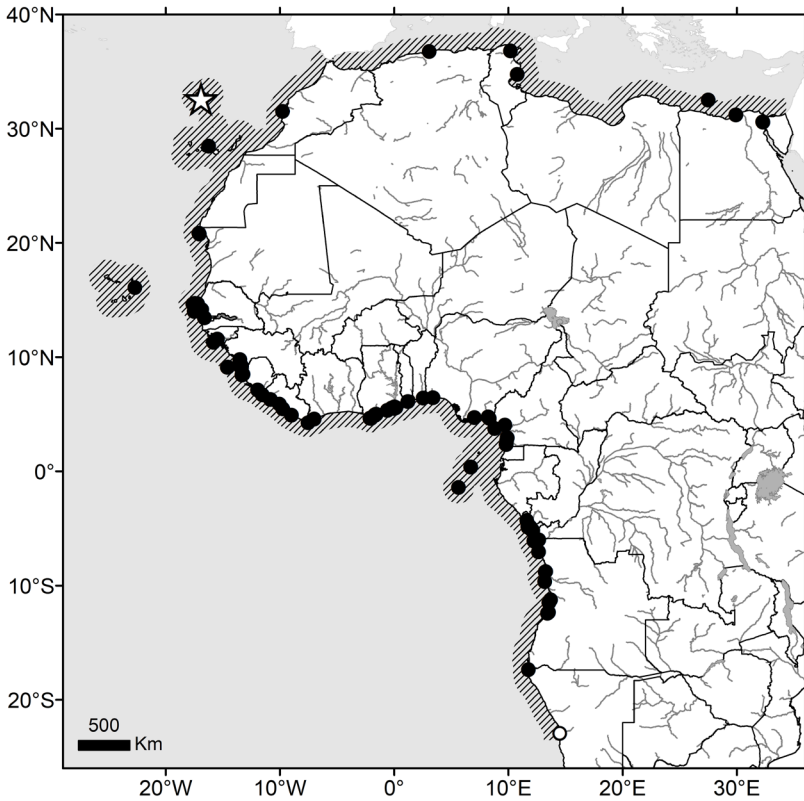


Figure 3-117. *Sardinella maderensis*, distribution map.



Figure 3-118. *Sardinella maderensis*, Campo Beach, Ntem River mouth, Cameroon, RMCA 93-082-P-0627. © RMCA.

Genus *Sauvagella* Bertin, 1940

The genus *Sauvagella* contains two species (Froese & Pauly 2021) that are known from the eastern coastal basins and north-western drainages in Madagascar, mainly in freshwater, although *S. madagascariensis* is sometimes found in brackish waters (Stiassny 2003). Species of *Sauvagella* have a pelvic scute with slender lateral arms but lack prepelvic and postpelvic scutes. The closely related *Spratellomorpha* is characterised by a separate anal finlet (Whitehead 1985).

1a. 17-19 anal-fin rays; body depth 15.8-21.1% SL; snout length 26.2-33.7% HL
 *Sauvagella madagascariensis*

1b. 13-17 anal-fin rays; body depth 20.8-27.4% SL; snout length 18.5-26.6% HL
 *Sauvagella robusta*

Sauvagella madagascariensis (Sauvage, 1883)

Common names: Madagascar round herring (E), Sprat de Madagascar (F), Espadin de Madagascar (S), Varilava (Madagascar), Vilimena (Madagascar), Vilivary (Madagascar), Vivari (Madagascar).

Description: body elongate, a little compressed, its depth 15.8-21.1% SL; belly rounded, without prepelvic scutes, but with one pelvic scute with slender lateral arms; 17-20 gill rakers on lower limb of first arch; pelvic fin with 1 unbranched

and 7 branched fin rays, set a little anterior to level of dorsal-fin origin (Whitehead 1985; Stiassny 2002). Snout length 26.2-33.7% HL; 17-19 anal-fin rays; 41-43 vertebrae (Stiassny 2002).

Maximum length: 6.6 cm SL (Stiassny 2002).

Colour: In life: rather nondescript uniformly pale yellow with silvery iridescence on head and flanks; some larger specimens dark orange, even reddish (Stiassny 2002). Preserved specimens: pale creamy yellow with varying amounts of pigment ringing dorsal scale margins, darkening the dorsum; thin midlateral band of dark pigment often present on flanks; dorsal, anal and caudal fins usually with a line of dark pigment along base on body; silvery or black peritoneal lining of abdominal cavity often visible through body wall; pupil situated anteriorly in eye, iris silver (Stiassny 2002).

Distribution: middle and lower reaches of eastern coastal rivers and the Pangalanes Canal network in Madagascar (Whitehead 1985; Stiassny 2002).

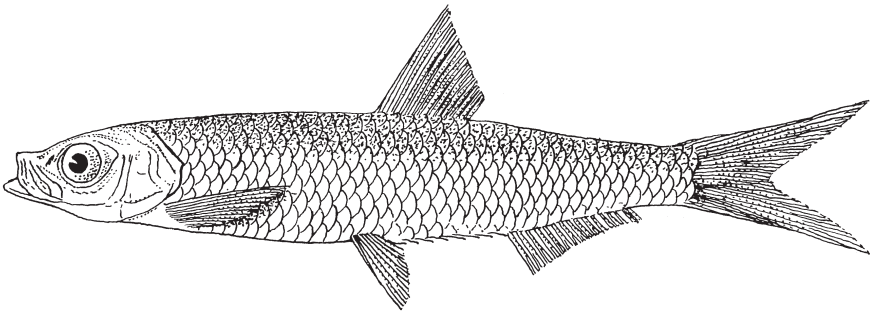


Figure 3-119. *Sauvagella madagascariensis* (from Whitehead 1985).



Figure 3-120. *Sauvagella madagascariensis*, small affluent of Mangoro River, at bridge ca. 5 km north on way to ferry, Madagascar, RMCA 97-038-P-0004-0006. © RMCA.

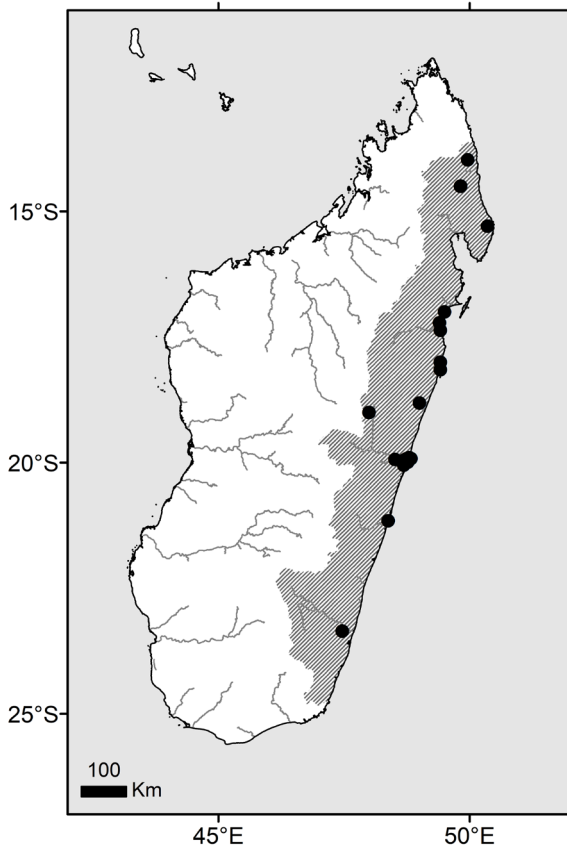


Figure 3-121. *Sauvagella madagascariensis*, distribution map.

Sauvagella robusta Stiassny, 2002

Common names: Amboaboa round herring (E), Varilava (Madagascar).

Description: body relatively elongate, body depth 20.8-27.4% SL; belly rounded, without prepelvic scutes, but a pelvic scute present with slender lateral arms; 15-19 gill rakers on lower limb of first arch; pelvic fin with 1 unbranched and 7 branched fin rays, a little anterior to dorsal-fin origin; snout length 18.5-21.1% HL; 13-17 anal-fin rays; 38-40 vertebrae (Stiassny 2002).

Maximum length: 4.7 cm SL (Stiassny 2002).

Colour: In life: uniformly pale creamy yellow with some silvery iridescence on chest and ventrum (Stiassny 2002). Preserved specimens: pale cream or dark yellow with faint pigment ringing dorsal scale margins, slightly darkening the dorsum; trace of thin midlateral band of dark pigment restricted to posterior half of body; dorsal, anal and caudal fins with a line of dark pigment along base; pupil situated more or less in mid-eye, iris silver or black (Stiassny 2002).

Distribution: Sofia River drainage in Madagascar (Stiassny 2002; Andriafidison *et al.* 2011).

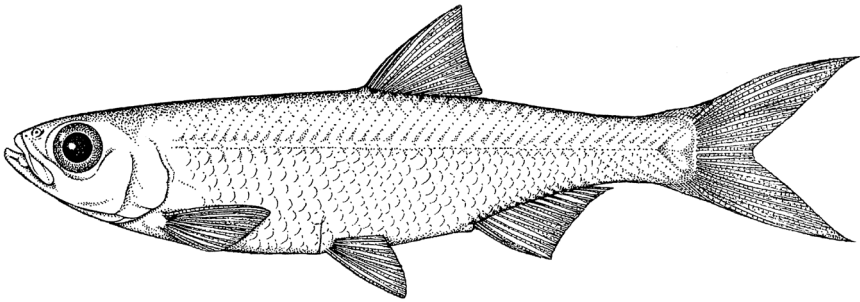


Figure 3-122. *Sauvagella robusta*, holotype, 47.1 mm SL, AMNH 231420 (from Stiassny 2002).



Figure 3-123. *Sauvagella robusta*, paratype, Ambombo River, Madagascar, RMCA 2001-066-P-0001-0002. © RMCA.

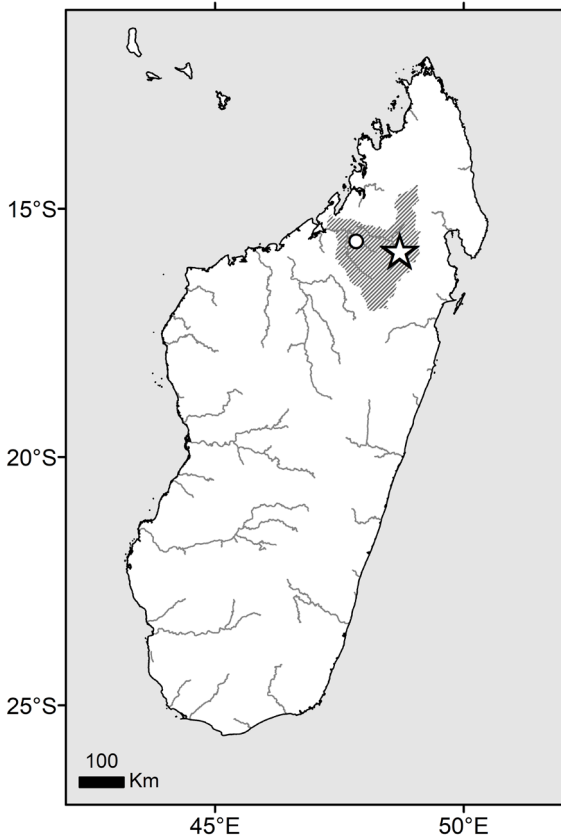


Figure 3-124. *Sauvagella robusta*, distribution map.

Genus *Sierrathrissa* Thys van den Audenaerde, 1969

The single species of this genus, *Sierrathrissa leonensis*, is a very small clupeid, reaching only 4 cm TL and already maturing at 1.8 to 2.0 cm SL (Otobo 1976; Whitehead 1985). It commonly occurs with *Pellonula*, but is characterised by the non-keeled prepelvic and postpelvic scutes without ascending arms, except for the W-shaped scute at the pelvic-fin base, and by the pelvic fin with 1 unbranched and 5-6 branched rays, inserted well before the dorsal-fin base (Whitehead 1985; Teugels 2007).

Sierrathrissa leonensis Thys van den Audenaerde, 1969

Common names: West African pygmy herring (E), Imboli (Nigeria), Ntita (Nigeria), Salanpore (Nigeria), Taga rana (Nigeria), Warangi (Nigeria), Worongi (Nigeria).

Description: small and slender, easily mistaken for juveniles of *Pellonula* (Whitehead 1985). Belly rounded, with 0-10 minute prepelvic scutes [varying between 4-10 according to Whitehead (1985), and between 0-6 according to Gourène & Teugels (2003) and Teugels (2007)], without arms, supporting a low, membranous keel, 6-11 postpelvic scutes similar, keel more apparent, and a W-shaped scute located at pelvic-fin bases; 13-16 lower gill rakers; pelvic-fin insertion well before dorsal fin with 1 unbranched and 5-6 branched rays; anal fin beginning under dorsal-fin base (Thys van den Audenaerde 1969; Whitehead 1985; Gourène & Teugels 2003; Teugels 2007).

Maximum length: 4.0 cm TL (Teugels 2007).

Colour: In life: golden-beige with lateral stripe of melanophores; iris silvery (Gourène & Teugels 2003; Teugels 2007). Preserved specimens: body pale brown with lighter lateral stripe; small melanophores present on snout, upper parts of head, opercles and caudal-fin base; double band of melanophores in predorsal area, another at anal-fin base; fins colourless (Thys van den Audenaerde 1969; Gourène & Teugels 2003; Teugels 2007).

Distribution: rivers of West Africa (Whitehead 1985) and Lower Guinea (Teugels 2007), from the Senegal to the Wouri in Cameroon, including the Gambia, Bia and Niger (Gourène & Teugels 2003; Teugels 2007). Also in the man-made lakes Kainji in Nigeria and Volta in Ghana (Whitehead 1985; Gourène & Teugels 2003). Possibly also present in the Sanaga in Cameroon (Vivien 1991), but no voucher specimens available and unconfirmed in Teugels (2007). A single record from the upper Benue in Cameroon (MNHN-B-3095), originally from a lot collected by Stauch with an additional 16 specimens now identified as *P. leonensis* (MNHN-1962-0546), is unconfirmed in Gourène & Teugels (2003) and needs verification.

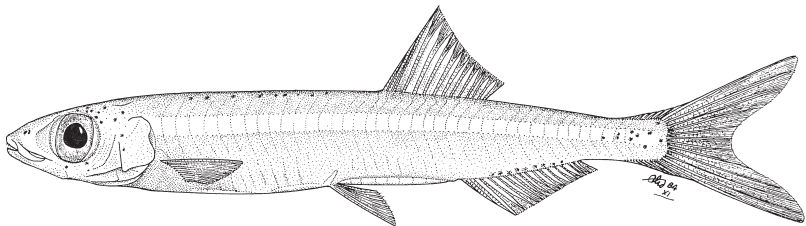


Figure 3-125. *Sierrathrissa leonensis* (from Whitehead 1985).



Figure 3-126. *Sierrathrissa leonensis*, Noe, Tano River, Côte d'Ivoire, RMCA 85-29-P-21-195. © RMCA.

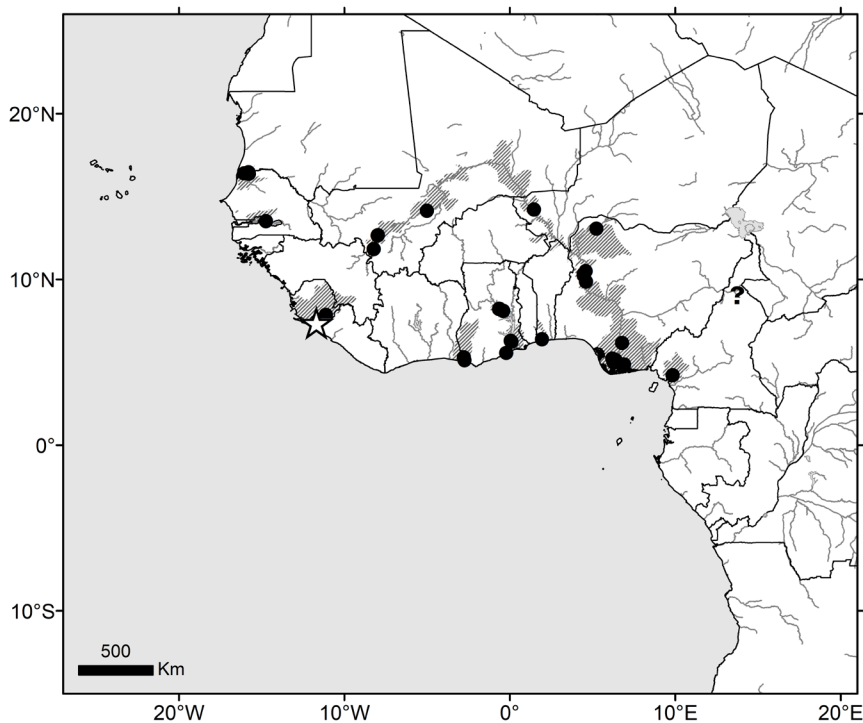


Figure 3-127. *Sierrathrissa leonensis*, distribution map.

Genus *Spratellomorpha* Bertin, 1946

The single species of this genus, *Spratellomorpha bianalis*, is distinguished from other clupeids by the presence of 2 anal fins, of which the second anal fin comprises 2 fin rays (Bertin 1943; Whitehead 1985). The species is considered to be euryhaline (Stiassny & Raminosoa 1994).

Spratellomorpha bianalis (Bertin, 1940)

Common names: Two-finned round herring (E), Dagua (Kenya), Estuarine sprat (Kenya), East African round herring (Madagascar).

Description: body elongate, a little compressed; belly rounded, without prepelvic and postpelvic scutes, but a pelvic scute present with slender vertical arms; 26-31 lower gill rakers; pelvic fin with 1 unbranched and 7-8 branched fin rays, well before dorsal-fin origin; last 2 anal-fin rays separate, forming a distinct little finlet (Bertin 1943; Losse 1968; Whitehead 1985).

Maximum length: 4.5 cm SL (Whitehead 1985).

Colour: Preserved specimens: dorsal side brown or grey-brown; faint, silvery midlateral stripe on flanks from operculum to caudal-fin base; ventral side whitish; sigmoid spot at caudal-fin base (Bertin 1943; Whitehead 1963).

Note: The description of the colour pattern in life is problematic. The account below is based on Losse (1968) for specimens from Port Tudor, Mombasa fish market, Kenya. At present it is not clear whether this species really occurs in that area. Therefore, the description below should be considered with caution.

Body mainly translucent; dorsal and lateral surfaces very light brown, peritoneum white; faint, poorly defined, silvery to golden lateral band from operculum to caudal-fin base, widest behind dorsal base, narrower than pupil of eye; few brown spots on head between orbits; postorbital surface of head brown; two parallel rows of minute black spots on median dorsal surface from nape to dorsal-fin origin and continued from last dorsal ray to caudal base; snout and tip of lower jaw faintly yellowish with few small dark spots; lower jaw, lateral parts of head and operculum silvery; bases of dorsal and caudal fins yellowish, caudal rays with minute orange spots and a few scattered melanophores; two black lines on caudal-fin base and a black streak on upper border of caudal peduncle; row of black spots along base of anal fin and first two rays of pectoral fin with few melanophores, rest of fins colourless (Losse 1968).

Distribution: north-western Madagascar (Poll *et al.* 1984; Whitehead 1985; Stiassny 2002) and western Madagascar, as far south as the Manambolo River (UMMZ collection). Also reported from the Kenyan coast at Port Tudor (Mombasa) (Losse 1968; Whitehead 1985), but conspecificity needs confirmation (Stiassny 2002). Other reports from Kenya (Mkurumudzi Estuary, SAIAB 82510) need confirmation.

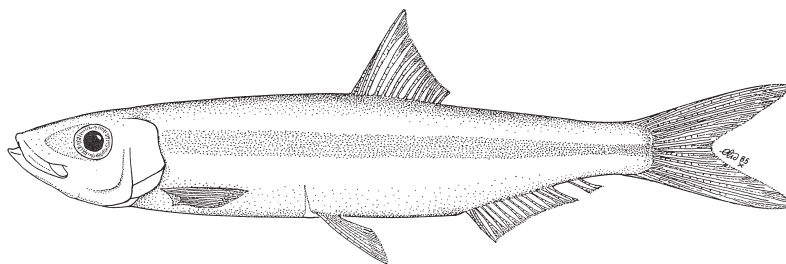


Figure 3-128. *Spratellomorpha bianalis* (from Whitehead 1985).

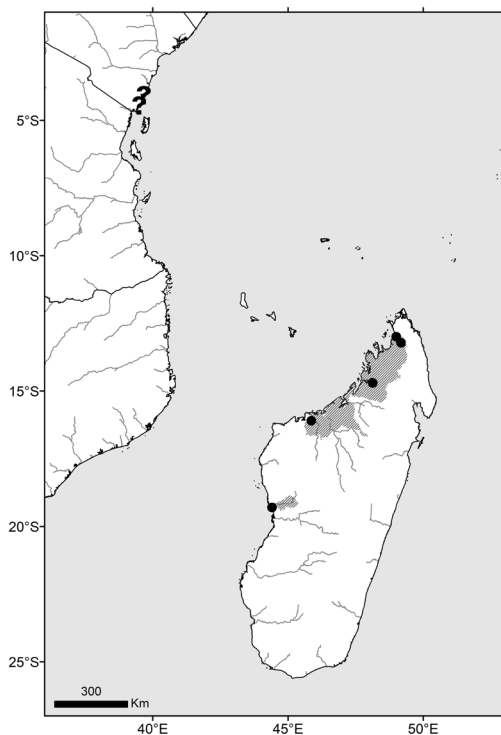


Figure 3-129. *Spratellomorpha bianalis*, distribution map.

Genus *Stolothrissa* Regan, 1917

The single species of this genus, *Stolothrissa tanganyicae*, resembles *Limnothrissa miodon*, also from Lake Tanganyika, but is more slender and has a smaller eye, a longer maxilla blade (slightly more than 2 times the length of its shaft, its depth more than 3 times in its length) with a ridge flared outwards on its upper edge, but not reaching forward to the posterior tip of the premaxilla, and a more symmetrical posterior supramaxilla (Whitehead 1985).

***Stolothrissa tanganyicae* Regan, 1917**

Common names: Lake Tanganyika sprat (E), Ndagala (Burundi, DRC, Rwanda, Tanzania), Kalumba (DRC), Ndakala (DRC, Tanzania), Daga (Tanzania), Lake Tanganyika sardine (Tanzania), Chilwe (Zambia), Kapenta (Zambia), Nsembe (Zambia).

Description: body slender, depth about 17-22% SL; 13-14 prepelvic and 8-9 postpelvic scutes, prepelvic scutes not strongly keeled, beginning behind base of last pectoral-fin ray, postpelvic scutes with sharp spines; maxilla blade about 2.25 times as long as shaft, but not continued forward to hind tip of premaxilla; posterior supramaxilla diamond shaped or more or less rhomboidal, approximately symmetrical; eye diameter less than postorbital length; 36-42 long and slender lower gill rakers; distinct silver stripe along flanks, broadest over tips of pelvic fins (Poll 1974; Whitehead 1985).

Maximum length: 9.8 cm SL (Poll 1953).

Colour: In life: body whitish, snout and upper side of head olive-yellow, dorsal side yellow-grey; side of head and lateral band silvery; ventral regions white; dorsal and caudal fin greyish (Poll 1953). Distinct silver stripe along flanks, broadest over tips of pelvic fins, bordered dorsally by a dark line (Poll 1953; Whitehead 1985).

Distribution: Lake Tanganyika (Poll 1946, 1953; Gourène & Teugels 1994), including the Lukuga River system downstream to the Kisimba-Kilia Falls (Kullander & Roberts 2012). Introduced in Lake Kivu between 1958 and 1960 (Collart 1960), but without success (Bell-Cross & Bell-Cross 1971; Gourène & Teugels 1994).

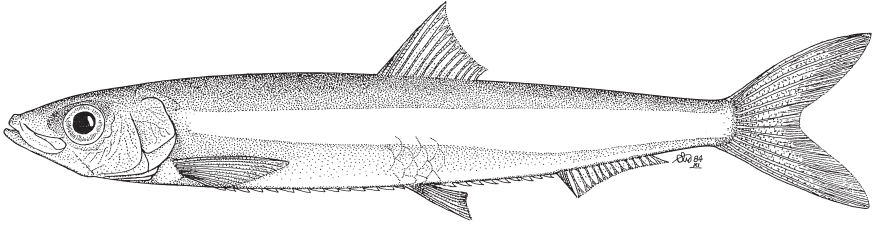


Figure 3-130. *Stoltothrisa tanganicae* (from Whitehead 1985).

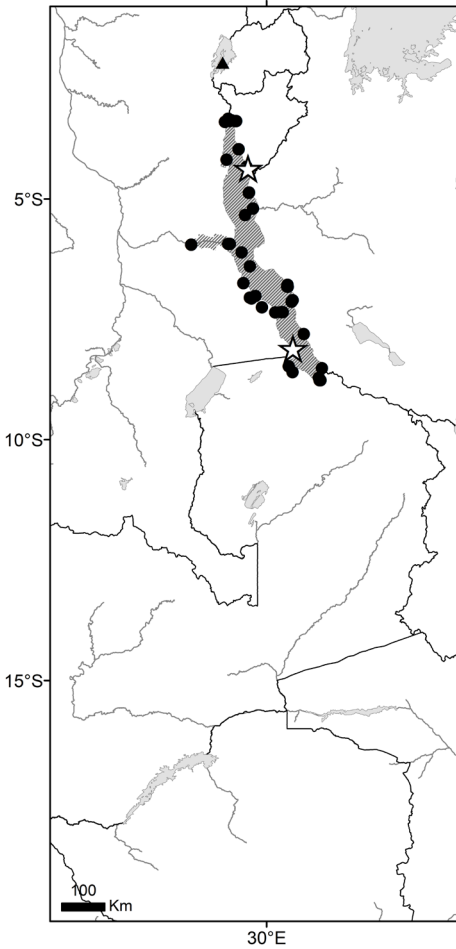


Figure 3-131. *Stoltothrisa tanganicae*, distribution map.



Figure 3-132. *Stolothrissa tanganicae*, Mwerasi, Lake Tanganyika, DRC, RMCA 89487-89491. © RMCA.

Genus *Thrattidion* Roberts, 1972

The single species in this genus, *Thrattidion noctivagus*, is distinguished from *Congothrissa gossei* by the presence of scutes, and from all other West or Central African pellonulines by the absence of a posterior supramaxilla (Whitehead 1985).

Thrattidion noctivagus Roberts, 1972

Common names: Sanaga pygmy herring (E).

Description: small and slender or moderately deep-bodied, depth 20-28% SL; belly rounded; 4-7 prepelvic scutes, with lateral arms but without keels; pelvic scute with 2 or 3 lateral arms; 3-5 postpelvic scutes, keeled and with arms; posterior supramaxilla absent; 10-12 lower gill rakers; pelvic-fin insertion well before level of dorsal fin; pelvic fin with 1 unbranched and 6-7 branched fin rays; anal-fin base starting under dorsal-fin base (Poll 1974; Whitehead 1985; Teugels 2007). Scales largely absent, restricted to about a dozen scales in 4-5 short rows immediately behind head, a double row of 4-9 scales superficial to lateral arms on each side of prepelvic scutes and a single row of 4-5 scales superficial to lateral arms on either side of postpelvic scutes (Roberts, 1972).

Maximum length: 2.1 cm SL (Whitehead 1985).

Colour: In life: peritoneum probably opaque white, body otherwise translucent (Roberts, 1972). Preserved specimens: opaque whitish, lacking melanophores or with few at anal-fin base and on caudal peduncle; silvery midlateral line absent; dense cluster of large melanophores on dorsal area of skull (Roberts 1972; Teugels 2007).

Distribution: known only from the type localities at the barrage at Edea on the Sanaga River in Cameroon (Gourène & Teugels 1994; Teugels 2007).

Note: The identification key for the genera of Clupeidae in Teugels (2007) contains an error. In step 2 the option ‘only one supramaxilla (posterior) present on upper jaw’ leads to the genus *Thrattidion*. This is incorrect since *Thrattidion* is characterised by the absence of a posterior supramaxilla (Roberts 1972; Whitehead 1985). This is correctly stated in the species text of *Thrattidion noctivagus* by Teugels (2007).

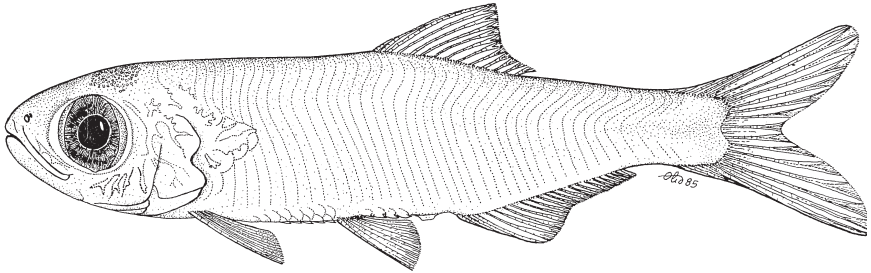


Figure 3-133. *Thrattidion noctivagus* (from Whitehead 1985).



Figure 3-134. *Thrattidion noctivagus*, paratype, Sanaga River, behind barrage at Edea, Cameroon, RMCA 76-51-P-1-9. © RMCA.

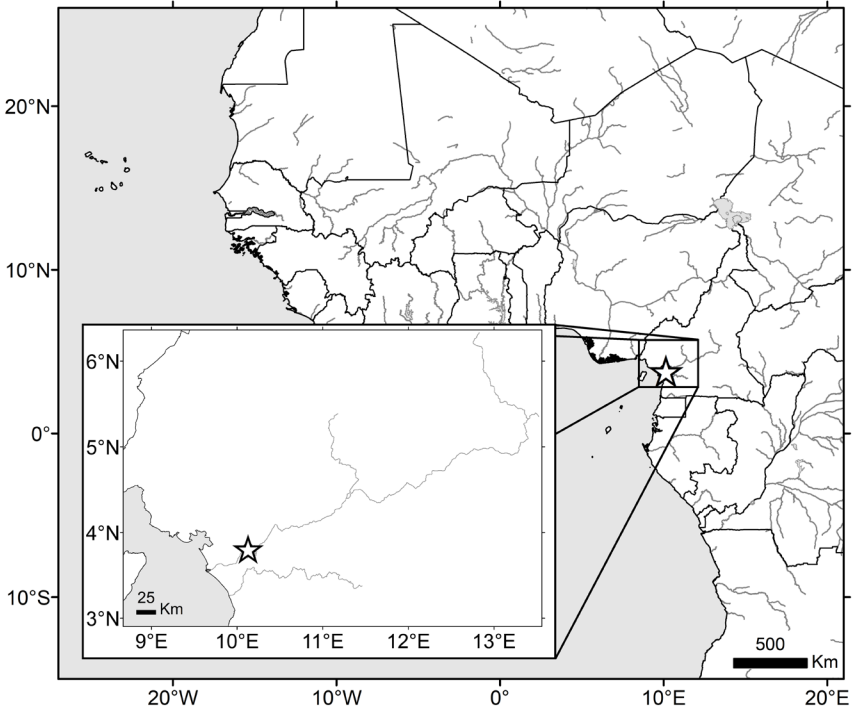


Figure 3-135: *Thrattidion noctivagus*, distribution map.

4. Discussion

Distribution patterns

It is clear that the clupeiform taxa occurring in African inland waters are not evenly distributed over the various families and groups, nor over the various regions of the continent. Below, we present an attempt to synthesise the available information.

Overall, two main categories can be discerned in African inland waters, though the distinction is somewhat arbitrary and not always clear cut. The first category includes species with a distribution limited to brackish and coastal fresh waters, the second includes taxa that are clearly well-adapted freshwater fishes.

Most species of the first category are marine species, not well adapted to a life in freshwater; their distribution in African inland waters is almost exclusively limited to brackish water coastal areas (lagoons and estuaries) and lower reaches of river systems. All species of Engraulidae (anchovies) and Pristigasteridae (longfin herrings) listed belong to this group. Such a distribution is roughly also found in *Ethmalosa fimbriata*, which has a different lifestyle, being a euryhaline species spawning mainly in lagoons and estuaries where fish complete their life cycle (Durand *et al.* 2005). *Hilsa kelee* also belongs to this group, though in contrast to the previous species, spawning usually occurs at sea (Charles-Dominique & Albaret 2003); the scarce data available do not exclude that it also reproduces in brackish waters.

A separate subcategory are the few species that are mainly temperate water species occurring in the Atlantic and Mediterranean waters and, as far as Africa is concerned, are restricted to the northern regions. These include the species of the genus *Alosa*, migrating upriver to spawn and also known from a few land-locked populations (Kottelat & Freyhof 2007). From the limited information available, no long-distance migration is known in African inland waters.

One species, *Sardinella maderensis*, is exceptional in having a combined tropical and temperate distribution, entering brackish waters along the Atlantic coast of western Africa and the Mediterranean coast of northern Africa.

No species has at the same time a large distribution on the Atlantic coast and the Indian Ocean coast of Africa. A few species occur on the eastern and western coasts

of southern Africa. These are species widespread in the Indian Ocean, such as *Stolephorus holodon* and *Herklotsichthys quadrimaculatus*, that apparently rounded the cape and occur in the western cape region on the Atlantic coast possibly to the area that corresponds to the border near Cape Columbine between two subregions of the Southern Benguela Ecoregion, the northwest Namaqua and the southwest Cape subregions (Sink *et al.* 2019).

The second main category within the African clupeiforms includes non-marine taxa that are clearly well-adapted to freshwaters.

A first subcategory is the merely euryhaline species (with *Sauvagella robusta* rather limited to freshwaters) with a narrow distribution, endemic to Madagascar and southern Africa. These include the two species of *Sauvagella* and *Spratello-morpha bianalis*, occurring mainly in lower and middle reaches of Malagasy freshwater systems. Whether the latter species is an exception and occurs in Kenya as well is not yet clear. Madagascar has a special endemic fresh and brackish water fish fauna, very different from mainland Africa; this particularity also seems reflected in its clupeiform fishes.

Gilchristella aestuaria is also included in this subcategory; it is an endemic to the eastern and western coastal areas of southern Africa. It can complete its entire life cycle in estuaries (Blaber 1997), but is also found far upstream in rivers.

A second subcategory consists of taxa from West and Central Africa, but curiously absent from North, East and Southern Africa (except for the introduction of *Limnothrissa tanganicae* in the Zambezi basin). Part of these species have a large distribution in freshwaters in western Africa, such as *Pellonula leonensis* and, to a lesser extent, *P. vorax* and *Sierrathrissa leonensis*. Others seem to ascend rivers less, such as *Odaxothrissa ansorgii*, *O. mento* and *Laeviscutella dekimpei*. Two are endemic species with a very narrow distribution. One of them is the enigmatic *Denticiceps clupeoides*, sole extant member of the monospecific family Denticipitidae. Its distribution is restricted to a few coastal rivers in western Africa and the family is even classified as a primary freshwater family by Berra (2007). The second species is *Thrattidion noctivagus*, a very small species only known from the type locality near Edea in the Sanaga River in Cameroon.

However, most species of this category are endemic to at least part of the Congo

basin. These include all taxa of the genera *Congothrissa*, *Limnothrissa*, *Stolothrissa*, *Microthrissa*, *Nannothrissa* and *Potamothrissa* and one of the species of *Odaxothrissa* (*O. losera*). This illustrates the distinctive character of the Congo basin as a special environment, facilitating the evolution of clupeids into specialised freshwater taxa.

Distribution and phylogeny

The above groupings and their associated distribution patterns, perhaps not unsurprisingly, do make sense in a phylogenetic context. However, the phylogeny of Clupeiformes is still a matter of debate and results differ largely, depending on the genetic markers used (see e.g. Li & Ortí 2007; Lavoué *et al.* 2013, 2014; Bloom & Egan 2018).

Denticeps clupeoides, in many aspects, is the odd one out within the Clupeiformes: in its morphology with the presence of a lateral line and a unique pattern of denticles scattered over the skull bones (for more particularities in its morphology see Di Dario & de Pinna (2006) and de Pinna & Di Dario (2010)), in its distribution being a narrow endemic in West Africa, in its taxonomy being the only extant species within a family and even a whole suborder, and in its phylogeny as a sistergroup to all other Clupeiformes (Wilson *et al.* 2008; Lavoué *et al.* 2014).

The Engraulidae and the Pristigasteridae are basal families to the Clupeidae (Lavoué *et al.* 2017); all taxa from the former two families discussed here are within the category of coastal species entering only lower reaches of rivers, five species in eastern Africa and *Ilisha africana* in western Africa.

The last and largest family, Clupeidae, is subdivided at the moment into four subfamilies (Lavoué *et al.* 2014), which differs from the subdivision in Nelson *et al.* (2016). Three of these subfamilies are important for African inland waters.

The Malagasy and southern African endemics of the genera *Sauvagella*, *Spratellomorpha* and *Gilchristella* are members of the subfamily Ehiravinae. This subfamily (with the exception of some *Clupeonella* previously classified within the Clupeinae) includes relatively small species confined to fresh waters and estuaries in the Indo-West Pacific (Lavoué *et al.* 2014).

The second relevant subfamily is the Alosinae, which includes taxa from temperate waters, some of which support a great tolerance to low salinity (Lavoué *et al.* 2014). This group is represented by species of *Alosa* in northern Africa.

The remaining species are all part of the Dorosomatinae as newly defined by Lavoué *et al.* (2014). The bulk of the species of this subfamily discussed in this guidebook belong to the West and Central African freshwater tribe Pellonulini (Wilson *et al.* 2008; is Pellonulinae sensu Nelson *et al.*, 2016), while the others, *Sardinella maderensis*, *Herklotsichthys quadrimaculatus*, *Ethmalosa fimbriata* and *Hilsa kelee*, are all relatively large marine species occasionally or frequently entering estuaries.

The Pellonulini are a clear monophyletic group of relatively small sardines highly adapted to freshwaters, though some of them are not indicated as such by Bloom & Egan (2018). The Tanganyika endemics *Limnothrissa miodon* and *Stolothrissa tanganyicae* together form a sistergroup to a clade containing Congo basin and western African endemics (Wilson *et al.* 2008). In a more recent analysis (Lavoué *et al.* 2014), the Tanganyika endemics form with other Congo endemics a sistergroup to a mixture of clades of other Congo endemics and western African species. Remarkable is that in both studies, the two species of *Microthrissa* included, *M. royauxi* and *M. congica*, are not sister groups and phylogenetically distinct. This finding echoes the earlier classification of both species in separate genera (respectively *Microthrissa* and *Poecilothrissa*, now subgenera) and confirms their morphological differences (see Gourène & Teugels 1989).

An attempt was made by Wilson *et al.* (2008) to reconstruct the colonization of African freshwaters by the Pellonulini (sensu Lavoué *et al.*, 2014). Wilson *et al.* (2008) postulated a marine invasion via West Africa somewhere between 25 and 50 million years ago and linked this to a marine incursion dated at about 37 million years ago. However, clearly a lot of work still needs to be done to unravel the phylogenetics of the Pellonulini and their evolutionary history.

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References

- Andriafidison, D., Jenkins, R.K.B., Loiselle, P.V., McCaskie, T., Rakotoarivelo, A.A., Rahalambomanan, J., Ravelomanana, T., Raminosoa, N. & Saunders, A. 2011. 'Preliminary fish survey of Lac Tseny in north-western Madagascar'. *Madagascar Conservation & Development* 6 (2): 83-87.
- Angot, M. 1950. 'Poissons littoraux de Soalara. Carte des fonds, systématique, observations biologiques, possibilités de pêche européenne'. *Mémoires de l'Institut scientifique de Madagascar, série A* 4 (1): 175-196.
- Aprahamian, M.W., Aprahamian, C.D., Baglinière, J.L., Sabatié, R. & Alexandrino, P. 2003. *Alosa alosa* and *Alosa fallax* spp. *Literature Review and Bibliography*. R&D Technical Report W1-014/TR. Bristol: Environment Agency, 349 p.
- Baglinière, J.-L., Sabatié, M.R., Rochard, E., Alexandrino, P. & Aprahamian, M.W. 2003. 'The allis shad *Alosa alosa*: biology, ecology, range and status of populations'. *American Fisheries Society Symposium* 35: 85-102.
- Baissac, J. de B. 1990. *Checklist of the Marine Fishes of Mauritius*. RAF/87/008/WP/54/90.
- Banister, K.E. & Bailey R.G., 1979. 'Fishes collected by the Zaire River Expedition 1974-1975'. *Zoological Journal of the Linnean Society* 66: 205-249.
- Barnard, K.H. 1925. 'A monograph of the marine fishes of South Africa. Part 1 (Amphioxus, Cyclostomata, Elasmobranchii, and Teleostei Isospondyli to Heterosomata)'. *Annals of the South African Museum* 21 (1): 1-418.
- Bell-Cross, G. 1965. 'Additions and amendments to the check list of the fishes of Zambia'. *The Puku, Occasional Paper, Department of Game and Fisheries, Zambia* 3: 29-43.
- Bell-Cross, G. & Bell-Cross, B. 1971. 'Introduction of *Limnothrissa miodon* and *Limnocaridina tanganyicae* from Lake Tanganyika into Lake Kariba'. *Fisheries Research Bulletin, Zambia* 5: 207-214.
- Berra, T.M. 2007. *Freshwater Fish Distribution*. Chicago/London: University of Chicago Press, 606 p.
- Bertin, L. 1940. 'Catalogue des types de poissons du Muséum national d'Histoire naturelle. 2^e partie. Dipneustes, Chondrostéens, Holostéens, Isospondyles'. *Bulletin du Muséum national d'Histoire naturelle, Série 2* 12 (6): 244-322.
- Bertin, L. 1943. 'Revue critique des dussumériidés actuels et fossiles. Description d'un genre nouveau'. *Bulletin de l'Institut océanographique de Monaco* 853: 1-31.

- Bills, R. 1999. *An Inventory of Fishes from the Lower Zambezi River, Mozambique (27/7/1999 to 14/8/1999)*. Investigational Report 62. Grahamstown: J.L.B. Smith Institute of Ichthyology, 60 p.
- Blaber, S.J.M. 1997. *Fish and Fisheries of Tropical Estuaries*. London: Chapman & Hall (series 'Fish and Fisheries', no. 22), 367 p.
- Bloom, D.D. & Egan, J.P. 2018. 'Systematics of Clupeiformes and testing for ecological limits on species richness in a trans-marine/freshwater clade'. *Neotropical Ichthyology* 16 (3): e180095. DOI: <https://doi.org/10.1590/1982-0224-20180095>
- Boulenger, G.A. 1899. 'Matériaux pour la faune du Congo. Poissons nouveaux du Congo. Quatrième Partie. Polyptères, Clupes, Mormyres, Characins'. *Annales du Musée du Congo, Série Zoologie*, 1 (4): 59-96.
- Boulenger, G.A. 1900. 'Descriptions of new fishes from the Cape of Good Hope'. *Marine Investigations in South Africa* (8): 10-12.
- Boulenger, G.A. 1905. 'A list of the freshwater fishes of Africa'. *Annals and Magazine of Natural History, Series 7* 16: 36-60.
- Boulenger, G.A. 1906. 'Fourth contribution to the ichthyology of Lake Tanganyika. Report on the collection of fishes made by Dr. W.A. Cunningham during the Third Tanganyika Expedition, 1904-1905'. *Transactions of the Zoological Society of London* 17 (6): 537-600.
- Boulenger, G.A. 1909. *Catalogue of the Fresh-Water Fishes of Africa in the British Museum (Natural History)*, vol. 1. London: printed by order of The Trustees, 373 p.
- Boulenger, G.A. 1910. 'On a large collection of fishes made by Dr. W.J. Ansorge in the Quanza and Bengo rivers, Angola'. *Annals and Magazine of Natural History, Series 8* 6: 537-561.
- Boulenger, G.A. 1916. *Catalogue of the Fresh-Water Fishes of Africa in the British Museum (Natural History)*, vol. 4. London: printed by order of The Trustees, 392 p.
- Bowdich, S.L. 1825. 'Fishes of Madeira'. In T.E. Bowdich (ed.), *Excursions in Madeira and Porto Santo, During the Autumn of 1823, While on his Third Voyage to Africa*. London: George B. Whittaker, pp. 121-125, 233-238.
- Charles-Dominique, E. & Albaret, J.-J. 2003. 'African shads, with emphasis on the West African shad. *Ethmalosa fimbriata*'. *American Fisheries Society Symposium* 35:27-48.
- Clausen, H.S. 1959. 'Denticipitidae, a new family of primitive Isospondylous teleosts from West African fresh-water'. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening I Kjøbenhavn* 121: 141-151.

- Collart, A. 1960. 'L'Introduction du *Stolothrissa tanganycae* (Ndagala) au lac Kivu'. *Bulletin agricole du Congo belge* 51 (4): 975-985.
- Cuvier, G. & Valenciennes, A. 1847. *Histoire naturelle des poissons*. Tome 20. Paris: P. Bertrand, 472 p.
- Daget, J. & Iltis, A. 1965. 'Poissons de Côte d'Ivoire (eaux douces et saumâtres)'. *Mémoires de l'Institut français d'Afrique noire* 74: 1-385.
- De Kimpe, P. 1964. *Contribution à l'étude hydrobiologique du Luapula-Moero*. Tervuren: MRAC (series 'Annales du Musée royal de l'Afrique centrale, série in-8, Sciences zoologiques', no. 128), 238 p.
- de Pinna, M. & Di Dario, F. 2010. 'The branchial arches of the primitive clupeomorph fish, *Denticeps clupeoides*, and their phylogenetic implication (Clupeiformes, Denticipitidae)'. In J.S. Nelson, H.-P. Schultze & M.V.H. Wilson (eds), *Origin and Phylogenetic Interrelationships of Teleosts*. München: Verlag Dr. Friedrich Pfeil, pp. 251-268.
- Decru, E., Vreven, E., Danadu, C., Walanga, A., Mambo, T. & Snoeks, J. 2017. 'Ichthyofauna of the Itimbiri, Aruwimi, and Lindi/Tshopo rivers (Congo basin): diversity and distribution patterns'. *Acta Ichthyologica et Piscatoria* 47 (3): 225-247.
- Di Dario, F. & de Pinna, M.C.C. 2006. 'The supratemporal system and the pattern of ramification of cephalic sensory canals in *Denticeps clupeoides* (Denticipitoidei, Teleostei): additional evidence for monophyly of Clupeiformes and Clupeoidei'. *Papéis Avulsos de Zoologia* 46 (10): 107-123.
- Durand, J.-D., Tine, M., Panfili, J., Thiaw, O.T. & Laë, R. 2005. 'Impact of glaciations and geographic distance on the genetic structure of a tropical estuarine fish, *Ethmalosa fimbriata* (Clupeidae, S. Bowdich, 1825)'. *Molecular Phylogenetics and Evolution* 36 (2): 277-287.
- FAO. 2012. 'Global Ecological Zones for FAO forest reporting: 2010 update'. *Forest Resources Assessment Working Paper* 179: 1-42.
- FAO. 2020. *The State of World Fisheries and Aquaculture 2020. Sustainability in Action*. Rome: Food and Agriculture Organization of the United Nations, 244 p. DOI: <https://doi.org/10.4060/ca9229en>
- Fricke, R. 1999. *Fishes of the Mascarene Islands (Réunion, Mauritius, Rodriguez): An Annotated Checklist, with Descriptions of New Species*. Königstein: Koeltz Scientific Books (series 'Theses Zoologicae', no. 31), 759 p.
- Fricke, R., Eschmeyer, W.N. & van der Laan, R. 2020. *Eschmeyer's Catalog of Fishes: Genera, Species, References*. Online: <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp> (accessed 04/11/2020).

- Fricke, R., Mahafina, J., Behivoke, F., Jaonalison, H., Léopold, M. & Ponton, D. 2018. 'Annotated checklist of the fishes of Madagascar, southwestern Indian Ocean, with 158 new records'. *FishTaxa* 3 (1): 1-432.
- Froese, R. & Pauly, D. 2021. FishBase. World Wide Web electronic publication. Online: www.fishbase.org, version (01/2021).
- GBIF. 2020. GBIF Home Page. Available from: <https://www.gbif.org> (accessed 20/11/2020).
- Golani, D. & Fricke, R. 2018. 'Checklist of the Red Sea fishes with delineation of the Gulf of Suez, Gulf of Aqaba, endemism and Lessepsian migrants'. *Zootaxa* 4509 (1): 1-215.
- Gosse, J.-P. 1968. *Les Poissons du bassin de l'Ubangi*. Tervuren: Musée royal de l'Afrique centrale (series 'Documentation zoologique', no. 13), 56 p.
- Gourène, G. & Teugels, G.G. 1988. 'A new species of herring-like fish *Microthrissa* (Pisces, Clupeidae, Pellonulinae) from the Zaire basin, Central Africa'. *Cybium* 12 (4): 357-363.
- Gourène, G. & Teugels, G.G. 1989. 'Révision systématique du genre *Microthrissa* Boulenger, 1902 des eaux douces africaines (Pisces, Clupeidae)'. *Revue d'hydrobiologie tropicale* 22 (2): 129-156.
- Gourène, G. & Teugels, G.G. 1991a. 'Révision systématique des genres *Odaxothrissa* Boulenger, 1899 et *Cynothrissa* Regan, 1917 (Pisces: Clupeidae) des eaux douces et saumâtres de l'Afrique'. *Journal of African Zoology* 105: 439-459.
- Gourène, G. & Teugels, G.G. 1991b. 'Révision du genre *Pellonula* des eaux douces africaines (Pisces: Clupeidae)'. *Ichthyological Exploration of Freshwaters* 2 (3): 213-225.
- Gourène, G. & Teugels, G.G. 1993. 'Position taxinomique de *Limnothrissa stappersii*, un clupéidé lacustre d'Afrique centrale'. *Ichthyological Exploration of Freshwaters* 4 (4): 367-374.
- Gourène, G. & Teugels, G.G. 1994. 'Synopsis de la classification et phylogénie des Pellonulinae de l'Afrique occidentale et centrale (Teleostei; Clupeidae)'. *Journal of African Zoology* 108: 77-91.
- Gourène, G. & Teugels, G.G. 2003. 'Clupeidae'. In D. Paugy, C. Lévêque & G.G. Teugels (eds), *Faune des poissons d'eaux douces et saumâtres de l'Afrique de l'Ouest*, tome 1. Paris/Tervuren: Institut de recherche pour le développement/Muséum national d'histoire naturelle/MRAC (series 'Faune et Flore tropicales', no. 40), pp. 125-142.
- Günther, A. 1868. *Catalogue of the Fishes in the British Museum*, vol. 7. London: Printed by order of The Trustees, 512 p.

- Hata, H., Lavoué, S. & Motomura, H. 2021. 'Taxonomic status of nominal species of the anchovy genus *Stolephorus* previously regarded as synonyms of *Stolephorus commersonnii* Lacepède 1803 and *Stolephorus indicus* (van Hasselt 1823), and descriptions of three new species (Clupeiformes: Engraulidae)'. *Ichthyological Research*. DOI: <https://doi.org/10.1007/s10228-020-00792-0>
- Heemstra, P.C. 1995. 'Additions and corrections for the 1995 impression'. In M.M. Smith & P.C. Heemstra (eds), *Revised Edition of Smiths' Sea Fishes*. Berlin: Springer-Verlag, pp. 5-15.
- Ibala Zamba, A. 2010. 'Faune des poissons des rivières Luki et Léfini (bassin du Congo): diversité et écologie'. PhD thesis, *Katholieke Universiteit Leuven, Faculty of Sciences*, 452 p.
- Jackson, P.B.N. 1961. *The Fishes of Northern Rhodesia. A Check List of Indigenous Species*. Lukasa: The Government Printer, 140 p.
- Jenness, J., Dooley, J., Aguilar-Manjarrez, J. & Riva, C. 2007a. 'African Water Resource Database. GIS-based tools for inland aquatic resource management. 1. Concepts and application case studies'. *CIFA Technical Paper* 33 (1): 1-167.
- Jenness, J., Dooley, J., Aguilar-Manjarrez, J. & Riva, C. 2007b. 'African Water Resource Database. GIS-based tools for inland aquatic resource management. 2. Technical manual and workbook'. *CIFA Technical Paper* 33 (2): 1-308.
- Kartas, F. 1991. '*Alosa fallax algeriensis* (Regan 1916)'. In H. Hoestlandt (ed.), *The Freshwater Fishes of Europe*, vol. 2: *Clupeidae, Anguillidae*. Wiesbaden: AULA-Verlag, pp. 213-224.
- Kottelat, M. 1997. 'European freshwater fishes. An heuristic checklist of the freshwater fishes of Europe (exclusive of former USSR), with an introduction for non-systematists and comments on nomenclature and conservation'. *Biologia, Bratislava* 52 (Supplement 5): 1-271.
- Kottelat, M. 2013. 'The fishes of the inland waters of Southeast Asia: a catalogue and core bibliography of the fishes known to occur in freshwaters, mangroves and estuaries'. *The Raffles Bulletin of Zoology* supplement 27: 1-663.
- Kottelat, M. & Freyhof, J. 2007. *Handbook of European Freshwater Fishes*. Cornol/Berlin: Publications Kottelat and Freyhof, 646 p.
- Kuiter, R.H. & Tono-zuka, T. 2001. *Pictorial Guide to Indonesian Reef Fishes. Part 1. Eels – Snappers, Muraenidae – Lutjanidae*. Australia: Zoonetics, 302 p.

- Kullander, S.O. & Roberts, T.R. 2012. 'Out of Lake Tanganyika: endemic lake fishes inhabit rapids of the Lukuga River'. *Ichthyological Exploration of Freshwaters* 22 (4): 355-376.
- Laë, R. & Lévêque, C. 2006. 'La Pêche'. In C. Lévêque & D. Paugy (eds), *Les Poissons des eaux continentales africaines. Diversité, écologie, utilisation par l'homme*. Paris: IRD, 564 p.
- Lavoué, S., Bertrand, J.A.M., Chen, W.-J., Ho, H.-C., Motomura, H., Sado, T. & Miya, M. 2017. 'Phylogenetic position of the rainbow sardine *Dussumieria* (Dussumeriidae) and its bearing on the early evolution of the Clupeoidei'. *Gene* 623 (2017) : 41-47. DOI: <https://doi.org/10.1016/j.gene.2017.04.032>
- Lavoué, S., Konstantinidis, P. & Chen, W.-J. 2014. 'Progress in clupeiform systematics'. In K. Ganas (ed.), *Biology and Ecology of Sardines and Anchovies*. Boca Raton: CRC Press, Taylor & Francis Group, pp. 3-42.
- Lavoué, S., Miya, M., Musikasinthorn, P., Chen, W.-J. & Nishida, M. 2013. 'Mitogenomic evidence for an Indo-West Pacific origin of the Clupeoidei (Teleostei: Clupeiformes)'. *PLoS ONE* 8 (2): e56485. DOI: <https://doi.org/10.1371/journal.pone.0056485>
- Lehner, B. & Grill, G. 2013. 'Global river hydrography and network routing: baseline data and new approaches to study the world's large river systems'. *Hydrological Processes* 27 (15): 2171-2186. DOI: <https://doi.org/10.1002/hyp.9740>
- Lehner, B., Verdin, K. & Jarvis, A. 2008. 'New global hydrography derived from spaceborne elevation data'. *Eos, Transactions, American Geophysical Union* 89 (10): 93-94.
- Lévêque, C., Paugy, D., Teugels, G.G. & Romand, R. 1989. 'Inventaire taxinomique et distribution des poissons d'eau douce des bassins côtiers de Guinée et de Guinée Bissau'. *Revue d'hydrobiologie tropicale* 22 (2): 107-127.
- Li, C. & Ortí, G. 2007. 'Molecular phylogeny of Clupeiformes (Actinopterygii) inferred from nuclear and mitochondrial DNA sequences'. *Molecular Phylogenetics and Evolution* 44: 386-398.
- Losse, G.F. 1968. 'The elopoid and clupeoid fishes of East African coastal waters'. *Journal of the East Africa Natural History Society* 27: 77-115.
- Lowenstein, J.H., Osmundson, T.W., Becker, S., Hanner, R. & Stiassny, M.L.J. 2011. 'Incorporating DNA barcodes into a multi-year inventory of the fishes of the hyperdiverse Lower Congo River, with a multi-gene performance assessment of the genus *Labeo* as a case study'. *Mitochondrial DNA* 22 (S1): 52-70.

- Matthes, H. 1964a. *Les Poissons du lac Tumba et de la région d'Ikela. Étude systématique et écologique*. Tervuren: MRAC (series 'Annales du Musée royal de l'Afrique centrale, série in-8°, Sciences zoologiques', no. 126), 204 p.
- Mdaihli, M., du Feu, T. & Ayeni, J.S.O. 2003. 'Fisheries in the southern border zone of Takamanda Forest Reserve, Cameroon'. In J.A. Comiskey & T.C.H. Sunderland (eds), *Takamanda: the Biodiversity of an African Rainforest*. Washington DC: Smithsonian Institution ('SI/MAB Series', no. 8), pp. 141-154.
- Micha, J.-C., Nabwenge Bangulu, B.-L., Ibofa, R., Mumba, F., Mutambwe, S., Zanga, N., Willem, E., Svennsson, J.-E. & Wilander, A. 2020. 'Une ressource surexploitée, *Nannothrissa stewarti*, sardine endémique du lac Maï-Ndombe (RD Congo), résultat innatendu du Programme national de Lutte contre le Paludisme'. *Bulletin des Séances de l'Académie royale des Sciences d'Outre-mer* 64 (1): 61-91. DOI: <https://doi.org/10.5281/zenodo.3980731>
- Monsembula Iyaba, R.J.C. & Stiassny, M.L.J. 2013. 'Fishes of the Salonga National Park (Congo basin, central Africa): a list of species collected in the Luilaka, Salonga, and Yenge Rivers (Equateur Province, Democratic Republic of Congo)'. *Check List* 9 (2): 246-256. DOI: <https://doi.org/10.15560/9.2.246>
- Nelson, G. & McCarthy, L.J. 1995. 'Two new species of gizzard shads of the genus *Nematalosa* (Teleostei, Clupeidae, Dorosomatinae) from the Persian/Arabian Gulf'. *Japanese Journal of Ichthyology* 41 (4): 379-383. DOI: <https://doi.org/10.11369/jji1950.41.379>
- Nelson, G. & Rothman, M.N. 1973. 'The species of gizzard shads (Dorosomatinae) with particular reference to the Indo-Pacific region'. *Bulletin of the American Museum of Natural History* 150 (2): 133-206.
- Nelson, J.S., Grande, T.C. & Wilson, M.V.H. 2016. *Fishes of the World. Fifth Edition*. Hoboken: John Wiley & Sons, Inc., 707 p. DOI: <http://doi.org/10.1002/9781119174844>
- OBIS 2020. Ocean Biodiversity Information System. Intergovernmental Oceanographic Commission of UNESCO. Online: www.obis.org (accessed on 20/11/2020).
- Offem, B.O., Samsons, Y.A. & Omoniyi, I.T. 2008. 'Reproductive aspects of common freshwater fishes in the Cross River, Nigeria'. *Journal of Animal and Plant Sciences* 18 (4): 130-138.

- Offem, B.O., Samsons, Y.A. & Omoniyi, I.T. 2009. 'Fish composition and abundance in the wetlands of Cross River, Nigeria'. *Aquatic Ecology* 43 (4): 1155-1166. DOI: <https://doi.org/10.1007/s10452-009-9240-0>
- Otobo, F.O. 1976. 'Observations on meristic characters separating *Pellonula afzeliusi* Johnels, 1954 from *Sierrathrissa leonensis* Thys Van den Audenaerde, 1969'. *Journal of Fish Biology* 8: 303-310.
- Pellegrin, J. 1933. 'Les Poissons des eaux douces de Madagascar et des îles voisines (Comores, Seychelles, Mascareignes)'. *Mémoires de l'Académie malgache* 14: 1-222.
- Pfeffer, G. 1896. 'Die Fische Ost-Afrikas'. In K. Möbius (ed.), *Deutsch-Ost-Afrika. Band III. Die Tierwelt Ost-Afrikas und der Nachbargebiete. Lieferung V.* Berlin: Geographische Verlagshandlung Dietrich Reimer, pp. 1-72.
- Poll, M. 1933. 'Contribution à la faune ichthyologique du Katanga'. *Annales du Musée du Congo belge, Zoologie, Série I* 3 (3): 101-152.
- Poll, M. 1946. 'Révision de la faune ichthyologique du lac Tanganika'. *Annales du Musée du Congo belge, Zoologie, Série I* 4 (3): 141-364.
- Poll, M. 1948. 'Poissons recueillis au Katanga par H.J. Bredo'. *Bulletin du Musée royal d'Histoire naturelle de Belgique* 24 (21): 1-24.
- Poll, M. 1953. 'Poissons non Cichlidae'. *Exploration hydrobiologique du lac Tanganika (1946-1947). Résultats scientifiques* 3 (5): 1-251. Brussels: Institut royal des Sciences naturelles de Belgique.
- Poll, M. 1964. 'Une famille dulcicole nouvelle de poissons africains: les Congothrissidae'. *Académie royale des Sciences d'Outre-Mer, classe des Sciences naturelles et médicales, nouvelle série* 15 (2): 1-40.
- Poll, M. 1974. 'Synopsis et distribution géographique des Clupeidae d'eau douce africains, descriptions de trois espèces nouvelles'. *Bulletin de la Classe des sciences de l'Académie royale de Belgique, 5^e Série*, 60 (2): 141-161.
- Poll, M. & Roberts, T. 1976. '*Nannothrissa stewarti*, espèce nouvelle de Clupeidae du lac Mai-Ndombe (Zaïre) (Pisces, Clupeidae)'. *Revue de zoologie africaine* 90 (1): 235-239.
- Poll, M., Teugels, G.G. & Whitehead, P.J.P. 1984. 'Clupeidae'. In J. Daget, J.-P. Gosse & D.F.E. Thys van den Audenaerde (eds), *Check-List of the Freshwater Fishes of Africa (CLOFFA)*, vol. 1. Paris/Tervuren: ORSTOM/MRAC, pp. 41-55.
- Poll, M., Whitehead, P.J.P. & Hopson, A.J. 1965. 'A new genus and species of clupeoid fish from West Africa'. *Bulletin de la Classe des sciences de l'Académie royale de Belgique, 5^e série* 51 (3): 277-292.

- Quignard, J.P. & Douchement, C. 1991a. '*Alosa alosa* (Linnaeus 1758)'. In H. Hoestlandt (ed.), *The Freshwater Fishes of Europe*, vol. 2: *Clupeidae, Anguillidae*. Wiesbaden: AULA-Verlag, pp. 89-126.
- Quignard, J.P. & Douchement, C. 1991b. '*Alosa fallax fallax* (Lacépède 1803)'. In H. Hoestlandt (ed.), *The Freshwater Fishes of Europe*, vol. 2: *Clupeidae, Anguillidae*. Wiesbaden: AULA-Verlag, pp. 225-253.
- Quignard, J.P. & Douchement, C. 1991c. '*Alosa fallax nilotica* (Geoffroy Saint-Hilaire, 1808)'. In H. Hoestlandt (ed.), *The Freshwater Fishes of Europe*, vol. 2: *Clupeidae, Anguillidae*. Wiesbaden: AULA-Verlag, pp. 265-273.
- Quignard, J.P. & Tomasini, J.A. 2000. 'Mediterranean fish biodiversity'. *Biologia Marina Mediterranea* 7 (3): 1-66.
- Randall, J.E. 1995. *Coastal Fishes of Oman*. Honolulu: University of Hawaii Press, 439 p.
- Randall, J.E. 2005. *Reef and Shore Fishes of the South Pacific. New Caledonia to Tahiti and the Pitcairn Islands*. Honolulu: University of Hawaii Press, 720 p.
- Regan, C.T. 1917. 'A revision of the clupeid fishes of the genus *Pellonula* and of related genera in the rivers of Africa'. *Annals and Magazine of Natural History, Series 8* 19: 198-207.
- Reiner, F. 1996. 'Catálogo dos peixes do arquipélago de Cabo Verde'. *Publicações Avulsas do Instituto Português de Investigação Marítima* 2: 1-339.
- Reynolds, J.D. 1969. 'The biology of the clupeids in the new Volta lake, Ghana'. In L.E. Obeng (ed.), *Man-made lakes: the Accra Symposium*. Accra: Ghana University Press, pp. 195-203.
- Roberts, T.R. 1972. 'Osteology and description of *Thrattidion noctivagus*, a minute, new freshwater clupeid fish from Cameroon, with a discussion of pellonulin relationships'. *Breviora* 382: 1-25.
- Roberts, T.R. & Stewart, D.J. 1976. 'An ecological and systematic survey of fishes in the rapids of the Lower Zaire or Congo River'. *Bulletin of the Museum of Comparative Zoology* 147 (6): 239-317.
- Sabaj, M.H. 2020. 'Codes for natural history collections in ichthyology and herpetology'. *Copeia* 108 (3): 593-669. DOI: <https://doi.org/10.1643/ASIHCODONS2020>
- Sink, K.J., van der Bank, M.G., Majiedt, P.A., Harris, L.R., Atkinson, L.J., Kirkman, S.P. & Karenyi, N. 2019. *South African National Biodiversity Assessment 2018 Technical Report*, vol. 4: *Marine Realm*. Pretoria: South African National Biodiversity Institute, 555 p.

- Skelton, P.H. 2001. *A Complete Guide to the Freshwater Fishes of Southern Africa*. Cape Town: Struik Publishers, 395 p.
- Skelton, P.H. 2019. 'Chapter 11. The freshwater fishes of Angola'. In B.J. Huntley, V. Russo, F. Lages & N. Ferrand (eds), *Biodiversity of Angola. Science & Conservation: a Modern Synthesis*. Cham: Springer Nature Switzerland AG, pp. 207-242.
- Smith, J.L.B. 1949. *The Sea Fishes of Southern Africa*. Port Elizabeth: Central News Agency Ltd., 550 p.
- Snoeks, J., Kaningini, B., Masilya, P., Nyinza-wamwiza, L. & Guillard, J. 2012. 'Chapter 8. Fishes in Lake Kivu: Diversity and Fisheries'. In J.-P. Descy, F. Darchambeau & M. Schmid (eds), *Lake Kivu: Limnology and Biogeochemistry of a Tropical Great Lake*. Dordrecht: Springer ('Aquatic Ecology Series', no. 5), pp. 127-152.
- Stiassny, M.L.J. 2002. 'Revision of *Sauvagella* Bertin (Clupeidae; Pellonulinae; Ehiravini) with a description of a new species from the freshwaters of Madagascar and diagnosis of the Ehiravini'. *Copeia* 2002 (1): 67-76.
- Stiassny, M.L.J. 2003. 'Clupeidae: *Sauvagella*, *Varilava*, *Vilvari*, and *Vilimena*'. In S.M. Goodman & J.P. Benstead (eds), *The Natural History of Madagascar*. Chicago/London: University of Chicago Press, 1728 p.
- Stiassny, M.L.J. & Raminosoa, N. 1994. 'The fishes of the inland waters of Madagascar'. In G.G. Teugels, J.-F. Guégan & J.-J. Albaret (eds), *Biological Diversity of African Fresh- and Brackish Water Fishes. Geographical Overviews Presented at the PARADI Symposium, Senegal, 15-20 November 1993* (series 'Annales du Musée royal de l'Afrique centrale, Sciences zoologiques', no. 275), pp. 133-148.
- Talwar, P.K. & Kacker, R.K. 1984. *Commercial Sea Fishes of India*. Calcutta: Zoological Survey of India, 997 p.
- Teugels, G.G. 2003a. 'Denticipitidae'. In D. Paugy, C. Lévêque & G.G. Teugels (eds), *Faune des poissons d'eaux douces et saumâtres de l'Afrique de l'Ouest*, tome 1. Paris/Tervuren: Institut de recherche pour le développement/Muséum national d'histoire naturelle/MRAC (series 'Faune et Flore tropicales', no. 40), pp. 122-124.
- Teugels, G.G. 2003b. 'Pristigasteridae'. In D. Paugy, C. Lévêque & G.G. Teugels (eds), *Faune des poissons d'eaux douces et saumâtres de l'Afrique de l'Ouest*. Tome 1. Paris/Tervuren: Institut de recherche pour le développement/Muséum national d'histoire naturelle/MRAC (series 'Faune et Flore tropicales', no. 40), pp. 143-144.

- Teugels, G.G. 2007. 'Clupeidae'. In M.L.J. Stiassny, G.G. Teugels & C.D. Hopkins (eds), *Poissons d'eaux douces et saumâtres de basse Guinée, ouest de l'Afrique centrale*, vol. 1. Paris/Tervuren: Institut de recherche pour le développement/Muséum national d'histoire naturelle/Musée royal de l'Afrique centrale (series 'Faune et Flore tropicales', no. 42), pp. 186-204.
- Thys van den Audenaerde, D.F.E. 1969. 'Description of a new genus and species of clupeoid fish from Sierra Leone'. *Revue de zoologie et de botanique africaines* 80 (3-4): 385-390.
- Thys van den Audenaerde, D.F.E. 1994. *Introduction of Aquatic Species into Zambian Waters, and their Importance for Aquaculture and Fisheries*. ALCOM Field Document No. 24, Rome: Food and Agriculture Organization of the United Nations, 29 p.
- van der Elst, R. 1993. *A Guide to the Common Sea Fishes of Southern Africa. Third edition*. Cape Town: Struik Publishers, 398 p.
- Vivien, J. 1991. *Faune du Cameroun: guide des mammifères et poissons*. Yaoundé/Paris: GICAM/Ministère de la Coopération et du Développement, 271 p.
- Vreven, E.J. & Teugels, G.G. 2007. 'Denticipitidae'. In M.L.J. Stiassny, G.G. Teugels & C.D. Hopkins (eds), *Poissons d'eaux douces et saumâtres de basse Guinée, ouest de l'Afrique centrale*, vol. 1. Paris/Tervuren : Institut de recherche pour le développement/Muséum national d'histoire naturelle/Musée royal de l'Afrique centrale (series 'Faune et Flore tropicales', no. 40), pp. 205-208.
- Whitehead, P.J.P. 1963. 'A revision of the recent round herrings (Pisces: Dussumieriidae)'. *Bulletin of the British Museum (Natural History), Zoology* 10 (6): 307-380.
- Whitehead, P.J.P. 1965a. 'A preliminary revision of the Indo-Pacific Alosinae (Pisces: Clupeidae)'. *Bulletin of the British Museum (Natural History), Zoology* 12 (4): 115-156.
- Whitehead, P.J.P. 1965b. 'A review of the elopoid and clupeoid fishes of the Red Sea and adjacent regions'. *Bulletin of the British Museum (Natural History), Zoology* 12 (7): 225-281.
- Whitehead, P.J.P. 1967a. 'The clupeoid fishes described by Lacepède, Cuvier & Valenciennes'. *Bulletin of the British Museum (Natural History), Zoology Supplement* 2: 1-180.
- Whitehead, P.J.P. 1967b. 'The West African shad, *Ethmalosa fimbriata* (Bowdich, 1825): synonymy, neotype'. *Journal of Natural History* 1 (4): 585-593. DOI: <https://doi.org/10.1080/00222936700770551>

- Whitehead, P.J.P. 1974a. 'Clupeidae'. In W. Fischer & P.J.P. Whitehead (eds), *FAO Species Identification Sheets for Fishery Purposes. Eastern Indian Ocean (Fishing Area 57) and Western Central Pacific (Fishing Area 71)*, vol. 1. Rome: Food and Agriculture Organization of the United Nations.
- Whitehead, P.J.P. 1974b. 'Engraulidae'. In W. Fischer & P.J.P. Whitehead (eds), *FAO Species Identification Sheets for Fishery Purposes. Eastern Indian Ocean (Fishing Area 57) and Western Central Pacific (Fishing Area 71)*, vol. 2. Rome: Food and Agriculture Organization of the United Nations.
- Whitehead, P.J.P. 1981. 'Clupeidae'. In W. Fischer, G. Bianchi & W.B. Scott (eds), *FAO Species Identification Sheets for Fishery Purposes. Eastern Central Atlantic. Fishing Areas 34, 47 (in part)*, vol. 2. Ottawa: Canada Funds-in-Trust Department of Fisheries and Oceans Canada, by arrangement with the Food and Agriculture Organization of the United Nations.
- Whitehead, P.J.P. 1985. *FAO Species Catalogue*, vol. 7: *Clupeoid Fishes of the World (Suborder Clupeoidei). An Annotated and Illustrated Catalogue of the Herrings, Sardines, Pilchards, Sprats, Shads, Anchovies and Wolf-Herrings. Part 1. Chirocentridae, Clupeidae and Pristigasteridae*. Rome: United Nations Development Programme/Food and Agriculture Organization of the United Nations (series 'FAO Fisheries Synopsis', no. 125), 303 p.
- Whitehead, P.J.P. 1990. 'Clupeidae'. In J.C. Quérou, J.C. Hureau, C. Karrer, A. Post & L. Saldanha (eds), *Check-List of the Fishes of the Eastern Tropical Atlantic (CLOFETA)*, vol. 1. Paris: JNICT/SEI/UNESCO, pp. 208-227.
- Whitehead, P.J.P. & Bauchot, M.L. 1985. 'Catalogue critique des types de poissons du Muséum national d'histoire naturelle (suite). Ordre des Clupéiformes (familles des Clupeidae, Engraulididae et Denticipitidae)'. *Bulletin du Muséum national d'Histoire naturelle, Série 4, Section A: Zoologie, Biologie et Écologie animales* 7 (supplément 4): 1-77.
- Whitehead, P.J.P. & Wongratana, T. 1984a. 'Clupeidae'. In W. Fischer & G. Bianchi (eds), *FAO Species Identification Sheets for Fishery Purposes. Western Indian Ocean. Fishing Area 51. Bony Fishes*, vol. 1: Acanthuridae to Clupeidae. Rome: Food and Agriculture Organization of the United Nations.
- Whitehead, P.J.P. & Wongratana, T. 1984b. 'Engraulidae'. In W. Fischer & G. Bianchi (eds), *FAO Species Identification Sheets for Fishery Purposes. Western Indian Ocean. (Fishing Area 51)*, vol. 2. Rome: Food and Agriculture Organization of the United Nations.
- Whitehead, P.J.P. & Wongratana, T. 1986a. 'Clupeidae'. In M.M. Smith & P.C. Heemstra (eds), *Smiths' Sea Fishes*. Berlin: Springer-Verlag, pp. 199-204.

- Whitehead, P.J.P. & Wongratana, T. 1986b. 'Engraulidae'. In M.M. Smith & P.C. Heemstra (eds), *Smiths' Sea Fishes*. Berlin: Springer-Verlag, pp. 204-207.
- Whitehead, P.J.P., Nelson, G.J. & Wongratana, T. 1988. *FAO Species Catalogue, vol. 7: Clupeoid Fishes of the World (Suborder Clupeoidei). An Annotated and Illustrated Catalogue of the Herrings, Sardines, Pilchards, Sprats, Shads, Anchovies and Wolf-Herrings. Part 2. Engraulididae*. Rome: United Nations Development Programme/Food and Agriculture Organization of the United Nations (series 'FAO Fisheries Synopsis', no. 125), pp. 305-579.
- Whitfield, A.K. 1994. 'A review of ichthyofaunal biodiversity in Southern African estuarine systems'. In G.G. Teugels, J.-F. Guégan & J.-J. Albaret (eds), *Biological Diversity of African Fresh- and Brackish Water Fishes. Geographical Overviews Presented at the PARADI Symposium, Senegal, 15-20 November 1993. Annales du Musée royal de l'Afrique centrale, Sciences zoologiques* (275):149-168. Tervuren/Paris: RMCA/ORSTOM.
- Whitfield, A.K. 1999. 'Ichthyofaunal assemblages in estuaries: a South African case study'. *Reviews in Fish Biology and Fisheries* 9: 151-186.
- Whitfield, A.K. 2005. 'Preliminary documentation and assessment of fish diversity in sub-Saharan African estuaries'. *African Journal of Marine Science* 27 (1): 307-324.
- Whitfield, A.K. 2007. 'Estuary associated fish species'. In M.L.J. Stiassny, G.G. Teugels & C.D. Hopkins (eds), *Poissons d'eaux douces et saumâtres de basse Guinée, ouest de l'Afrique centrale*, vol. 1. Paris/Tervuren: Institut de recherche pour le développement/Muséum national d'histoire naturelle/MRAC (series 'Faune et Flore Tropicales', no. 42), pp. 46-56.
- Wilson, A.B., Teugels, G.G. & Meyer, A. 2008. 'Marine incursion: the freshwater herring of Lake Tanganyika are the product of a marine invasion into West Africa'. *PLoS One* 3 (4): e1979. DOI: <https://doi.org/10.1371/journal.pone.0001979>
- Winterbottom, R. 1976. 'Additions to, and range extensions of, the south African marine ichthyofauna'. *Zoologica Africana* 11 (1): 59-73.

References describing species, otherwise not used in text

- Angel, F., Bertin, L. & Guibé, J. 1946. 'Note relative à la nomenclature d'un amphibien et d'un poisson'. *Bulletin du Muséum national d'histoire naturelle, Série 2* 18 (6): 473-474.

- Bloch, M.E. 1795. *Naturgeschichte der ausländischen Fische. Neunter Theil*. Berlin: Im Verlage der Morinoschen Kunsthandlung, 192 p.
- Bloch, M.E. & Schneider, J.G. 1801. *M.E. Blochii, Systema Ichthyologiae iconibus cx illustratum. Post obitum auctoris opus inchoatum absolvit, correxit, interpolavit Jo. Gottlob Schneider, Saxo.Berolini*. Berlin: Sumtibus Auctoris Impressum et Bibliopolio Sanderiano Commissum, 584 p.
- Boulenger, G.A. 1902. 'Additions à la faune ichthyologique du bassin du Congo. Matériaux pour la faune du Congo'. *Annales du Musée du Congo belge, Zoologie, Série I 2* (2): 19-57.
- Broussonet, P.M.A. 1782. *Ichthyologia sistens Piscium descriptiones et icones*. London: Prostat, Londini apud Petr. Elmsly. Parisiis apud P. Franc. Didot, Juni. Viennæ et Lipsiæ apud Rudolph. Græffer. Lugduni Batav. apud Andr. Koster et soc.
- Cuvier, G. 1829. *Le Règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Avec figures dessinées d'après nature. Nouvelle édition, revue et augmentée*. Tome 2. Paris: Déterville, 406 p.
- Delsman, H.C. 1931. 'Fish eggs and larvae from the Java Sea. 17. The genus *Stolephorus*'. *Treubia* 13 (2): 217-243.
- Forsskål, P. 1775. *Descriptiones animalium, avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit Petrus Forskål. Post mortem auctoris edidit Carsten Niebuhr*. Hauniae: Mölleri, 164 p.
- Fowler, H.W. 1935. 'South African fishes received from Mr. H.W. Bell-Marley in 1935'. *Proceedings of the Academy of Natural Sciences of Philadelphia* 87: 361-408.
- Gilchrist, J.D.F. 1913. 'Review of the South African clupeidae (herrings) and allied families of fishes'. *Marine Biological Report* 1: 46-66.
- Gilchrist, J.D.F. & Thompson, W.W. 1908. 'Descriptions of fishes from the coast of Natal'. *Annals of the South African Museum* 6 (2): 145-206.
- Lacepède, B.G.E. 1803. *Histoire naturelle des poissons*. Tome 5. Paris: Plassan, 803 p.
- Linck, H.F. 1790. 'Versuch einer Eintheilung der Fische nach den Zähnen'. *Magazin für das Neueste aus der Physik und Naturgeschichte* 6 (3): 28-38.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. Stockholm (Holmiae): Impensis Direct. Laurentii Salvii, 824 p.

- Lowe, R.T. 1839. 'A synopsis of the fishes of Madeira; with the principal synonyms, Portuguese names, and characters of the new genera and species'. *Transactions of the Zoological Society of London* 2 (3): 173-200. DOI: <https://doi.org/10.1111/j.1469-7998.1839.tb00017>.
- Poll, M. 1965. 'Un genre nouveau de Clupeidae (Pellonulinae) du bassin central du Congo'. *Revue de zoologie et de botanique africaines* 72 (3-4): 309-315.
- Regan, C.T. 1916. 'The British fishes of the sub-family Clupeinae and related species in other seas'. *Annals and Magazine of Natural History, Series 8* 18 (103): 1-19.
- Regan, C.T. 1917. 'A revision of the clupeoid fishes of the genera *Pomolobus*, *Brevoortia* and *Dorosoma*, and their allies'. *Annals and Magazine of Natural History, Series 8* 19: 297-316.
- Richardson, J. 1846. *Report on the ichthyology of the seas of China and Japan*. Report of the British Association for the Advancement of Science 1845. London: Richard & John E. Taylor, pp. 187-320.
- Rüppell, W.P.E.S. 1837. *Neue Wirbelthiere zu der Fauna von Abyssinien gehörig, entdeckt und beschrieben: Fische des Rothen Meeres*. Frankfurt am Main: Siegmund Schmerber, pp. 53-80.
- Sauvage, H.E. 1883. 'Description de quelques poissons de la collection du Muséum d'histoire naturelle'. *Bulletin de la Société philomatique de Paris, Série 7* 7: 156-161.
- Swainson, W. 1839. *The Natural History and Classification of Fishes, Amphibians, and Reptiles or Monocardian Animals*, vol. 2. London: Longman, Orme, Brown, Green & Longmans, 452 p.
- van Hasselt, J.C. 1823. 'Uittreksel uit een brief van Dr. J.C. van Hasselt aan den Heer C.J. Temminck'. *Algemeene Konst- en Letter-Bode Deel* 1 (21): 328-331.
- Whitley, G.P. 1951. 'New fish names and records'. *Proceedings of the Royal Zoological Society of New South Wales, 1949-1950*: 61-68.

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