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The West African Pygmy Herring
Sierrathrissa leonensis: General Features, Visceral Anatomy, and Osteology

PETER J. P. WHITEHEAD[1] AND GUY G. TEUGELS[2]

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[1] Research Associate, Department of Ichthyology, American Museum of Natural History. Current address: Zoology Department, British Museum (Natural History), London SW7 5BD.
[2] Ichtyologie Générale et Appliquée, Muséum National d'Histoire Naturelle, 75231 Paris.

ABSTRACT

The minute freshwater herring *Sierrathrissa leonensis* Thys van den Audenaerde, 1969, first recorded from Sierra Leone, has sometimes been claimed as nothing more than the ummetamorphosed larva of a species of *Pellonula* (or perhaps *Cynothrissa*). Fully mature specimens with ripe gonads at only 21–26 mm SL are described and the distinction from juvenile *Pellonula* clarified. General features of the species are given, as well as descriptions and illustrations of its visceral organs and most of the 900 bony or cartilaginous elements of its anatomy.

INTRODUCTION

The largest evolutionary radiation of freshwater Clupeidae occurs in the rivers and lakes of West Africa, where 13 genera comprising about 23 species have been recorded (Poll, 1974; Poll, Teugels, and Whitehead, 1984). This is in striking contrast to the paucity of marine Clupeidae and Engraulidae off West African coasts, where only four genera are found (*Sardinella, Ethmalosa, Ilisha,* and *Engraulis*—all but the first monotypic in this area). By comparison, there are 14 marine clupeoid genera and about 24 species known from the Guianas area on the Western side of the Atlantic (Whitehead, 1973, pp. 10–11).

Although the West African freshwater clupeids appear to belong to a single subfamily, the Pellonulinae,[3] they show considerable diversity. There are carnivores with large canine teeth and the dorsal gill arch elements separated in the midline (*Cynothrissa,*

Odaxothrissa); genera with the characteristic clupeid scutes greatly reduced (*Laeviscutella*) or even absent except for the ubiquitous pelvic scute (*Congothrissa*); genera with scales almost entirely lacking (*Thrattidion*); genera with the usual six or seven branchiostegal rays reduced to three (*Congothrissa*); and genera with the 2nd supramaxilla small (*Microthrissa, Poecilothrissa*), minute (*Potamothrissa*), or absent (*Congothrissa, Thrattidion*). This general tendency toward reduction is also found in overall size and is carried to an extreme in *Thrattidion noctivagus,* which is mature at under 20 mm SL.

Thus, when Thys van den Audenaerde (1969) described *Sierrathrissa leonensis* from Sierra Leone, a species which he believed matured at about 20 mm SL, it seemed that this was merely another example of pellonuline dwarfism and reduction (of scutes, pelvic finrays, branchiostegal rays, etc.). However, Roberts (1972, pp. 19–20) denied rather categorically that these were adults and he claimed that *Sierrathrissa* was nothing more than the unmetamorphosed form of a well-known species of *Pellonula* (or perhaps *Cynothrissa*). He equated the juvenile *Pellonula* described from the Gambia river by Svensson (1933, pp. 47–48, fig. 16) with "*Sierrathrissa*" and noted that Svensson, and later

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[3] As yet inadequately defined, but uniting species that lack an anterior supramaxilla (and occasionally the posterior also), have i7 pelvic finrays (occasionally i6), and retain the posterior frontal fontanelles in adults. *Congothrissa gossei,* originally placed in a separate family by Poll (1964), was later relegated to a tribe of the Pellonulinae (Poll, 1974); Taverne (1977) disagreed but, being the most recent statement, his acceptance of the family Congothrissidae had to be followed by Poll and Teugels (1984).
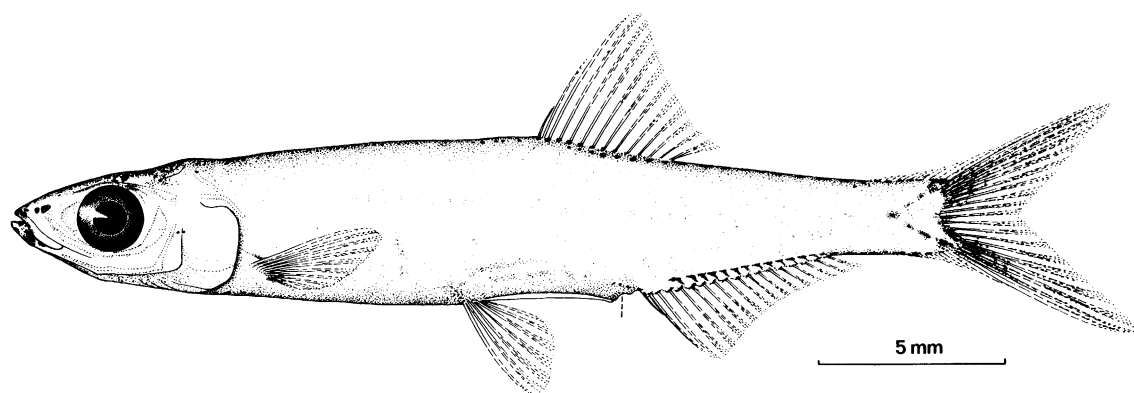
FIG. 1. *Sierrathrissa leonensis,* 25.4 mm SL, *ex* Sandje River at Tondé, Wouri system, Cameroon (MRAC 73-29-P-2059-2107).

Johnels (1954, pp. 16–17), who named the adults as *Pellonula afzeliusi,* both commented on the larval features of specimens less than about 30 SL. Similarly, Daget (1954, p. 68) supposed that his *Microthrissa miri* (i.e., *P. afzeliusi*) underwent metamorphosis. As Roberts pointed out (*in litt.* and during a visit to London in 1976), the most distinctive features of *Sierrathrissa* (only three branchiostegal rays, rudimentary scutes, few gillrakers, and one less pelvic finray than usual) are precisely those one would expect in a larval stage. Moreover, it was unlikely that a small divergent species would occur in rivers as far apart as the Gambia and the Niger, and in any case he knew of no fully mature specimens of *Sierrathrissa* and conversely, no descriptions of very small *Pellonula* that did not include the diagnostic features of *Sierrathrissa.*

The problem was in part resolved by Otobo (1978), who reported sexually mature *Sierrathrissa* of both sexes in Lake Kainji, Nigeria, and also by Teugels and Thys van den Audernaerde (1979), who compared small *P. afzeliusi* with similar sized *Sierrathrissa* and showed that, in addition to the differences already noted, *Sierrathrissa* lacks postcleithra, has a quite different growth pattern of the frontals, and has the dorsal fin much further back on the body (behind the pelvic insertion). One of us (PJPW) received a Nigerian sample in fairly fresh condition, which included sexually mature and fully ripe individuals of both sexes, thus confirming Otobo's observations, and not long afterwards

Prof. Alf Johnels very kindly donated 14 syntypes of *P. afzeliusi* to the British Museum (Natural History), of which four were that species (25.0–30.2 mm SL), but 10 were *Sierrathrissa* (13.2–28.4 mm SL, the largest being a ripening female). There could be no doubt that *Sierrathrissa leonensis* is a distinct species of dwarf herring in West African fresh waters.

The additional specimens and the dissections prompted further investigation of *Sierrathrissa,* so that the original description can now be enlarged to include more morphometric and meristic data, as well as a description of the visceral anatomy and osteology of this minute species. Presumably its nearest modern relative is among the other 20 or so freshwater clupeids of West Africa, perhaps a species of *Pellonula,* but until the juveniles of these have been studied in comparable detail, it is unwise to speculate on what may be advanced characters in *Sierrathrissa* or broach the philosophical question of whether its larval features are primitive or derived.
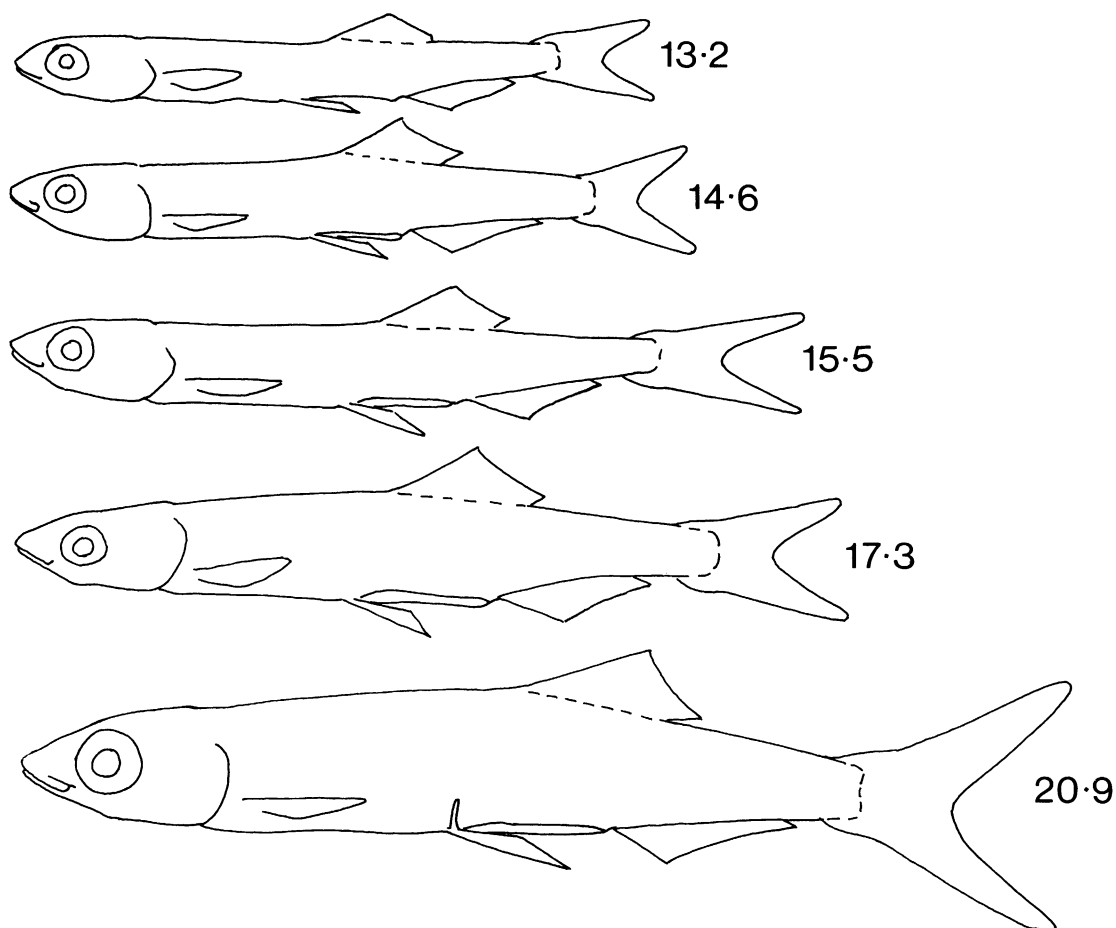
FIG. 2. *Sierrathrissa leonensis,* 13.2–20.9 mm SL, *ex* Gambia River, part of syntypical series of *Pellonula afzeliusi* (BMNH 1977.11.29.5–9).

paper and for offering many helpful criticisms and suggestions.

Acknowledgment is made to the British Council (Brussels) for a grant-in-aid that enabled the junior author to work in London.

ABBREVIATIONS

Since most anatomical parts appear in only one of the figures, we prefer to give their abbreviations and explanation in the captions rather than make the reader search through a list at the end. The following institutional abbreviations have been used:

BMNH, British Museum (Natural History), London

MNHN, Muséum National d'Histoire Naturelle, Paris

MRAC, Musée Royale de l'Afrique Centrale

EXTERNAL FEATURES (figs. 1–5)

An adult ♂ of 25.4 mm SL is shown in figure 1 and a series of five specimens 13.2–20.9 mm SL in figure 2. The species is immediately distinguished from juvenile *Pellonula afzeliusi* by the posterior position of the dorsal fin, which originates well behind the pelvic fin insertion. The postpelvic keel of armless scutes distinguishes it from all West African pellonulines except *Laeviscutella dekimpei* Poll, Whitehead, and Hopson, 1965, which has i7 pelvic finrays (cf. i6), 6 branchiostegal rays (cf. 2–4), more gillrakers (21–26, cf. 13–15 on the lower part of the arch), and the dorsal fin more advanced.

Measurements of body parts follow standard practice, except that body depth was taken just before the pelvic fin base. Fine
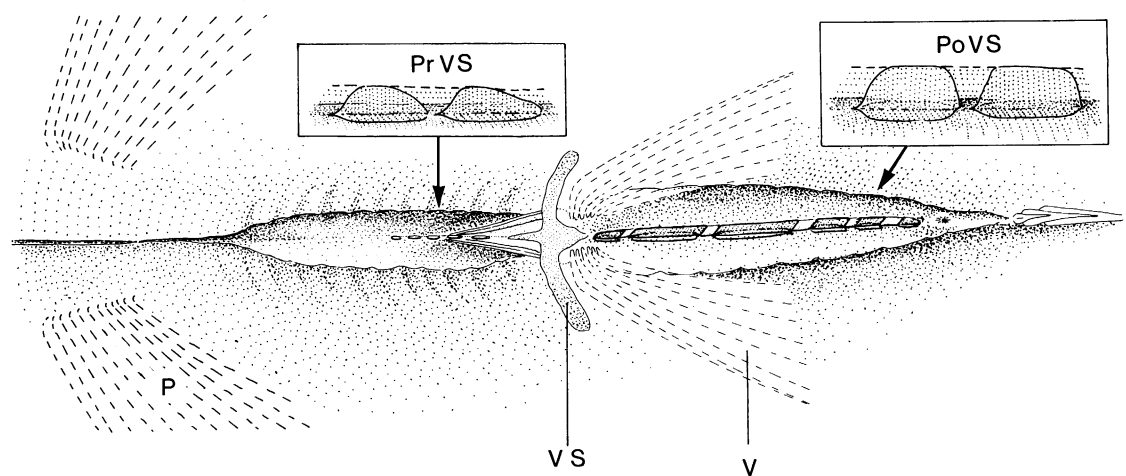
FIG. 3.   Abdominal scutes (ventral view, head to left), with insets (enlarged ventrolateral views from right side). **P**, pectoral fin; **PoVS**, postpelvic scutes; **PrVS**, prepelvic scutes; **V**, pelvic fin; **VS**, pelvic scute.

pointed dial calipers were used under low magnification. Unusually high or low counts and measurements are placed in parentheses, as are all frequencies (preceded by f.); the counts for upper and lower procurrent caudal finrays are also placed in parentheses. Counts for paired fins were sometimes made on both sides, hence totals may exceed the number of specimens. Additional meristic counts for 116 specimens are given in table 1.

Description based on 20 fishes, 22.5–26.7 mm SL (BMNH 1970.9. 24.177–216, *ex* Aklor, Volta Lake, Ghana—see Study Material, p. 42) and also five alizarin-stained specimens, 20.8–25.8 mm SL, from the same batch (meristic counts only).

Br. St. 3 (f.7), D iii (iv) 10 (f.3), 11 (f.21), 12 (f.1), P i8 (f.1), 9 (f.28), 10 (f.3), V i6 (f.36), 7 (f.1), A iii14 (f.3), 15 (f.5), 16 (f.9), 17 (f.6), 18 (f.1), C upper (10–11) and i + 9, lower 7–8 + i and (9), g.r. 13 (f.2), 14 (f.2), 15 (f.1) on lower arm, scutes 0–6 + 6–11, vert. (22–23) 24 + (17) 18 (19).

In percentages of standard length: head length 23.0–27.4 (M 25.18), body depth (13.2) 14.2–18.0 (M 16.74); snout length (5.2) 6.2–7.2 (M 6.57), eye diameter (6.6) 7.1–8.1 (M 7.47), upper jaw (5.2) 5.9–7.3 (M 6.68), lower jaw 9.9–11.4 (M 10.95); pectoral fin length 12.2–14.5 (15.9) (M 13.56), pelvic fin length 10.4–12.7 (M 11.49), length of anal fin base 17.4–21.2 (M 19.39); predorsal distance (57.6) 59.0–63.0 (M 60.72), prepelvic distance 49.0–

TABLE 1

Additional Meristic Counts in *Sierrathrissa*, Based on 138 Specimens of 9.8–30.4 mm SL Selected from Study Material (see p. 42)

Branchiostegal Rays: 2 + 2 (f. 1)
2 + 3 (f. 2)
3 + 3 (f. 43)
3 + 4 (f. 3)

Total Numbers of Branched and Unbranched Rays

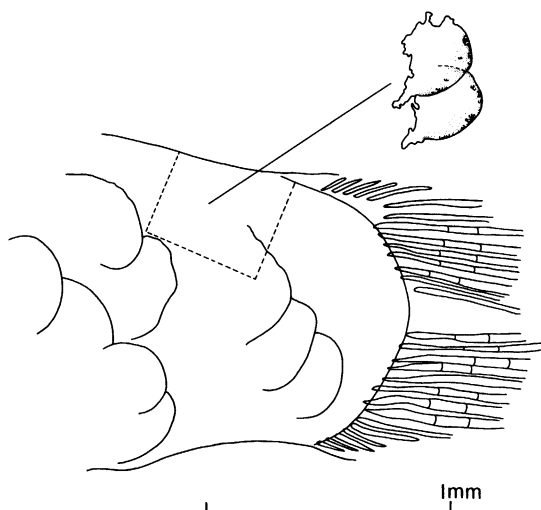|	7	8	9	10	11	12	13	14	15	16	17	18	19	20	n
Dorsal	–	–	–	–	–	2	4	82	18	–	–	–	–	–	106
Pectoral	–	–	10	85	18	2	–	–	–	–	–	–	–	–	115
Pelvic	119	–	–	–	–	–	–	–	–	–	–	–	–	–	119
Anal	–	–	–	–	–	–	–	–	–	–	2	41	36	12	91

FIG. 4.   Scales on caudal peduncle (left lateral view).

54.4 (M 52.56), preanal distance 69.0–73.1 (M 71.09).

Body fairly compressed, its width 1.7–2.2 times in its depth, the latter 1.3–1.8 times in head length. Belly rounded, usually with a shallow median depression with an almost transparent floor between pectoral and pelvic fin bases; the pelvic bones and associated tissues rise out of this depression and make a distinct break in the ventral outline; a similar depression with a semitransparent floor behind the pelvic fins (fig. 3). A series of minute, elongate scutes with narrow armless bases before the pelvic fins (PrVS), usually 5 or 6 (4–10 in additional specimens), of which the first 2–3 are in advance of the pelvic bone, the whole supporting a very low membranous keel about 0.6 mm deep (no prepelvic scutes seen in a fish of 20.8 mm SL); pelvic scute (VS) with distally rounded lateral arms and in the midline a slender antrorse and broader retrorse triangular projection, the former keeled; postpelvic scutes (PoVS) 6–11 (8–12 in additional specimens; two or three fused in some cases) with slender armless bases, the whole supporting a membranous keel from pelvic base to anus (about 0.18 mm deep).

Snout somewhat pointed, a little shorter than eye diameter, the latter 3.0–3.5 times in head length. Mouth small, terminal or lower jaw projecting a little; premaxillae subtrian-

gular but with a low dorsal articulating lobe offset from midline, lower edge with a single series of 9 or 10 small conical teeth on each side reaching almost to distal tip of bone; maxillae short, failing to reach vertical from anterior margin of eye by about ½ pupil diameter, the proximal head of the bone accommodated by a slight inward flexure of the premaxilla, lower edge of expanded portion with a single series of about 15–20 very small conical teeth; first supramaxilla absent, second about as long as pupil diameter, sharply pointed anteriorly, bluntly rounded posteriorly, its depth a little less than expanded portion of maxilla. Lower jaw about three times as long as deep, its articulation just before vertical through eye center, its upper profile rising in two steps to the coronoid process, the dentary bearing a single series of 4–6 small conical teeth on either side of the symphysis. No teeth on tongue, vomer, or pterygoids; three very small conical teeth on inner edge of palatines.

Gill cover with evenly rounded fleshy margin concealing strong posterodorsal and posterior excavations in operculum; suboperculum more or less rectangular; fine cutaneous canals radiating back over gill cover.

Hind border of gill opening smoothly rounded, without a cleithral lobe; sternohyoideus muscle tapering evenly forward, reaching forward to the point at which left and right branchiostegal membranes join (left overlaps right). Gillrakers slender, bladelike, and distally pointed, without serrae; longest raker about twice as long as corresponding gill filaments and about 3.5 in eye or 1.5 in pupil diameter; six short triangular rakers on posterior face of 3rd epibranchial. Pseudobranch present, a little less than eye diameter in length and not reaching to hyomandibular facet, with up to 10 filaments covered for half their length by a thin membrane. Dorsal surface of head with a long triangular anterior frontal fontanelle, also two broad posterior fontanelles (together heart-shaped).

Dorsal fin origin 2–3 eye diameters behind midpoint of body, the longest ray about equal to length of fin base; first unbranched finray (articulating with first pterygiophore) minute or sometimes absent, the 2nd about half length of 3rd, the latter almost equal to the 4th (if present). Pectoral fins set rather low
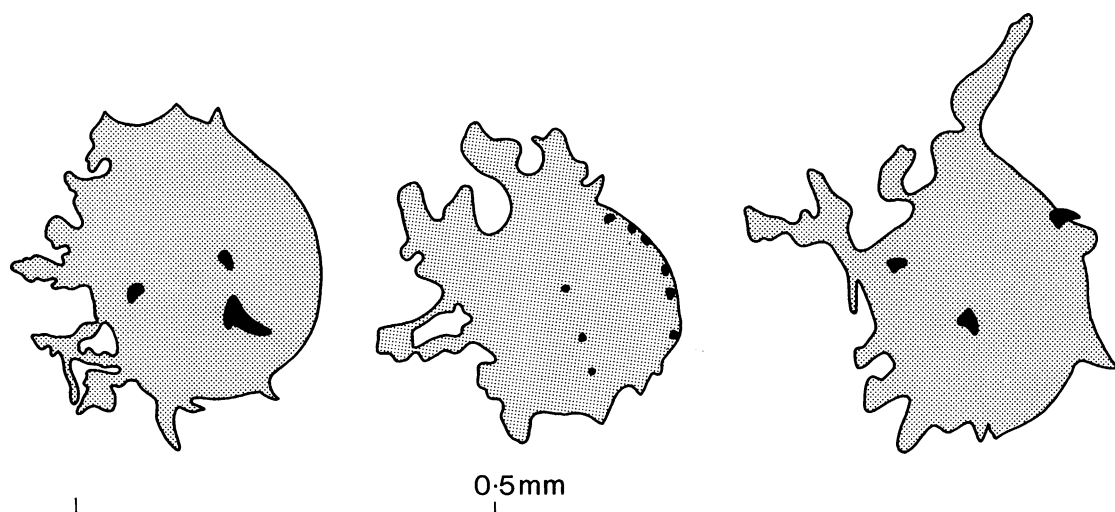
FIG. 5. Three scales from caudal peduncle. Possible denticles shown in black.

on body, their tips failing to reach pelvic fin base by 1.8–2.0 eye diameters; no axillary scale or groove above first finray. Pelvic fins almost an eye diameter before vertical from dorsal fin origin and nearer to anal origin than to pectoral base by about ¾ eye diameter. Anal fin origin below last quarter of dorsal fin base and on a vertical below 7th or 8th branched dorsal finrays, much nearer to pelvic than to caudal fin bases.

Scales present on at least hind part of body, although small, extremely thin, and scarcely visible. They are more easily observed on the caudal peduncle (fig. 4); an elongate scale is often present immediately before the upper and lower 1st procurrent caudal finrays. The peduncle scales illustrated here (fig. 5) have very irregular anterior margins, but perhaps this was caused by their removal from the scale pocket; indicated in black are what appear to be denticles on the scales.

Color (fresh): general body color a warm translucent golden-beige, with a complete absence of silver on the flanks, but a distinct midlateral band of melanophores, most intense anteriorly; swimbladder clearly visible through the flank. Iris intensely silvery. Fins hyaline, but entire lower caudal lobe and lower quarter of upper lobe densely spotted with melanophores (Paul Loiselle, in litt., 11 November 1970—based on observations at Akosombo, Lake Volta, Ghana).

Color (alcohol preserved fishes): body pale brown, with a slightly lighter midlateral stripe;

myosepta clearly visible. A sprinkling of small melanophores on snout, upper part of head and gill cover, as well as on caudal base; a double line of predorsal melanophores and another series at the bases of the anal finrays. The degree of pigmentation variable. Fins hyaline.

VISCERAL ANATOMY (figs. 6–8)

The following description is based on dissection of a number of specimens of both sexes. In parentheses are given measurements and some counts from a ripe male of 24.8 mm SL.[4]

The body cavity is roughly oblong and its length is about 10 times greater than its depth. The foregut and associated organs occupy the lower part of the anterior third. In sexually mature and ripe individuals, the remainder of the body cavity is largely taken up with the gonads and to a lesser extent by the swimbladder. In some specimens there is a certain amount of fatty tissue in spaces between or-

[4] Dissection of such small fishes posed manipulative problems since the entire body cavity in adults is only a little more than a centimeter long. The finest entomological pins make excellent seekers, while minute scalpels can be produced by slicing small wedges from a soft and flexible brand of razor blade by means of sharp scissors (the resulting curl of metal can be gently straightened with fine forceps and mounted in a small corked specimen tube or other holder).
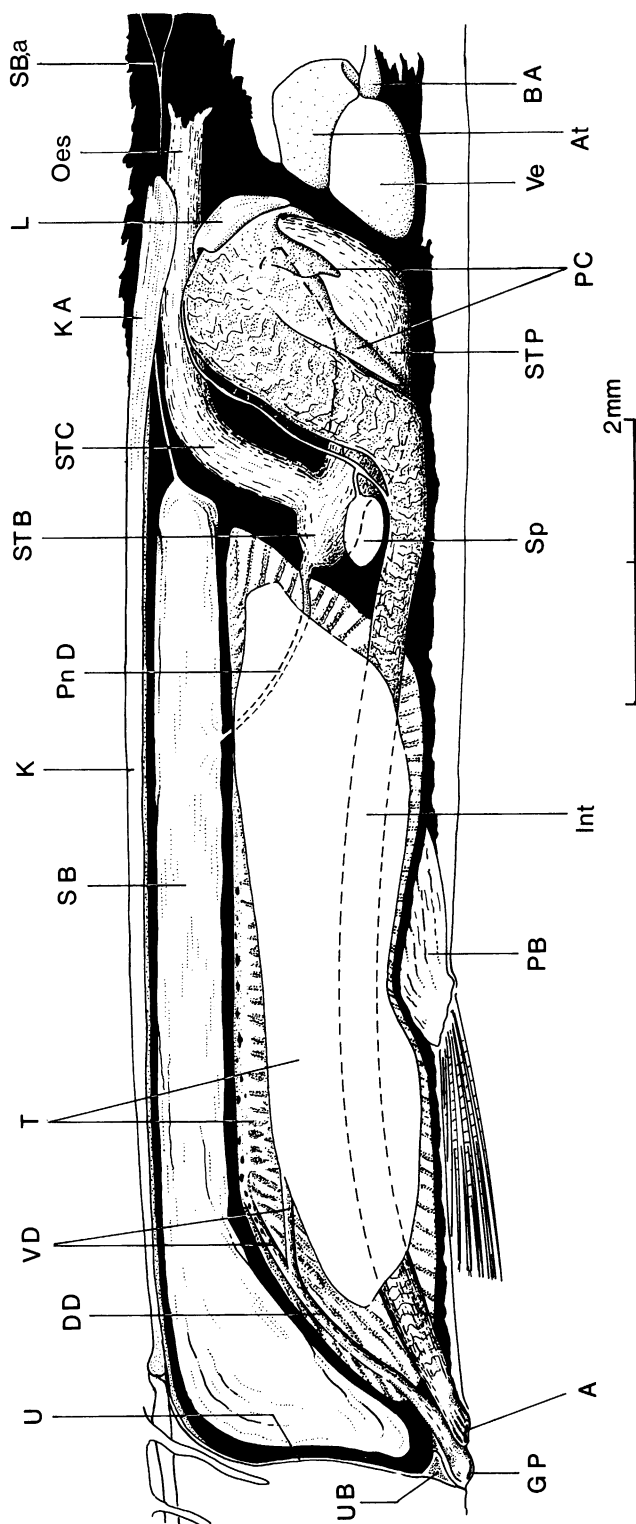
FIG. 6. Visceral organs (right lateral view) in a ripe male, 24.8 mm SL (BMNH 1984.4.24.1–8). **A**, anus; **At**, atrium of heart; **BA**, bulbus arteriosus; **DD**, ductus deferens; **GP**, genital pore; **Int**, intestine; **K**, kidney; **KA**, "head kidney"; **L**, liver; **Oes**, esophagus; **PB**, pelvic bone; **PC**, pyloric caeca; **PnD**, pneumatic duct; **SB**, swimbladder, and **a**, its anterior part; **Sp**, spleen; **STB**, stomach blindsac; **STC**, cardiac stomach; **STP**, pyloric stomach; **T**, testes; **U**, ureter; **UB**, urinary bladder; **VD**, vasa deferentia; **Ve**, ventricle of heart.

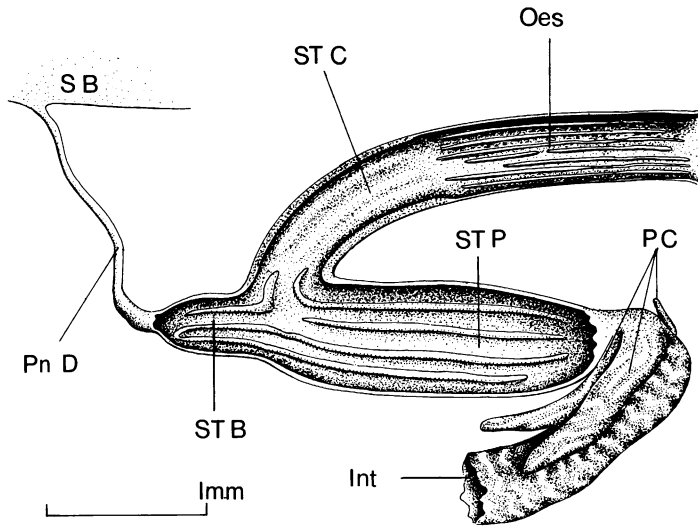FIG. 7. Stomach, showing pattern of mucosal folds (right lateral view, the intestine and pyloric caeca displaced ventrad); same fish as in figure 6. Symbols the same.

gans (white, yellow, or orange globules in alcohol-preserved material).

The *esophagus* (Oes) is a straight, moderately thick-walled and wide tube (1.9 mm long, 0.5 mm outside diameter). Its inner surface bears a number of thin and well-defined longitudinal epithelial folds (17 or 18), most of which run the complete length of the esophagus; in places they appear as fused lines of papillae.

The *cardiac stomach* (STC) (1.6 mm long, 0.5 mm outside diameter), although hardly differentiated from the esophagus externally, has rather thicker walls and only a few (4 or 5) very faint indications of longitudinal folds. Posteriorly it curves ventrad and joins the pyloric stomach at the latter's junction with the blind sac; the posterior end of the cardiac stomach is quite obvious externally.

The *stomach blind sac* (STB) or gastric diverticulum is a well-defined conical projection (0.5 mm long, 0.5 mm diameter at its base) lying horizontally at the angle formed by the cardiac and pyloric portions of the stomach. The mucosa bears a few longitudinal folds (7), which are thicker than those of the esophagus; dorsally, these continue for a short distance into the cardiac stomach, while ventrally they are contiguous with those of the pyloric stomach.

The *pyloric stomach* (STP) is a moderately thick-walled tube (1.8 mm long, 0.8 mm outside maximum diameter). It bulges slightly at its midpoint and is constricted anteriorly at its junction with the intestine (about 0.5 mm outside diameter). Internally there are a number of rather broad longitudinal epithelial folds (7).

The *pyloric caeca* (PC) are asymmetrically arranged, with two large caeca on the right side (longest 1.6 mm) and one large caecum on the left; in some individuals there are one or two very small additional caeca on the left. The caeca are tapering digitiform tubes, thin-walled with vermiform epithelial ridges that are quite visible from the outside.

The *intestine* (Int) rises steeply from its junction with the pyloric stomach (0.6 mm outside diameter). It then forms an inverted U on the right of the cardiac stomach, descends at a steep angle, rises slightly again, and then descends gradually as an almost straight tube to the anus (about 0.4 mm outside diameter). In ripe males it passes between the two testes, while in ripe females it lies in a groove down the right of the single ovary; in all the specimens examined the intestine was strongly compressed. From its origin almost to the anus it bears transverse and approximately zigzag epithelial folds,
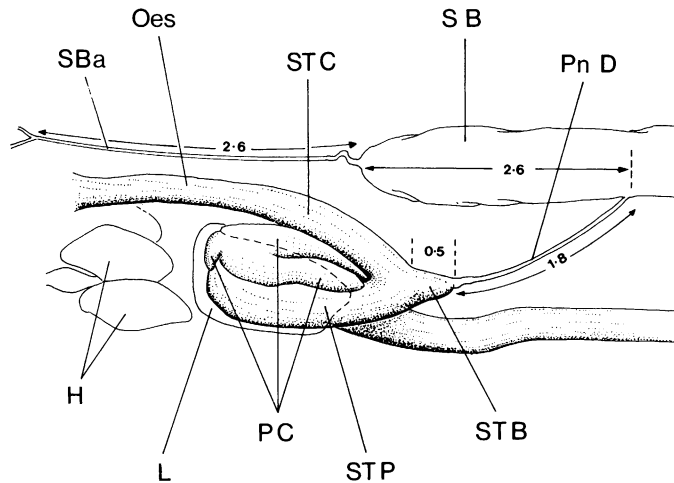
FIG. 8. Anterior portion of digestive tract and swimbladder (left lateral view); same fish as in figure 6. **H,** heart; other symbols the same.

which are clearly visible from the outside; posteriorly, the folds become more annular. Straightened out, the intestine is about 45 percent of SL (about 11 mm long). The entire alimentary tract is about 65 percent of SL (about 16.3 mm long).

The *liver* (L) is asymmetrically placed on the anterior face of the junction between the pyloric stomach and the intestine; on both sides it partly invests the pyloric caeca. The left lobe is larger than the right (1.7 mm long; cf. 0.8 mm) and it reaches more than halfway along the pyloric stomach.

The *pneumatic duct* (PnD) arises from the posterior tip of the stomach blindsac (in the vertical midline but displaced slightly ventrally) and runs diagonally upward to join the expanded portion of the swimbladder at a point about ⅓ along its ventral surface (duct 1.8 mm long). The anterior third of the duct is an irregularly tapering bulb (0.17 mm at widest point), while the remainder is of even and slender bore (0.09 mm outside diameter); the lumen of the bulb appears to be interrupted by several dorsal and ventral septa.

The *spleen* (Sp) is a small oval body on the right of the stomach blindsac just above the intestine.

The *swimbladder* (SB) comprises a large single-chambered posterior sac with a slender anterior tube. The former is extremely thin-walled, transparent, and delicate, barely maintaining its shape in dissected specimens. It is eight times longer than deep (8.3 mm long, 1.1 mm deep), tapers a little anteriorly, but is rounded at its origin below the 5th vertebra (and just above the junction between the esophagus and the cardiac stomach). At about its midpoint the swimbladder is somewhat forced dorsally by the gonads in ripe fishes, but thereafter it expands again and posteriorly curves ventrad, the tip being evenly rounded and without a caecum or tubular extension to the exterior. The anterior portion of the swimbladder (SBa) is a very thin tube (2.9 mm long, 0.05 mm outside diameter), passing (after a small upward convolution) forward beneath the kidneys and bifurcating at the hind end of the skull (presumably to enter across or through the exoccipitals, but this was not seen; see also p. 25).

The *testes* (T) in ripe individuals are paired, laterally compressed, and somewhat elongate organs lying immediately below the swimbladder and closely applied to its ventral surface; there is a distinct ventral excavation in each testis to accommodate the pelvic bone. The left testis is invariably longer than the right (7.2 mm long, 1.6 mm deep; 6.2 mm long, 1.4 mm deep). The numerous vasa efferentia appear white or cream/white, as also does the vas deferens along the dorsal margin of each testis. Left and right testes are sepa-

rate in their anterior third (with the pneumatic duct passing up between them) but are dorsally united by connective tissue after this. Posteriorly the two *vasa deferentia* (VD) merge into a common *ductus deferens* (DD), although each testis has a triangular lobe projecting beyond this. The ductus descends diagonally to the genital pore, lying for the last part of its length just above and closely bound to the intestine. Mature and ripe males were found to range from 23.2 to 26.2 mm SL.

The single (left) *ovary* lies mesially in the body cavity, immediately below the swimbladder and closely applied to it. Anteriorly, the ovary becomes dorsoventrally bilobed following the line of a shallow groove down its right side, along which the intestine passes; the upper and lower lobes of the ovary are slightly displaced to the left and right, respectively. The lower lobe is thinner and shorter than the upper (3.6 mm to tip of lower lobe, 4.2 mm to tip of upper lobe, greatest depth of ovary 1.05 mm in a female of 22.5 mm SL). The division of the ovary into upper and lower lobes is perhaps not the result of fusion of left and right ovaries in early ontogeny, for in a female of 18.1 mm SL, a minute and presumably atrophied right ovary was found (main body of ovary 1.23 mm long, 0.11 mm deep) which was quite separate from the much larger left ovary (2.05 mm long, 0.4 mm deep); the latter, however, was not (yet?) lobed anteriorly. Eggs in an apparently ripe female of 23.0 mm SL were 0.2 mm in diameter and almost all appeared to be at the same stage of development; the ovary contained about 200 eggs. The single oviduct descends diagonally as a wide but tapering tube which is closely applied to the final part of the intestine. Mature females were 21.5–24.0 mm SL.

The *kidneys* (K) form a slender, strap-shaped organ lying retroperitoneally between the swimbladder and the vertebral column and extending the whole length of the abdominal cavity. The pars anterior or "head kidney" (KA) is bifurcated, parting above the anterior third of the esophagus, with the tubular portion of the swimbladder passing forward between the fork; the right lobe is the larger. Left and right sides of the kidney are more or less separate over most of their length (with possible fusion or contact in places), but are quite separate in the posterior third, being divided by the posterior cardinal vein; at the termination of the kidney the two sides merge, the caudal vein immediately after its exit from the first hemal arch, passing over this loop and continuing forward as the posterior cardinal vein. In preserved material the kidneys are white or cream, with large stellate chromatophores on the underlying peritoneum.

The *ureters* (U) follow the slightly crenellated lateral margins of the final third of the kidneys before descending the posterior boundary of the body cavity as a pair of narrowly separated slender tubes to enter the pyriform *urinary bladder* (UB) at the extreme posteroventral corner of the abdominal cavity; the point at which the ureters pass through the peritoneum appears to be close to their entrance to the bladder. The latter is closely wedged between the posterior end of the swimbladder and the dorsal wall of the genital duct.

The *anus* (A) is immediately behind the termination of the postpelvic keel; its rim projects slightly and its anterior surface bears part of the final postpelvic scute. At the extreme end of the intestine, the mucosal folds become longitudinal and reach the rim of the anus, usually with an alternation of deep and narrow folds. The *genital opening* (GP) is immediately behind the anus, in females being a simple pore, but in males bearing a fleshy lip on each side to form a genital papilla. The *urinary pore* is minute and lies just behind. All three openings are on the midline and are bypassed on either side by the protractor analis muscle, which is very clearly seen anterior to the level of the genital pore.

SKELETON

The following description is based mainly on the five alizarin specimens used for the meristic counts (22.5–26.7 mm SL, BMNH 1970.9.24.177–216). Three further alizarin specimens were counter-stained with alcian blue to show cartilage (26.8–29.0 mm SL, BMNH 1973.11.13.11–32), although to some extent cartilage boundaries can be explored in alizarin specimens by shifting a very small black object (plastic strip) back and forth below the body part in question. Some dissec-
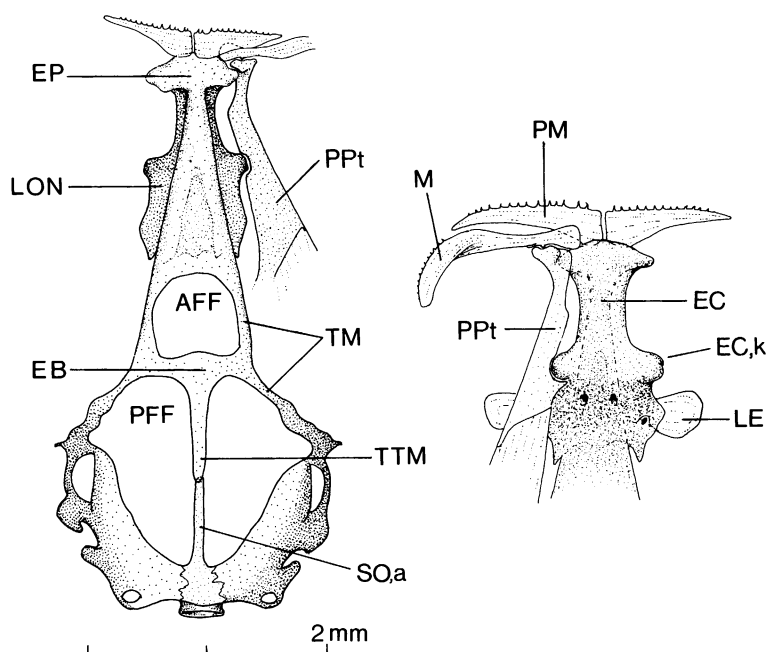
FIG. 9. Chondrocranium (dorsal view on left, slightly more enlarged ventral view on right showing ethmoid region). **EB,** epiphysial bar; **EC,** ethmoid cartilage and **k,** its lateral "knob"; **EP,** ethmoid plate; **LE,** lateral ethmoid; **LON,** lamina orbitonasalis; **M,** maxilla; **PFF,** left posterior frontal fontanelle; **PM,** premaxilla; **PPt,** palatopterygoid cartilage; **SO,a,** anterior extension of supraoccipital; **TM,** taenia marginalis; **TTM,** taenia tecti medialis.

tion was achieved using the microscalpels described earlier (hyopalatine arch, gill basket, circumorbital series, etc.), but disarticulation of the braincase proved impossible without damage to its elements, so that this region is described more superficially. It was possible, however, to clarify some details from the scanning electron microscope (SEM) photographs of a fish about 25 mm SL (from BMNH 1971.11.26.1–12).

CHONDROCRANIUM (fig. 9, also fig. 10)

Although the head bones (especially the dermal bones) are more or less well-ossified in the adults, most of the larval cartilaginous template of the skull persists without resorption or mineralization. The *ethmoid cartilage* (EC) is triangular in lateral view. Dorsally, it continues on each side as a supraorbital bar, the *taenia marginalis* (TM), that underlies the frontal and frames a *frontal fontanelle* (AFF), which is broader but shorter than that

framed by the frontal bones. Ventrally, the ethmoid cartilage tapers back as a median bar, the *trabecula communis* (TC), overlying about the first third of the parasphenoid. The *ethmoid plate* (EP), forming an anchorage or point of articulation for virtually all the bones of the snout, has prominent lateral projections (EP,l) on which lie part of the maxilla head and against which the clubbed head of the *palatopterygoid cartilage* (PPt) articulates; the latter runs back quite broadly to an oblique junction with the endopterygoid, then continues as a slender mesial edge to that bone before joining the extensive cartilage of the quadrate/symplectic area. The dorsal portion of the ethmoid cartilage broadens behind the slender neck of the ethmoid plate and houses the conical *anterior myodome* (AM) for the superior oblique eye muscles (arrow in fig. 10), the myodome tube undivided by any septum. Below the myodome, the ethmoid cartilage narrows to a vertical plate, along the ventral edge of which on each
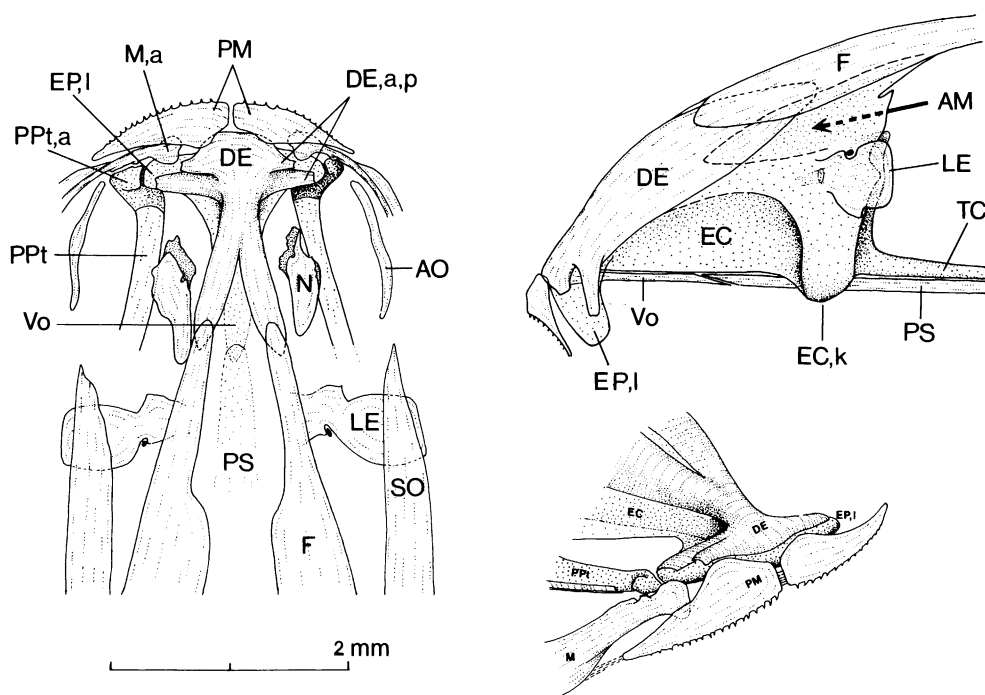
FIG. 10. Ethmoid region (dorsal, left lateral, and right anterolateral views). **AM,** anterior myodome; **AO,** antorbital; **DE,** dermethmoid and **a, p,** its anterior and posterior lateral processes; **EC,** ethmoid cartilage and **k,** its lateral "knob"; **EP,** ethmoid plate and **l,** its lateral projections; **F,** frontal; **LE,** lateral ethmoid; **M,** maxilla and **a,** its anterior expanded head; **N,** nasal; **PM,** premaxilla; **PPt,** palatopterygoid cartilage and **a,** its articular head; **PS,** parasphenoid; **TC,** trabecula communis cartilage; **Vo,** vomer.

side is a horizontal plate, the *lamina orbitonasalis* (LON), which expands below the lateral ethmoid into a prominent "knob" (EC,k) that fits closely into a recess on the inner edge of the palatopterygoid bar. From the knob, which marks the broadest point of the ethmoid cartilage, the hind lateral margin of the ethmoid block rises almost vertically, about halfway up producing a small wing supporting the lateral ethmoid bone. Two paired foramina penetrate the ethmoid cartilage in this region; the first emerges anterolaterally through an indentation on the upper edge of the lateral ethmoid bone (passage of orbitonasal vessels), while the second, which is larger and nearer to the midline, passes forward through the hind wall of the ethmoid block and conducts the olfactory nerves (I).

In dorsal view the taeniae laterales are bridged at their midlength by a moderately broad transverse *epiphysial bar* (EB), which is produced posteriorly as a tapering *taenia*

tecti medialis (TTM) that reaches back to meet the anterior extension of the supraoccipital bone. The hind part of the chondrocranium is extremely complex, and at this small size and with the rather heavy alcian blue stain tending to obscure both bone and internal contours, it proved impossible to explore it in detail.

ETHMOID REGION (fig. 10)

The principal (and probably only) dermal ossification, covering the anterior part of the ethmoid cartilage, is the *dermethmoid* (DE), a well-defined funnel-shaped plate that is pinched around the slender ethmoid neck. In front of the neck the dermethmoid expands over the rostral mass of the ethmoid plate to produce a triangular or rhomboid plate of bone that bears short paired lateral projections and, below and behind them, rather longer paired projections (DE,a,p). Poste-
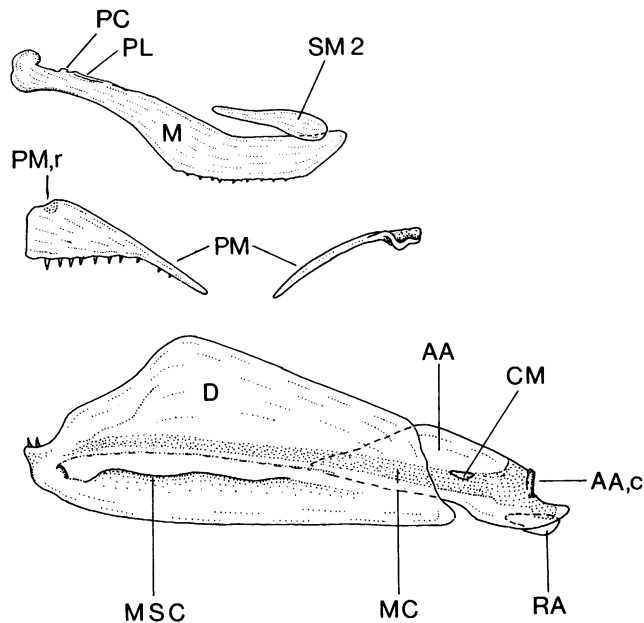
FIG. 11. Maxilla, premaxilla, and lower jaw (left lateral views, also dorsal view of premaxilla). **AA,** anguloarticular and **c,** its condyle for articulation with the quadrate; **CM,** coronomeckelian; **D,** dentary; **M,** maxilla; **MC,** Meckel's cartilage; **MSC,** mandibular laterosensory canal; **PC,** palatomaxillary condyle; **PL,** palatomaxillary ligament attachment; **PM,** premaxilla and **r,** recess for maxilla head; **RA,** retroarticular; **SM2,** 2nd supramaxilla.

riorly, the dermethmoid is bilobed, the two laminar wings being overlain at their tips by the frontals.

There is no indication of a "rhinal" element, such as has been claimed for *Congothrissa* by Taverne (1977).

The *lateral ethmoid* bones (LE) become increasingly well-ossified distally and emerge beyond the boundary of the ethmoid cartilage as rounded and almost vertical wings that mark the anterior boundary of the eye. As noted above, where the upper margin of the wing meets the ethmoid cartilage, there is a small foramen.

There appears to be no *mesethmoid* ossification (called ventral or hypoethmoid by some authors), although this might be represented by the horizontal plate of the ethmoid cartilage.

The *vomer* (Vo) is a thin toothless bone that tapers to a point posteriorly and has a slight thickening and two short lateral processes at its head. Anteriorly, it fails to contact the dermethmoid, being separated by the cartilaginous ethmoid plate, while posteriorly

it is held firm by the ethmoid cartilage until it is overlain by the anterior tip of the *parasphenoid* (PS); the vomer head seems to have incorporated ethmoid material (in *Clupea* the vomer head includes a distinct endoskeletal ossification of the ventral ethmoid; see Patterson, 1975, p. 501).

Jaws (figs. 10, 11)

The *premaxillae* (PM) are approximately triangular, the deepest point being slightly offset from the midline and the distal third being drawn out into a slender arm; the bones are slightly curved in both the horizontal and the vertical planes. Medially they are bound together; at their deepest point they are applied to the anterior edge of the dermethmoid. There is a slight flexure in the upper margin of the bone near its deepest point and this forms a small indentation on the inner face into which fits the lower half of the expanded maxilla head (PM,r). A single series of conical teeth (9 or 10) is present on each side of the upper jaw.

The *maxillae* (M) are fairly slender flattened bones with a well-defined proximal head, a more slender central shaft, and an expanded distal blade. The head bears a dorsal flange, which lies on the front edge of the ethmoid plate, and a ventral flange that fits into the indentation of the premaxilla. The shaft lies at about 60° to the horizontal and is slightly rounded along its upper margin; it bears a minute knob that forms the articulation with the head of the palatopterygoid cartilage (PC) and, distal to this, a low condyle for the palatomaxillary ligament (PL). The distal blade of the maxilla, which is approximately horizontal when the mouth is closed, is not greatly expanded (depth six times in the total length of bone); its ventral margin is enlarged to provide attachment for the pointed tip of the premaxilla, while distally it sweeps upward to form a rounded point. There are 15–20 small conical teeth irregularly spaced along the ventral margin of the blade.

There is a single *supramaxilla* (SM2), being the 2nd or posterior (1st or anterior lost); anteriorly it is slender and pointed, posteriorly expanded and spatulate, its greatest depth being 1½ times in the depth of the maxilla blade.

When the lower jaw is depressed, the maxilla swings downward, slightly outward, and twists slightly forward, pivoting at its dorsal edge on the pad of the palatopterygoid head, while the dorsal flange of the maxilla head appears to slide over the cartilaginous wing of the ethmoid; the ventral expansion of the maxilla head helps to rotate the premaxillae forward and their distal tips outward. The supramaxilla rotates upward, its anterior shaft apparently serving to reinforce the membrane at the side of the mouth.

In lateral view the lower jaw forms an irregular triangle, the highest point of the coronoid process being at the first quarter of the jaw; anteriorly, the dorsal profile rises by a small subsidiary step immediately after the toothed and thickened mental area; there are four to six small conical teeth. The *dentary* (D) accounts for four-fifths of the lower jaw; in its ventral third it has a longitudinal mesial inflexion and externally a flange that forms the roof of the mandibular laterosensory canal (MSC); the external walls of the canal are not clearly ossified and perhaps only exist anteriorly (there is a distinct anterior pore penetrating a bony bridge).

Meckel's cartilage (MC) appears as a slender cord running above the inflexion of the dentary; at its posterior tip (just before the lower jaw articulation) it appears to merge with a small mesial plate of bone that fuses with the condyle of the anguloarticular. A little posterior to the overlap between the dentary and the articular proper, the dorsal surface of Meckel's cartilage bears a small and irregularly shaped (occasionally double) ossification, the *coronomeckelian* or sesamoid articular (CM).

The *anguloarticular* (AA) (called angular or articular by some authors), which is about half the length of the lower jaw, is pointed anteriorly and penetrates almost half its length along the inner face of the dentary; dorsally, there is no gap between it and the dentary. Posteriorly, the articular bears a strong condyle for articulation with the head of the quadrate (AA,c); below the condyle the bone has a small and slender projection.

The *retroarticular* (RA) is a small discrete bone applied to the inner face of the posterior projection of the articular and hidden by it externally except for a small ventral portion; it makes no contribution to the articulation of the lower jaw and indeed it is difficult to see what function it can serve (except perhaps for attachment of the protractor hyoidei muscle—see fig. 13, m.ph).

CIRCUMORBITAL SERIES (fig. 12)

The *supraorbital* (SO) is a slender, well-ossified bone supported posteriorly by a lateral expansion of the frontal; it twists anteriorly from almost horizontal over the eye to vertical. The *antorbital* (AO), which is loosely attached to the anterior end of the supraorbital, is also a slender bone, of slightly varying shape but usually tapering anteriorly. The *lacrymal* (L) (first infraorbital), which is often rather poorly ossified anteriorly, is again slender; it has a narrow longitudinal flange on the lateral face that provides the roof of the infraorbital laterosensory canal and, posteriorly, a part of its lateral wall; with the jaws closed, the lacrymal conceals the upper part of the 2nd supramaxilla. The 2nd and 3rd
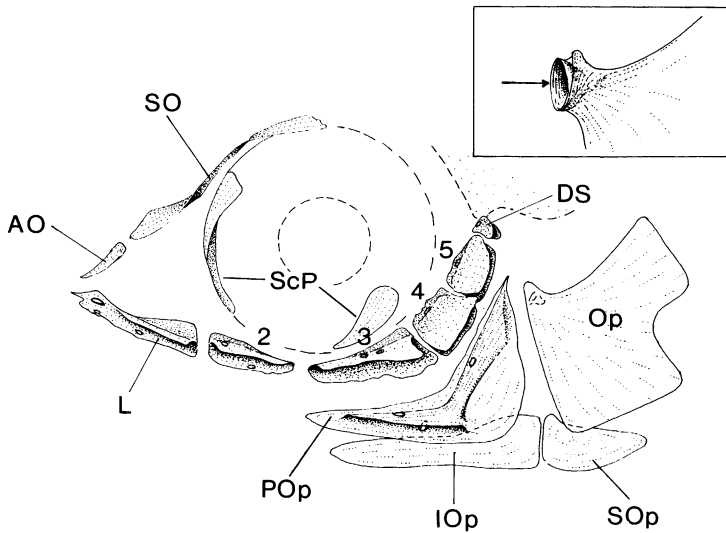
FIG. 12. Circumorbital and opercular bones (left lateral view) and inset of operculohyomandibular facet (arrowed). **AO,** antorbital; **DS,** dermosphenotic; **IOp,** interoperculum; **L,** lacrymal (1st infraorbital); **Op,** operculum; **POp,** preoperculum; **ScP,** sclerotic plates. Infraorbitals 2–5 numbered.

infraorbitals also bear a flange housing the canal and this becomes deeper posteriorly until it provides the entire lateral wall of the canal; the outer margins of these bones are well separated from the anterior edge of the preoperculum. The 4th and 5th infraorbital bones are saddle-shaped, the inner and outer walls almost equally embracing the canal. The *dermosphenotic* (DS) is a very small saddle-shaped bone whose dorsal tip is applied to the anterior corner of the frontal wing that covers the recessus lateralis. Along the upper margin of these six canal-bearing bones there are (from front to rear) 1,1,2,1,1,1 small round foramina for entry of the nerves serving the neuromasts. There are two *sclerotic plates* (ScP) in the eye, the larger anterior plate projecting laterally beyond the margin of the supraorbital.

OPERCULAR SERIES (fig. 12)

The *operculum* (Op) is relatively small, with a deep posterior excavation so that the bone is virtually bilobed, the upper lobe being the smaller and lying at an angle of about 45°; the anterodorsal angle of the bone is produced into a short and rounded projection (insertion of the dilatator operculi muscle), which supports internally a shallow cuplike articulation that hinges on a cartilaginous pad on the anterior face of the hyomandibula. The *suboperculum* (SOp) is triangular and is just overlapped by the anteroventral angle of the operculum; its anterior margin is more or less vertical and meets or is slightly overlapped by the longer and more heavily ossified *interoperculum* (IOp). The latter is overlain dorsally by the preoperculum (POp), an L-shaped bone with the preopercular canal entirely enclosed on the vertical limb but roofed and only partly walled by bone on the horizontal limb; there is a single foramen on the upper limb, while the lower limb bears two.

HYOPALATINE ARCH (fig. 13)

The *palatine* (PL), which is the only toothed bone of the palate, is short and flat, lying as a narrow plate on the underside of the palatopterygoid cartilage. Anteriorly, the cartilage has a mesial articulation with the lateral wing of the ethmoid plate while at its midlength it produces a medial wing or projection that fits around the lateroventral "knob" of the ethmoid cartilage (fig. 10, EC,k). The palatine bone is thus held very firmly to the ethmoid block. It has two or three small conical teeth on its inner edge.
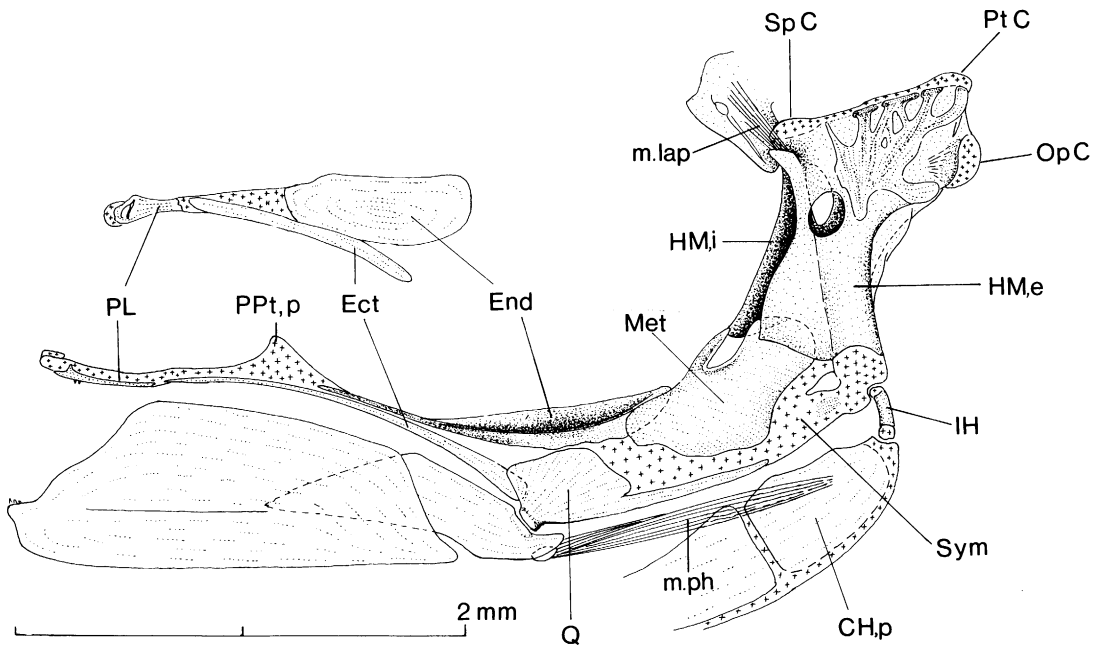
FIG. 13. Hyopalatine arch (left lateral view), with dorsal view of palatine and pterygoids (less enlarged). **CH,p,** ceratohyal, posterior part; **Ect,** ectopterygoid; **End,** endopterygoid; **HM,i** and **HM,e,** hyomandibula, internal and external walls; **IH,** interhyal; **Met,** metapterygoid; **m.lap,** levator arcus palatini muscle; **m.ph,** protractor hyoidei muscle; **OpC,** opercular condyle of hyomandibula; **PL,** palatine bone; **PPt,p,** palatopterygoid cartilage, process adjoining lateral "knob" of ethmoid cartilage; **PtC,** pterotic condyle of hyomandibula; **Q,** quadrate; **SpC,** sphenotic condyle of hyomandibula; **Sym,** symplectic.

The *ectopterygoid* (Ect) is long, flat, and slender, forming an evenly arched vault at the side of the mouth. Anteriorly, it underlies the palatopterygoid cartilage, but fails to meet the hind tip of the palatine; in its middle section it is closely applied to the edge of the endopterygoid, while posteriorly it is underlain by the quadrate. The *endopterygoid* (End) is much shorter and broader and at its widest point is depressed as a shallow cup under the eye. Anteriorly, it merges obliquely with the palatopterygoid cartilage; lateral to its midline it has a ridge along most of its length; ventrally, it makes a short and uneven contact with the quadrate, but does not overlap it. The *metapterygoid* (Met), which anteriorly just overlaps the endopterygoid, is an irregular but somewhat oval bone which is itself overlapped dorsally by the hyomandibula, but ventrally appears to overlie the cartilaginous plate of the symplectic; posteromesially, it has a small arm that rises up to contact the internal wall of the hyomandibula.

The *quadrate* (Q) is rhomboidal, with a long and slender posterior arm overlying the symplectic (and perhaps strengthening it); the bone becomes increasingly ossified and sturdy toward the condyle for the lower jaw articulation, which faces slightly downward.

The *symplectic* (Sym) is represented by a thin sheet of cartilage which extends from the main body of the quadrate backward to the ventral margin of the hyomandibula; a hint of ossification was seen as an oval patch at the posterior part of the sheet of cartilage, above which is a foramen.

The *hyomandibula* (HM, e and i) is inclined very slightly backward. Its upper edge is almost straight and bears a narrow strip of cartilage which swells at either end to form the sphenotic and pterotic condyles (SpC, PtC); below the latter is a third cartilaginous pad, the condyle for the opercular hinge (OpC). Reinforcing this upper part of the bone is a system of densely ossified coalescing struts. The lower part of the hyomandibula
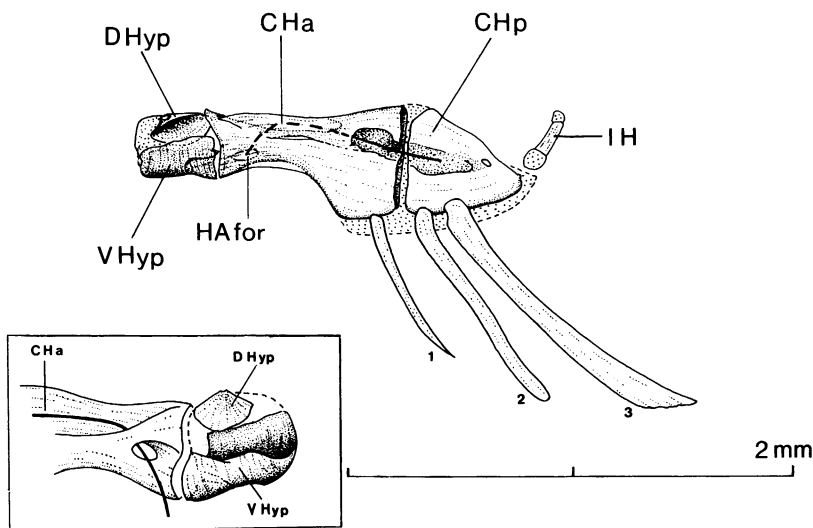
FIG. 14. Hyal arch and branchiostegal rays (left lateral view), with inset of hypohyals (left side in median view, more enlarged). **CHa,p,** anterior and posterior ceratohyals; **DHyp,** dorsal hypohyal; **HAfor,** foramen for hyoid artery; **IH,** interhyal; **VHyp,** ventral hypohyal. Heavy line shows course of hyoid artery.

comprises internal and external walls, with an open passage between them. The external wall has a small and dorsally directed projection just below the sphenotic condyle (for insertion of a part of the levator arcus palatini muscle, m.lap). Descending from this at a slight angle is a diagonal tubelike strut of bone which is continued a short distance ventrally as cartilage (where it joins the symplectic and provides a cup for the articulation of the interhyal). Dorsally, the internal wall of the hyomandibular has a large oval foramen, which is opposite a smaller and round foramen in the external wall (passage for the hyomandibula branch of the facial nerve).

HYAL ARCH AND BRANCHIOSTEGAL
RAYS (fig. 14)

The two paired hypohyals are platelike perichondral ossifications, each investing a cartilaginous mass. The *dorsal hypohyals* (DHyp) are patelloid caps of bone, tilted slightly inward toward the midline, with a small round knob of cartilage at the tip of the cone (which points directly into the interspace between the basihyal and the first basibranchial). The *ventral hypohyals* (VHyp)

lie in the vertical plane, forming somewhat V-shaped plates with the outer face a little higher than the inner, the space between being a block of cartilage that extends forward beyond the bone itself; posteriorly, there is a cartilage-filled cup (opposite to a similar cup in the lower part of the anterior ceratohyal) which is separated from the upper part of the bone by a triangular vane.

The two paired ceratohyals are bladelike and tilted outward at an angle of about 30°; they are slightly flexible at the cartilaginous joint between the anterior and posterior parts. The *anterior ceratohyals* (CH,a) are expanded anteriorly, waisted and laterally compressed in their central portion, and strongly expanded and compressed posteriorly. The inner and outer walls fail to meet in the final third of the ventral midline, while dorsally there is an open groove in the central part of the bone, the inner wall folding across to form the floor of the principal feature, the channel for the hyoid artery, which runs through the upper part of the bone; after entering from an oval anterior foramen on the inner face, it passes upward into the open channel, is roofed posteriorly, but ends with a lateral fenestra which extends to the posterior bound-

ary of the bone. In its posterior, expanded portion, the bone is fairly broadly edged with cartilage.

The *posterior ceratohyals* (CH,p) (epihyals of authors) are triangular and essentially thin pairs of plates joined along the dorsal midline but open ventrally and edged with cartilage; the outer plate is fenestrated anteriorly, being bent inward at this point to form the groove for the hyoid artery.

The *interhyal* (IH) is a slender, short, and hollow bone, clubbed at either end with a bulb of cartilage; it articulates with the cartilaginous tips of the posterior ceratohyal and the hyomandibular.

There are usually three *branchiostegal rays* (range two to four), increasing in width and length posteriorly, whose proximal tips are loosely applied to the outer faces of the anterior (1st) and posterior (2nd, 3rd) ceratohyals. The 1st and 2nd branchiostegals are clearly associated with their respective bones and do not lie in the interface between them (five specimens).

BRANCHIAL SKELETON (figs. 15–17)

As might be expected, there is a marked lack of ossification in many of the gill arch elements, especially on the floor of the branchial basket (basibranchial and hypobranchial series). Even the most heavily ossified elements have a fairly substantial ball or plate of cartilage at either end, so that most of the points of articulation are broadly cartilaginous.

The *basihyal* (BH) comprises a thin and elongate bony plate which is very slightly hollowed down the middle but posteriorly folds down into a hemicylinder. It overlies a much broader and posteriorly much thicker cartilaginous mass; since the clupeoid basihyal is an endochondral and not a dermal bone, and since it usually remains partly or completely unossified, the ossified portion is here interpreted as a dermal plate; it bears no teeth.

The *basibranchials* (BB1–4) are difficult to interpret and are rather different from the pattern found by Nelson (1970, p. 12) in seven other West African pellonuline genera, where teeth or toothplates are absent on basibranchials 1–4 (also on infrapharyngobranchials 1–4):
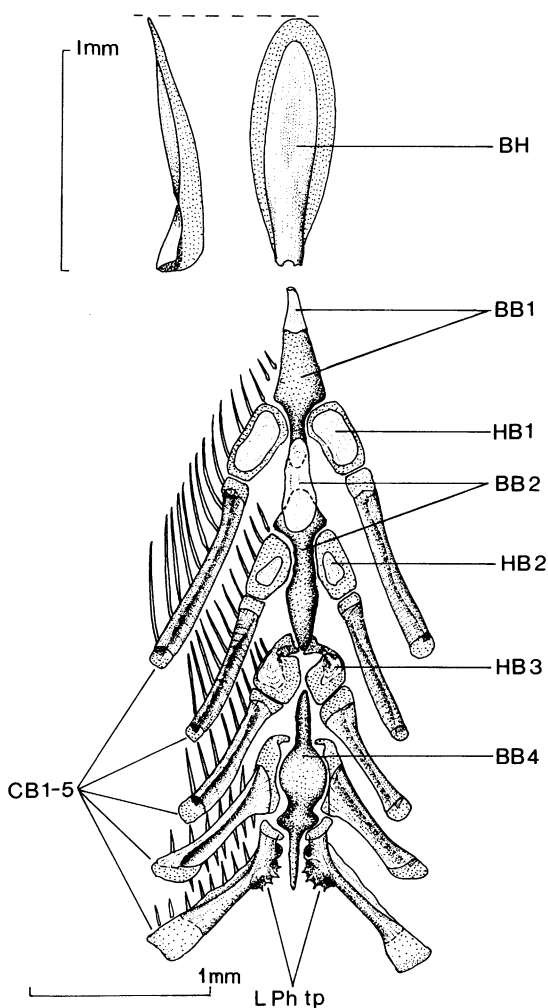

FIG. 15. Lower gill arch elements (dorsal view, basihyal slightly enlarged and also in right lateral view; gillrakers shown on left side only). **BB1-4,** basibranchials and their bony plates; **BH,** basihyal and its bony plate; **CB1-5,** ceratobranchials and their bony plates; **HB1-3,** hypobranchials and their bony plates; **L Ph tp,** lower pharyngeal toothplate.

BB1   A slender cartilage shaped like an arrowhead, the lateral excavations housing the heads of the 1st hypobranchials; anteriorly, there is a short triangular plate of bone, toothless and becoming poorly ossified posteriorly (perhaps a perichondral ossification and not a dermal plate); two short gillrakers on each side (fish of 25.6 mm SL, cited hereafter).
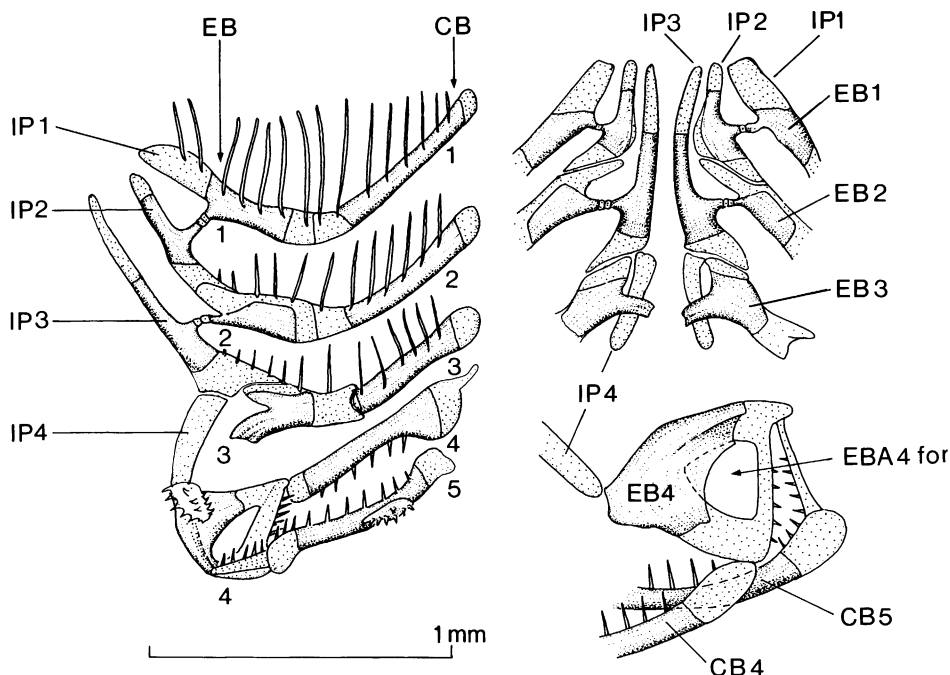
FIG. 16. Upper gill arch elements (on left, ventral view of left side, the ceratobranchials reflected outward; at top right, dorsal view; at bottom right, lateral view of left 4th epibranchial). **CB1-5,** ceratobranchials; **EB1-4,** epibranchials; **EBA4for,** foramen for 4th efferent branchial artery; **IP1-4,** infrapharyngobranchials.

BB2 A blunter arrowhead, the excavations housing the 2nd hypobranchials, the "tail" reaching back to the 3rd hypobranchials. Spanning BB1 and BB2 and overlapping the tips of each is an elongate bony plate without teeth. It is interpreted here as belonging to the 2nd cartilaginous basibranchial element and having extended forward.

BB3 No discrete cartilaginous element present; perhaps represented by the posterior "tail" of BB2, or the pointed anterior projection of BB4. No toothplate present.

BB4 A spindle-shaped cartilage, pointed at either end, with a larger anterior bulge (articulation of the 4th ceratobranchials) and smaller posterior one (articulation of 5th ceratobranchials). The anterior point is wedged between the 3rd hypobranchials. Clupeoids normally have four basibranchials; the present cartilage could be the 4th, perhaps with

the 3rd fused to it, rather than a 3rd that has migrated back.

There are three pairs of *hypobranchials* (HB1-3), as in other clupeoids, of which the last pair are the best ossified:

HB1 Slightly elongate rectangular plates with an upper and a lower bony portion (united along the medial edge) which sandwich the more extensive cartilaginous plate; four gillrakers along the outer edge.

HB2 Rather poorly ossified and vaguely rectangular plates, shorter than the preceding and with upper and lower portions not joined along the medial edge; the cartilaginous part is more extensive and much of its inner edge abuts the 2nd basibranchial; three gillrakers along outer edge and a fourth in front.

HB3 Small bony plates, each bearing a well-defined digitiform process that points downward and is surrounded by a me-

dially directed horn of cartilage that underlies the posterior tip of the 2nd basibranchial; the main plate of cartilage is rectangular; three short gillrakers on outer face.

There are five rather better ossified pairs of *ceratobranchials* (CB1–5), the usual number in clupeoids, and these form the largest and most robust elements in the gill basket; the last is a toothbearing bone:

CB1 The longest of all the paired bones of the gill arches; slightly curved, tubular, with a ventromedial cartilage-filled groove and cartilaginous tips; nine gillrakers along the anterior face.

CB2 About three-quarters the length of the previous pair and similar in shape, except that the tube is complete anteriorly; cartilage fills the tube and provides articulating pads at either end; eight gillrakers, the first borne on the cartilage.

CB3 Shorter, but similar in shape to the previous pair, except that the anterior head is slightly broader.

CB4 Similar, but with the anterior head much more expanded and ending in a very broad cartilaginous pad that hugs the anterior bulge of the 4th basibranchial and ends in a mesially pointing hook (somewhat similar to the hooks on the 3rd hypobranchials); six gillrakers on the anterior face and seven on the posterior face.

CB5 More complex in shape, being curved into the midline anteriorly, with a thin lamella of bone running laterally along the hollow of this curve; anteriorly, a knob of cartilage meets the posterior bulge of the 4th basibranchial and also approaches the cartilaginous pad at the base of CB4; just behind the anterior head of each bone and firmly fused to its dorsomedial edge is an approximately semicircular toothplate, the *lower pharyngeal toothplate* (L Ph tp), which projects toward the midline and bears two rows of small and very slightly curved conical teeth (about five or six in each row); eight gillrakers on the anterior face.
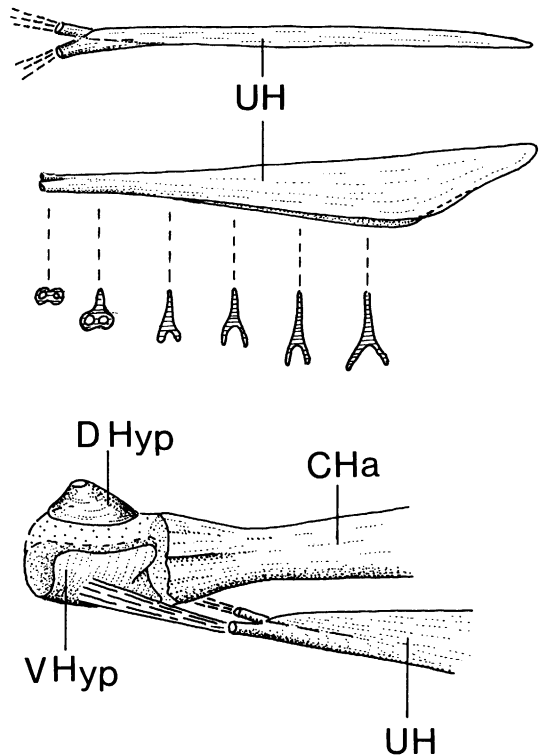

FIG. 17. Urohyal (dorsal and below it left lateral view, with approximate cross-sections) and enlarged view of its attachment to the ventral hypohyal. **CHa,** anterior ceratohyal; **DHyp,** dorsal hypohyal; **UH,** urohyal; **VHyp,** ventral hypohyal.

There are the usual four pairs of *epibranchials* (EB1–4) found in clupeoids, the first three not very strongly ossified and with rather substantial areas of cartilage at their ends:

EB1 The longest, with the upper portion ossified, bearing a small posteromedially directed limb whose cartilaginous tip meets a similar projection from the 2nd infrapharyngobranchial; four gillrakers on the bone and one in front.

EB2 Shorter, but of the same general shape, the small bony limb meeting that of the 3rd infrapharyngobranchial; three gillrakers.

EB3 Again similar in shape, but the bony limb is now as stout as the rest of the bone and is hooked medially to pass over the 4th infrapharyngobranchial; three gillrakers.

EB4 Essentially triangular, the inner part rather strongly ossified and Y-shaped, the outer part cartilaginous and forming an almost vertical bar between the two arms; between bony and cartilaginous parts there is a well-defined triangular foramen for the *4th efferent branchial artery* (EBA4for); at the dorsolateral apex of the triangle a slender support of connective tissue joins the posterior (cartilaginous) tip of the 5th ceratobranchial, with five short gillrakers along its inner edge; the ventrolateral angle of the triangle makes a broad junction with the posterior (cartilaginous) tip of the 4th ceratobranchial, with five short gillrakers on the vertical arm and facing those just mentioned; the inner (bony) angle of the triangle is joined to the 4th (cartilaginous) infrapharyngobranchial and overlapping this junction is the upper pharyngeal toothplate, a semicircle of bone only loosely attached, with about a dozen short, slightly curved, and conical teeth; whereas the lower pharyngeal toothplates are firmly fused to their supporting bones (5th ceratobranchials), the upper pharyngeals are free and capable of considerable independent movement.

There are four distinct *infrapharyngobranchials* (IP1–4), of which the 1st and 4th are entirely cartilaginous; since the upper pharyngeal plate should presumably be borne by the 5th infrapharyngobranchial, perhaps this element has become incorporated into the 4th epibranchial. In the midline, the infrapharyngobranchials are fairly closely apposed, although not actually joined:

IP1 Assumed to be the tapering and entirely cartilaginous rod joined to the tip of the 1st epibranchial; it bears two small gillrakers which continue the epibranchial series.

IP2 Fairly slender and slightly tapering, with a short anterolaterally directed arm articulating with that of the 1st epibranchial; the bone passes into cartilage at either end, the posterior tip being broadly united with the tip of the 2nd epibranchial. Two small gillrakers.

IP3 Longer and more slender, but again with a small anterolaterally directed arm, which articulates with that of the 2nd epibranchial; anteriorly the bone is continued as a slender cartilaginous rod lying sagittally and reaching as far forward as the cartilaginous tip of the preceding infrapharyngobranchial; there is a firm cartilaginous joint with the closely apposed tips of the 3rd epibranchial and IP4; four short gillrakers continue the epibranchial series.

IP4 A slender and entirely cartilaginous rod passing under the bony arm of the 3rd epibranchial and uniting the base of the 3rd infrapharyngobranchial to the tip of the 4th epibranchial; the upper pharyngeal toothplate (see under EB4 above) seems to lie as much on the tip of IP4 as on the 4th epibranchial.

According to the toothplate scheme used by Nelson (e.g., 1970, pp. 8–12), *Sierrathrissa* has the following formula:

		BP				UP				
H	1	2	[3]	4	LP 1	2	3	4	[5]
0	0?	0		–	*	–	–	–	–	T

(where H = basihyal; BP = basibranchials 1–4; LP = lower pharyngeal plate on 5th ceratobranchials; UP = upper pharyngeal plates on infrapharyngobranchials 1–5; * = fused toothplate; T = independent toothplate; missing elements in brackets).

The gillrakers are poorly ossified and even on the first arch are bony only in their basal third. There are six gillrakers on the posterior face of the 3rd epibranchial. The rakers themselves are slender pointed blades with no serrae or denticulations.

The *urohyal* (UH) is a slender and well-ossified bone, triangular in lateral view, the deepest point being in its final quarter. Anteriorly it has two short processes for the left and right ligamentous attachments to the ventral hypohyal; these two processes coalesce to form a strong ventral bar which, after the first third of the bone, gives way to ventral wings, so that in cross-section the bone is an inverted Y. Ventral elements of the sternohyoideus muscle attach within the groove
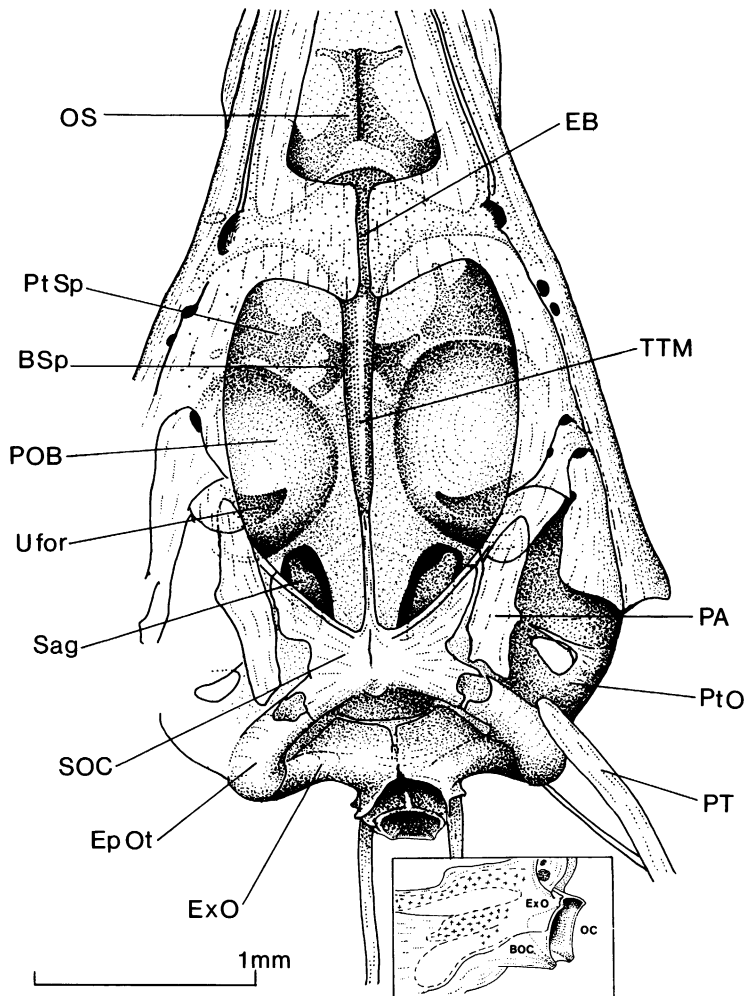
FIG. 18. Hind part of skull (dorsal view) and inset of occipital condyle (left lateral view). **BOC,** basioccipital; **BSp,** basisphenoid; **EB,** epiphysial bar; **EpOt,** epiotic; **ExO,** exoccipital; **OC,** occipital condyle; **OS,** orbitosphenoid; **PA,** parietal; **POB,** pro-otic bulla; **PT,** posttemporal; **PtO,** pterotic; **PtSp,** pterosphenoid; **Sag,** sagitta; **SOC,** supraoccipital; **TTM,** taenia tecti medialis cartilage; **Ufor,** utricular foramen.

of the Y, the dorsal elements attaching to the blade of the urohyal.

NEUROCRANIUM (figs. 18–21)

The slightly curved *parasphenoid* (PSp), slender anteriorly and underlain by the tip of the vomer, widens a little near its junction with the pro-otics and from about the mid-point of the pro-otic bullae produces lateral wings that separate in the midline, become increasingly slender and extend as pointed processes as far back as the 5th vertebra. Somewhat before meeting the pro-otics, the lower surface of the parasphenoid bears a small forward-pointing foramen (BHfor) which leads into the buccohypophysial canal (a feature retained in at least some clupeoids according to Misra and Sathyanesan, 1959); this foramen was only seen in the SEM photographs. On either side of the expanded part of the parasphenoid and linking it to the contour of the pro-otic bullae, are the *parachordal cartilages* (Par). These expand anteriorly
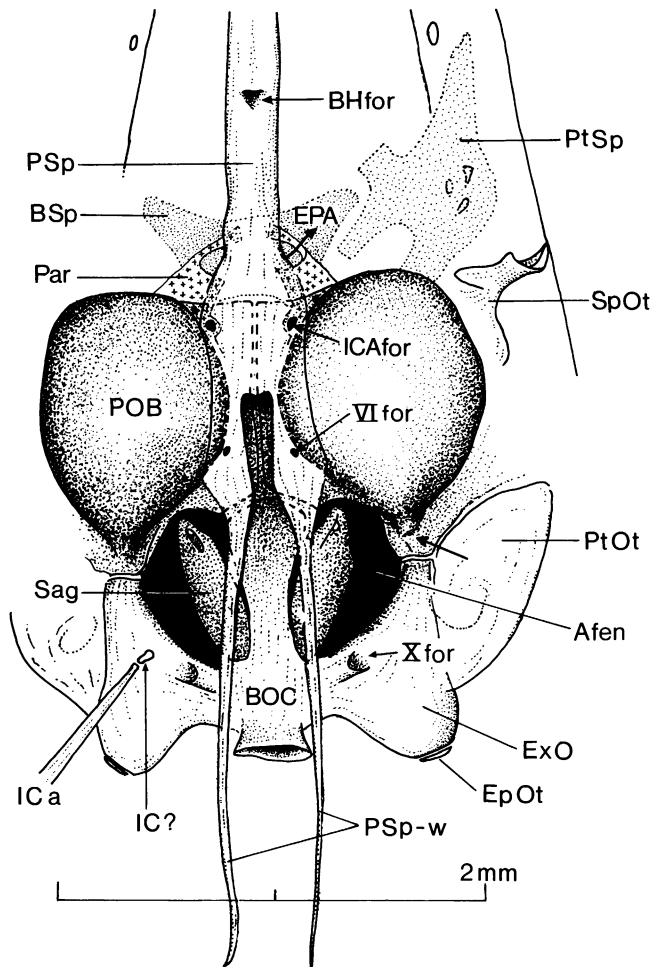
FIG. 19.   Hind part of skull (ventral view). **Afen,** auditory fenestra; **BHfor,** buccohypophysial foramen; **BOC,** basioccipital; **BSp,** basisphenoid; **EPA,** passage of efferent pseudobranchial artery; **EpOt,** epiotic; **ExO,** exoccipital; **IC?,** intercalar?; **ICAfor,** foramen for internal carotid artery; **ICa,** intercalar arm of posttemporal; **Par,** parachordal cartilage; **POB,** pro-otic bulla; **PSp** and **w,** parasphenoid and its posterior wings; **PtOt,** pterotic; **PtSp,** pterosphenoid; **Sag,** sagitta; **SpOt,** sphenotic; **VIfor,** foramen for abducens nerve; **Xfor,** foramen for vagus nerve. Arrow at hind end of pro-otic bulla suggests possible entry of swimbladder tube (see also fig. 21A).

to mark the front of the posterior myodome, with a dorsal excavation for the efferent pseudobranchial artery (EPA).

The *frontals* (F) are widely separated from each other except for the median expansion at their midlength where they roof the cartilaginous *epiphysial bar* (EB) and carry the paired epiphysial canals; the frontals frame a slender anterior and a broader posterior frontal fontanelle. The *parietals* (PA), whose slender anterior tips are overlain by the frontals, contribute little or sometimes nothing to the posterior border of the posterior frontal fontanelle; a small projection on their lateral margin marks the division between the temporal foramen and the pre-epiotic fossa.

The otic region is dominated by the paired *pro-otics* (PO) with their relatively enormous bullae (about 1 mm along the longest axis, which rise posterodorsally at about 45°). The pro-otics meet in the midline by means of a median flange; they abut the exoccipitals pos-
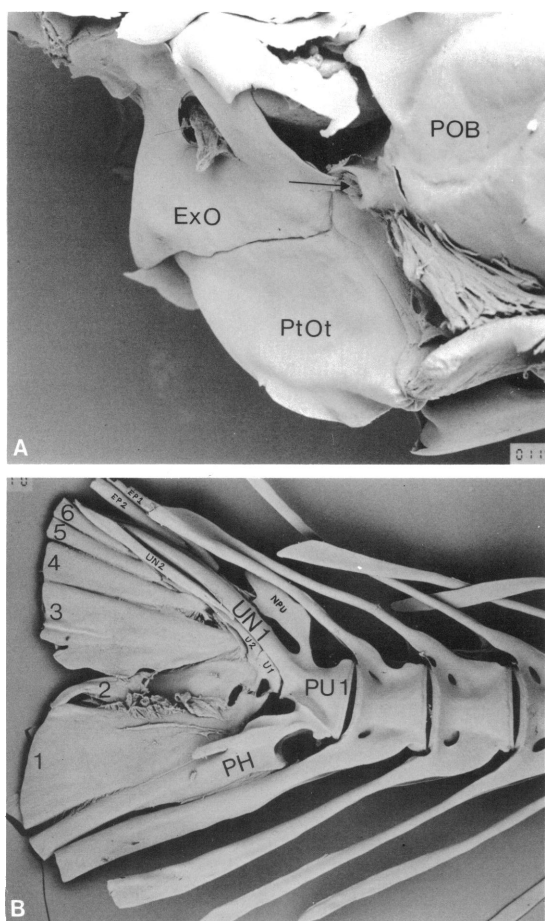
FIG. 20. A. Hind part of skull (left side, ventral view), with arrow indicating possible entrance of swimbladder tube into pro-otic; same specimen as in figure 21. B. Caudal skeleton. **EP1, 2,** epurals; **ExO,** exoccipital; **NPU,** neural spine of 1st preural centrum; **PH,** parhypural; **POB,** pro-otic bulla; **PtOt,** pterotic; **PU1,** 1st preural centrum; **U1, 2,** ural centra; **UN1, 2,** uroneurals. Hypurals labeled 1–6.
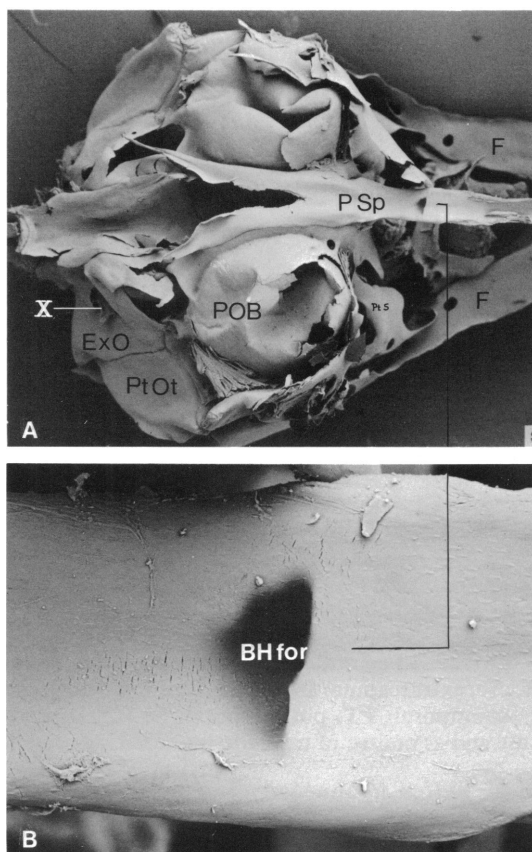
FIG. 21. A. Hind part of skull (ventral view), scanning electron microscope (SEM) photograph of specimen about 25 mm SL (BMNH 1971.11.26.1–12). B. Enlargement of parasphenoid. **BHfor,** buccohypophysial foramen; **ExO,** exoccipital; **F,** frontal; **POB,** pro-otic bulla; **PSp,** parasphenoid; **PtOt,** pterotic; **X,** exit of vagus nerve.

teriorly and the pterotics laterally. Dorsally, the pro-otic bullae have a large transverse crescentic *utricular foramen* (Utfor) connecting with the inner ear. The median flange of each pro-otic contributes to the myodome floor; penetrating this flange near its junction with the contour of the bulla is a large anterior foramen (ICAfor) (for the internal carotid arteries) and a smaller posterior foramen (VIfor) (passage of VI abducens nerve). In ventral view the pro-otic bullae are produced somewhat posteriorly and there is an indication (figs. 19, 20A, arrow) that it is at this point that the swimbladder tube may enter (rather than through the exoccipitals as in other clupeoids).

The *pterotics* (PtO) seem not to house a swimbladder bulla, but this could not be determined with certainty; it would be unusual (only species of *Sprattus* and *Clupeonella* are recorded among clupeoids to lack this bulla), but the pterotic bulla develops later than its pro-otic counterpart, is usually smaller, and
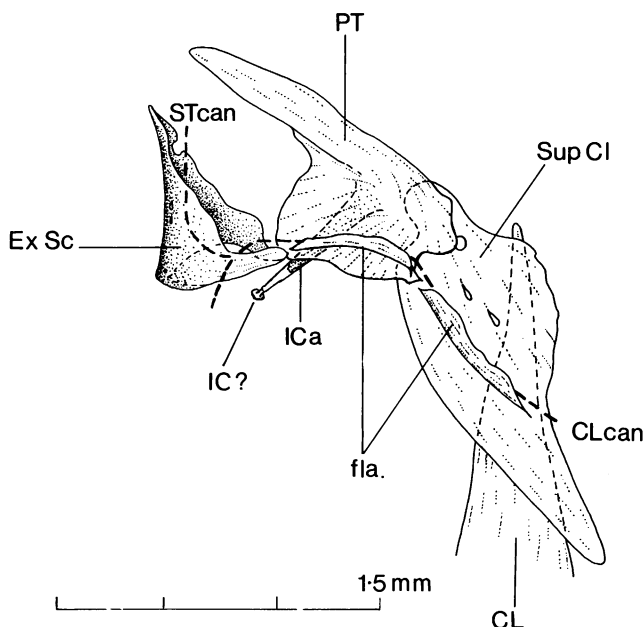
FIG. 22.   Pectoral girdle, upper part (left lateral view). **CL**, cleithrum; **CLcan**, cephalic lateralis canal; **ExSc**, extrascapula; **fla**, flange forming trough for sensory canal; **IC?**, intercalar?; **ICa**, intercalar arm of posttemporal; **PT**, posttemporal; **SupCl**, supracleithrum; **STcan**, supratemporal canal. Heavy broken line shows course of cephalic laterosensory canals.

perhaps has a less critical role to play. The *epiotics* (EpOt) mark the hind border of the pre-epiotic fossa; they chiefly roof the posterior semicircular canal and they provide attachment for the upper limb of the posttemporal.

The *supraoccipital* (SOC) is a well-ossified cap to the hind end of the skull; its anterior extension, dividing left from right fontanelles, has no trace of cartilage below it; laterally the supraoccipital approaches the parietal on each side, but is separated by cartilage. The *exoccipitals* (ExO) have a large foramen for the vagus nerve (X), but there is no sign (even in the SEM photographs, e.g., fig. 21A, which seem to show up foramina invisible in the alizarin preparations) of a foramen for the anterior tubes of the swimbladder; possibly they pass across the face of the exoccipital and enter the pro-otics directly (see under pro-otic above). The *basioccipital* (BOC) reaches forward to the median flanges of the pro-otics and thus provides the inner margins of the very large auditory fenestra (Afen).

The *occipital condyle* is difficult to interpret. Superficially, it would appear that the posterior half of a 1st vertebral centrum has become trapped by flanges from the exoccipitals and the basioccipital, a condition suspected by Ridewood (1904) in the six clupeoids that he examined. However, Patterson (1975, p. 318) argued that the notochordal pit in such fishes is merely lined with osteoid tissue, giving the false impression of a "half-centrum." In *Sierrathrissa* the upper rim of this "half-centrum" seems to be separate from the dorsal and lateral edges of the exoccipitals; nevertheless, the sides of the "half-centrum" and its floor apparently merge imperceptibly with the posterior projection of the basioccipital. The question is left open, but the numbering of the vertebrae in the text (p. 33) and figures ignores this half-centrum, the first vertebra to bear a neural arch being labeled here as centrum 1.

PECTORAL GIRDLE AND FINS (figs. 22–25)

The pectoral girdle, as in other clupeoids, forms an arch of five pairs of major, mostly

well-ossified bones (posttemporals, supra-cleithra, cleithra, scapulae, and coracoids), the whole anchored firmly to the hind end of the skull and united ventrally in the midline.

The *extrascapula* (ExSc), a dermal roofing bone but described here for convenience, is triangular, with thin inner and outer walls enclosing a right-angled channel for the su-pratemporal branch (STcan, vertical) and the cephalic lateralis branch (CLcan, horizontal) of the cephalic laterosensory canal system. The inner and outer walls are united down the vertical anterior margin of the bone by a strong ridge, whereas the posterodorsal mar-gins are ragged and poorly ossified except at their dorsal tips. Along the ventral margin there is a large semicircular opening in the inner wall where the main canal joins the supratemporal and cephalic lateralis branch-es. The upper limb of the extrascapula rises above the underlying dorsolateral face of the pterotic and spans, or almost spans, the pre-epiotic fossa, thus conducting the supratem-poral canal to (or from) its route across the parietal.

The *posttemporal* (PT) is a flat bone with a strongly ossified epiotic (upper) limb in-clined forward at about 45° and firmly bound at its tip to the epiotic. The lower portion is expanded into an irregular triangle whose an-terior tip just passes behind the extrascapula and serves to continue, by way of an external gutterlike flange, the course of the cephalic lateralis canal. Posteriorly, the posttemporal broadly overlaps the dorsal tip of the supra-cleithrum; the two bones are bound fairly firmly but are capable of slight vertical ro-tation. On the inner face of the posttemporal is a strong and slender spine, the *intercalar arm* (ICa), which points ventromedially down to the base of the braincase. In its final third, this arm is ligamentous. At its tip it makes an abrupt junction with a minute stem from an oval bony plate which is applied very firm-ly to the ventral face of the exoccipital (a short distance behind the anterior angle of that bone). It is not clear whether the small oval plate is the tip of the intercalar arm, or wheth-er it is indeed a separate ossification; if it is a true *intercalar* (IC), then it would appear to have migrated from its normal position at the interface between the exoccipital, pro-otic, and pterotic.
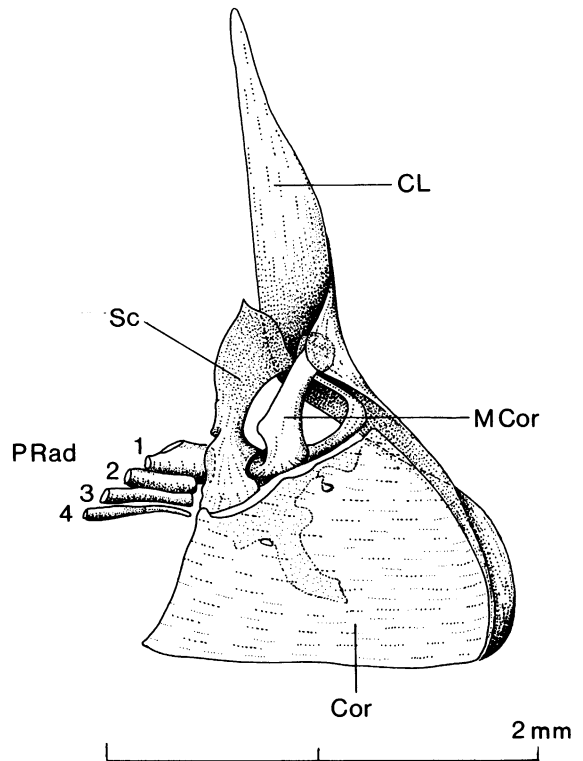

FIG. 23. Pectoral girdle, lower part (left side, medial view). **CL**, cleithrum; **Cor**, coracoid; **MCor**, mesocoracoid; **PRad**, proximal radials 1–4; **Sc**, scapula.

The *supracleithrum* (SupCl) is broadly dag-ger-shaped, with a spatulate dorsal "handle" underlying the posttemporal, an expanded central portion (but posterior margin ill-de-fined), and a tapering ventral blade. There is a small but distinct foramen just behind the junction with the posttemporal and one or two tear-shaped foramina a little below this. The cephalic lateralis branch of the canal sys-tem (CLcan) is continued from the posttem-poral by means of another gutterlike flange running obliquely downward across the su-pracleithrum.

There are no *postcleithra,* which in clu-peoids normally run as slender rods diago-nally down from the tip of the supracleithrum to a point behind the pectoral fin. There is, however, a minute perforated oval plate a little behind the midpoint of the supraclei-thrum which, although aligned transversely,
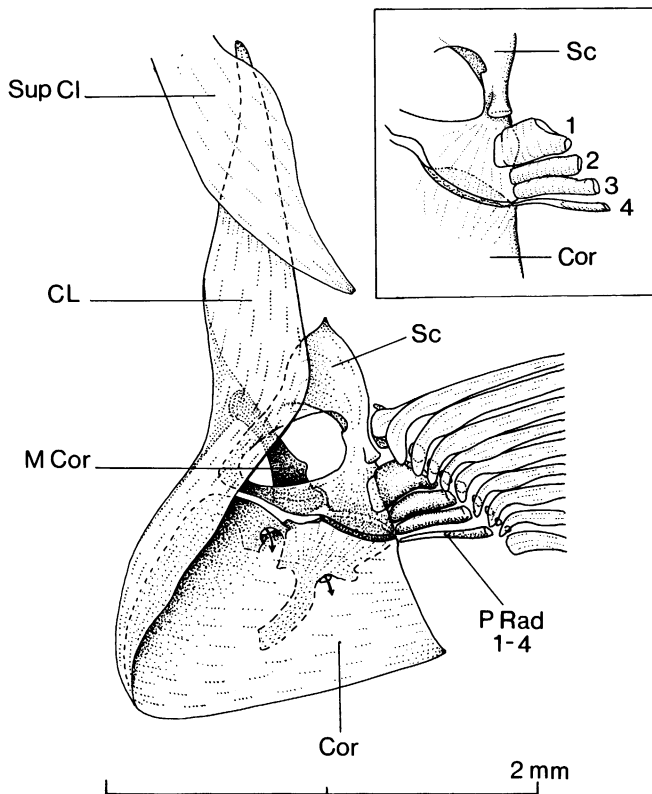
FIG. 24.   Pectoral girdle, lower part (left lateral view), with inset of proximal radials 1–4 (left lateral view). **CL,** cleithrum; **Cor,** coracoid; **MCor,** mesocoracoid; **PRad,** proximal radials 1–4; **Sc,** scapula; **SupCl,** supracleithrum.

must be a lateral line scale (but is absent in two of the five alizarin fishes).

The *cleithrum* (CL) is the longest bone in the arch, with upper and lower arms meeting at an obtuse angle, the upper approximately vertical and closely bound to the overlying and oblique blade of the supracleithrum. At its midpoint the cleithrum is bowed like a sail, the inner and outer margins meeting (respectively) the tips of the mesocoracoid and the scapula. The lower portion is similarly bowed and bears a narrow anteromedial flange.

The *scapula* (Sc) is triangular and encloses a large and almost circular foramen offset anteriorly from the vertical center of the bone. The anterior edge of the scapula, which is cartilaginous, is closely applied to the inner face of the cleithrum; the ventral edge overlaps the coracoid anteriorly by a broad triangle of cartilage, but posteriorly the inner

and outer walls of both scapula and coracoid swell to form cartilage-filled cups that join at this point. The posterior edge of the scapula has an irregular outline, with a prominent projection on which the 1st finray articulates, followed by an excavation and low median flange into which the 1st (upper) proximal radial nests.

The *mesocoracoid* (MCor) is a narrow curved bar with a small projection on its posterior edge. Dorsally, it is very firmly attached to the inner face of the median "wing" of the cleithrum; ventrally, it expands into a strong ball-shaped joint at the junction of the scapula and coracoid.

The *coracoid* (Cor) forms a dorsally truncated triangle, its anterior margin meeting the inner face of the cleithrum and its upper margin joined by cartilage to the scapula and mesocoracoid. The cuplike junction with the scapula is continued ventrally as a flattened
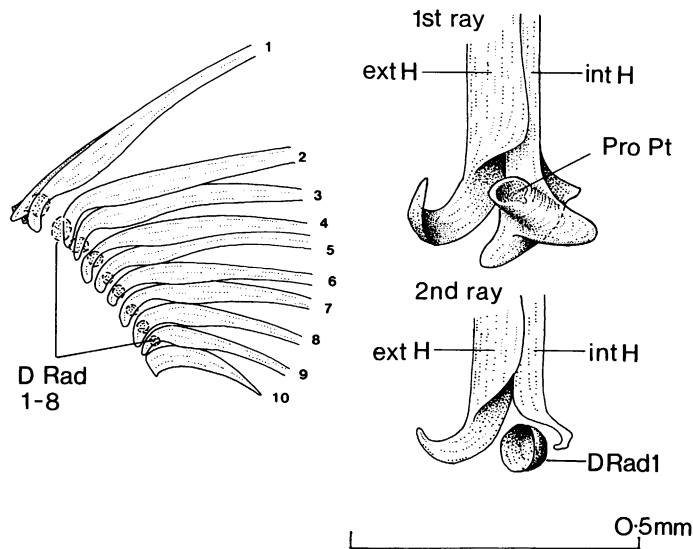
FIG. 25. Base of pectoral fin (left lateral view) and on right, articulation of 1st and 2nd finrays. **DRad,** distal radials 1–8; **extH** and **intH,** external and internal hemitrichs; **ProPt,** propterygium. Finrays labeled 1–10.

curved tube which has a well-defined foramen on the inner wall at the base of the cup; there is another small opening just anterior to the cup where inner and outer walls of the coracoid again separate. At the posteroventral tip of the coracoid there is no posterior projection such as is found in many clupeoids. Two foramina (arrows in fig. 24) allow entrance and exit of (upper) the anterior and (lower) the posterior branches of the subclavian artery and vein.

There are four tubular *proximal radials* (PRad), of which the 1st has a broad base and a lateral flange that embraces the scapula; distally, this radial has a broad upper and a rounded and concave lower articulating surface. The 2nd and 3rd radials are more slender, each with a round distal articular surface and both articulating proximally with the scapula. The 4th radial is even more slender, poorly ossified distally, but entirely cartilaginous toward its base, which articulates with the upper corner of the coracoid.

There are eight *distal radials* (DRad), the upper ones rather barrel-shaped, the lower ones rounder and increasingly poorly ossified. These radials lie in a groove between the bases of the inner and outer hemitrichs of the 2nd to 8th finrays. A *propterygium* (ProPt) is

present as a cylindrical projection fused to the base of the inner hemitrich of the 1st (marginal) finray; it appears to provide the articulation for that finray against the edge of the scapula.

There are 9–11 *pectoral finrays,* of which the first is unbranched. The bases of the outer hemitrichs are hooked and point downward, being almost at right angles to the direction of the abductor superficialis muscles. The bases of the inner hemitrichs are all (except the 1st) hooked inward toward the midline of the fin base. The 1st hemitrich has a more complex base, with three small projections. The 1st ray articulates directly with the posterior edge of the scapula; the next two rays articulate (via their distal radials) with the first (upper) proximal radial; the remaining finrays articulate irregularly with the lower three proximal radials, again via the distal radials; the final finray, which is not hooked at its base, is free. The base of the fin, i.e., the alignment of its articulation, is set at about 30° to the horizontal.

PELVIC GIRDLE AND FINS (figs. 26, 27)

The paired pelvic bones (PB), which lie below the tips of the 8th–11th ribs, are tri-
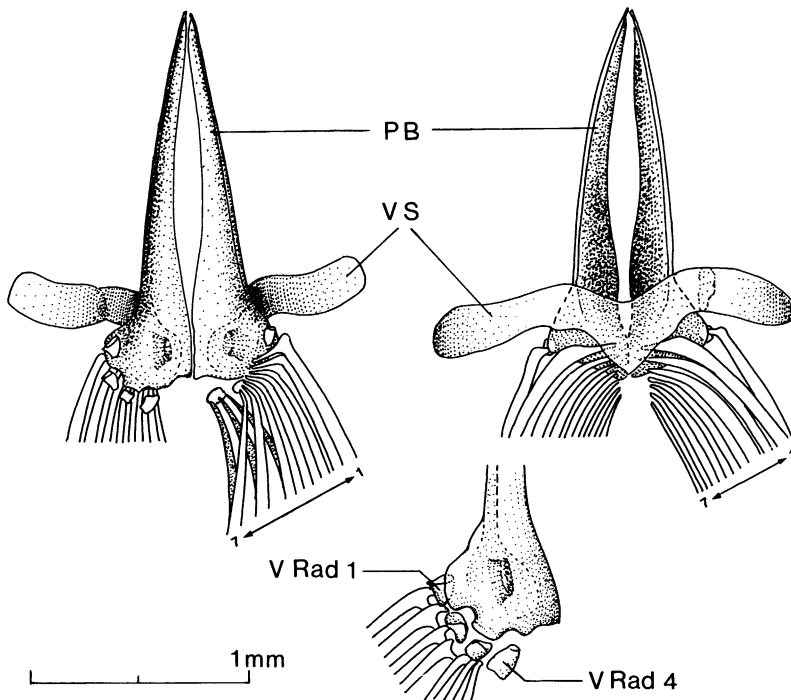
FIG. 26. Pelvic girdle (dorsal view on left, ventral view on right) and below, the ischial region (right half, ventral view, enlarged). **PB,** pelvic bone; **VRad,** pelvic radials 1–4; **VS,** pelvic scute. Lower hemitrichs labeled 1–7; pelvic radials 2–4 slightly displaced posteriorly.

angular and well-ossified plates with straight and tubular ventral margins and slightly convex dorsal margins viewed laterally, the former distorting the otherwise straight ventral boundary of the body cavity. Dorsally, the two pelvic bones are inclined inward toward each other, their dorsal edges almost meeting anteriorly, then separating, but curving inward to meet again posteriorly (without fusion). The ventral part of the expanded posterior region of these bones has a dark-staining line which bounds a possible separate *ischial ossification* (ISC), irregularly oval in shape, with an anterior spine, the oval portion bearing on its medial face a short and flattened bony tube projecting inward at 45° toward the ventral midline (but not nearly meeting its partner on the other side); this ischial ossification appears to be fused at its lateral boundary (or along its whole lateral face) to the main pelvic bone and encloses a cartilaginous mass (which also fills the bony ischial tube).

At the widest (posterolateral) point of the girdle, each pelvic bone has a rounded lateral wing, on the top of which lies the tubular but flattened and roughly conical 1st *pelvic radial* (VRad1); the latter appears to be free to rock over the surface of the lateral wing. Beyond this point the hind margin of the pelvic bone is first indented (for reception of the more cylindrical 2nd radial), then expanded into an articular surface (for the cylindrical 3rd radial), and finally indented once more (for reception of the cylindrical 4th radial). This hind margin slopes very gently upward to the midline, so that the pelvic fin bases are at a slight angle to the horizontal.

The W-shaped *pelvic scute* (VS) is fairly firmly bound in its central triangular portion to the ventral edges of the pelvic bones (see Scutes, p. 6).

There are seven *pelvic finrays,* the 1st unbranched. The *ventral hemitrichs* have a prominent and medially directed bladelike "foot" (less pronounced in the inner rays and scarcely apparent in the last). The seven "feet" on which insert the arrector ventralis pelvicus

muscle (1st ray) and the abductor pectoralis superficial and presumably also deep muscles (the other rays), lie in close succession across the ventral face of the expanded ischial region, with the tips of the first two ventral hemitrichs overlapped by the pelvic scute. These ventral hemitrichs lie immediately below the 2nd–4th pelvic radials, but only the 4th radial appears to provide a pivotal surface (for the inner two rays). The 1st ventral hemitrich also has a well-defined "heel," whereas the 2nd–5th hemitrichs have a minute knob at the base of the "foot" and there is nothing on the final two hemitrichs. The 1st and subsequent dorsal hemitrichs also have a medially directed "foot" respectively for insertion of the erector and adductor muscles and there is a short and ventrally directed spur at the "heel" (most pronounced in the 1st ray, barely apparent in the last). The first two dorsal hemitrichs articulate basally with the 1st radial, the next two with the 2nd radial, and the final three with the 3rd radial; the 4th radial does not support any dorsal hemitrichs, with the result that the dorsal and ventral hemitrichs of the two innermost finrays are widely separated at their bases (which presumably prevents these inner finrays from spreading too far laterally when the fin is spread outward). In one of the five alizarin specimens there is an 8th dorsal hemitrich (but no matching ventral half), while in another fish the 1st radial is missing on both sides.

DORSAL FIN (fig. 28)

There are iii 10–12 finrays supported by a series of proximal, middle, and distal pterygiophores, the posterior finrays and supports becoming increasingly poorly ossified. The fin begins somewhat behind the midpoint of the body and lies over neural spines about 18–27.

There are 13 or 14 *proximal pterygiophores* (PPt), of which the 1st is an expanded plate, roughly triangular; in some specimens this pterygiophore has an oblique narrow lateral wing on each side parallel with the hind margin. The succeeding proximal pterygiophores are more slender in the anteroposterior plane (anterior expansion long and narrow, posterior short and near base of pterygiophore),
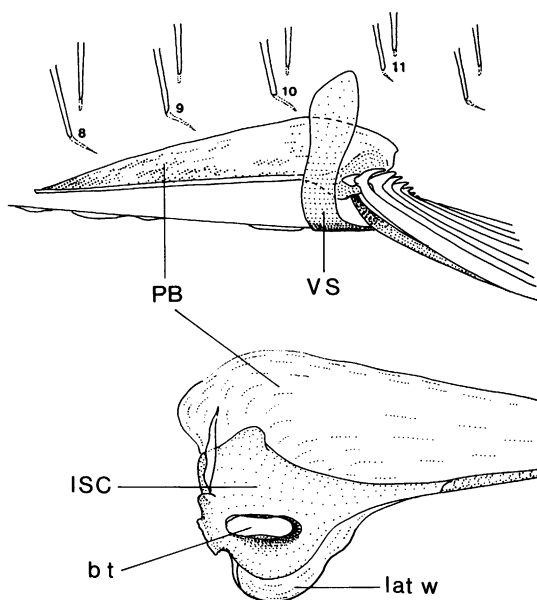

FIG. 27. Pelvic girdle (left lateral view) and below, the ischial region (left half, median view, enlarged). **bt,** bony tube; **ISC,** ischial ossification; **latw,** lateral wing; **PB,** pelvic bone; **VS,** pelvic scute. Tips of pleural ribs labeled 8–11.

but lateral wings occur on the 2nd–4th pterygiophores (progressively lost after this). The final pterygiophore has a short posterior extension.

The *middle pterygiophores* (MPt) are short cylindrical elements. The 1st is fused to the 1st pterygiophore and has two small lateral flanges pointing forward; the 2nd, 3rd, and 4th, as well as the last four, are also fused to the tip of their proximal pterygiophore, but the remainder are separate, cylindrical, and slightly waisted perichondral ossifications (posterior rim distinctly thickened in the more anterior ones).

The *distal pterygiophores* (DPt) are formed from two lateral perichondral plates (not quite meeting in the dorsal midline and not at all ventrally), each plate with an overhanging lateral flange. The middle and distal pterygiophores are inclined backward and become almost horizontal posteriorly. The cartilage core of the middle pterygiophores appears to be almost continuous with that of the proximal pterygiophores, but the rather conical core of the distal pterygiophores is quite distinct.
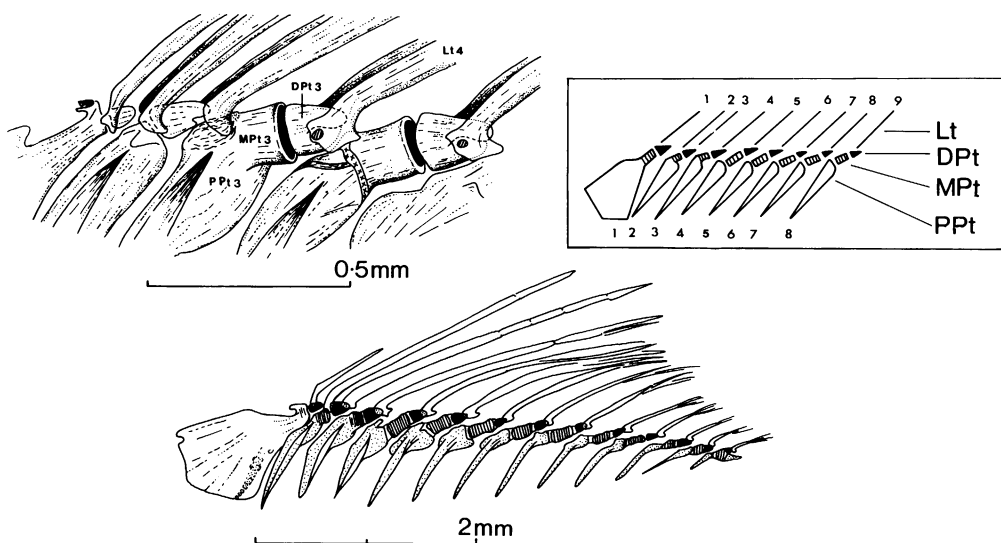
FIG. 28. Dorsal fin supports (left lateral view) and above left, the articulation of the first five finrays, with inset showing schematic arrangement of pterygiophore elements. DPt, distal pterygiophores; Lt, lepidotrichia; MPt, middle pterygiophores; PPt, proximal pterygiophores.

The finrays or *lepidotrichia* (Lt) are expanded proximally like a grasping hand, but with the "thumb" projecting inward as a pivot that rests underneath the overhanging lateral flange of the distal pterygiophores; a broad anterior and a slender posterior process serve as attachment for the levator and depressor muscles of each finray. In some specimens there is a minute 1st unbranched finray which articulates with the 1st (fused) median pterygiophore; in other specimens it is longer and articulates with the 1st distal pterygiophore. The 2nd and 3rd finrays share their articulation on the 2nd distal pterygiophore; each of those remaining articulates with a successive distal pterygiophore.

ANAL FIN (fig. 29)

There are iii 14–18 finrays supported, as in the dorsal fin, by a series of proximal, middle, and distal pterygiophores, the posterior elements again becoming increasingly poorly ossified. The fin begins under the 3rd caudal vertebra (under the final two or three dorsal finrays) and its pterygiophores are more or less associated with the first 10 hemal spines.

There are 16–20 *proximal pterygiophores* (PPt), of which the 1st is expanded into a

slender triangle (or sometimes a crescent), its hind margin a distinct strut (occasionally with a small posterior wing); the succeeding proximal pterygiophores are spindle-shaped and the final one has a small posterior extension (almost entirely cartilage and perhaps part of the final middle pterygiophore).

The presumed *middle pterygiophores* (MPt) show no discontinuity with the tips of the proximal pterygiophores and their identity is based on analogy with those of the dorsal fin. The 1st has a bony distal head, on which articulates the first unbranched finray and against which abuts the first distal pterygiophore; the 2nd has an irregular bony plate, which provides articulation for both the bony head of the 1st and the cartilaginous upper surface of the 1st distal pterygiophore; the 3rd and succeeding middle pterygiophores pass imperceptibly from bone to cartilage and become increasingly cartilaginous in the posterior ones, as well as increasingly footlike, the "heel" being a ball of cartilage abutting the cartilaginous upper surface of the preceding distal pterygiophore.

The *distal pterygiophores* (DPt) are approximate cones of cartilage with the apex pointing posteriorly and the base closely ap-
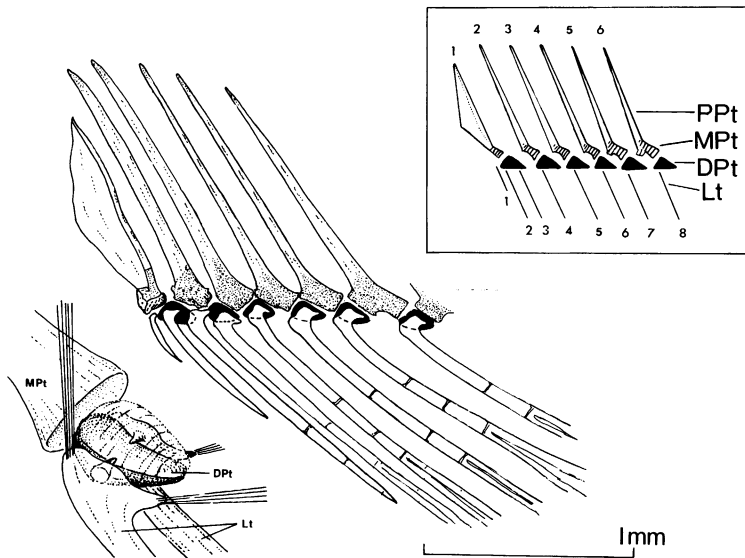
FIG. 29.   Anal fin supports (left lateral view) and below, the articulation of the 3rd finray (enlarged), with inset showing schematic arrangement of pterygiophore elements. **DPt,** distal pterygiophores; **Lt,** lepidotrichia; **MPt,** middle pterygiophores; **PPt,** proximal pterygiophores.

posed to the tip of the middle pterygiophore; in the anterior cones the ventral surface bears a pair of bony plates (left and right) which together resemble a "bucket seat."

The finrays or *lepidotrichia* (Lt) have the same handlike base as in the dorsal fin and, similarly, there are anterior and posterior processes for attachment of erector and depressor muscles, as well as an internal peg which, at least in the anterior finrays, serves as a pivot that rotates against the edge of the bony ventral plates of the distal pterygiophores.

VERTEBRAL COLUMN AND INTERMUSCULAR BONES (figs. 30–35)

There are 22–24 (usually 24) abdominal vertebrae and 17–19 (usually 18) caudal vertebrae (the last being preural 1, followed by three small ural centra). The *vertebrae,* which are peripherally ossified, have a strong constriction in the middle of the centrum, on either side of which is a ventral lateral plate of bone (VPZ) which thus encloses a small hollow, especially in the abdominal vertebrae; from preural 6 backward this lateral flange contributes to the bases of the hemal

arches. The dorsal counterparts to these flanges are paired wings or zygapophyses at the hind end of each centrum (DPZ); from preural 5 backward these contribute to the bases of the neural arches. The possibility that an abdominal (half) centrum is locked in the occipital condyle has been discussed (p. 26). The 1st centrum is short, the 2nd longer, and the remainder are about 1½ times as long as deep. The centra are amphicoelous; presumably they are pierced by a notochordal foramen, but this could not be seen.

Paired *neural spines* (NSp) begin on the 1st vertebra, but only from about the 22nd vertebra do they become fully fused to the centrum; the spines on the anterior vertebrae arch inward, but do not fuse together distally until about the 20th vertebra, thereafter forming a complete neural arch with spine. The neural arch bases lie near the anterior rim of the centrum, but at preural 5 the main axis of the arch has shifted to the middle of the centrum and on preurals 4–2 it arises from near the posterior rim of the centrum; the elongate neural plate on preural 1 merely continues this process.

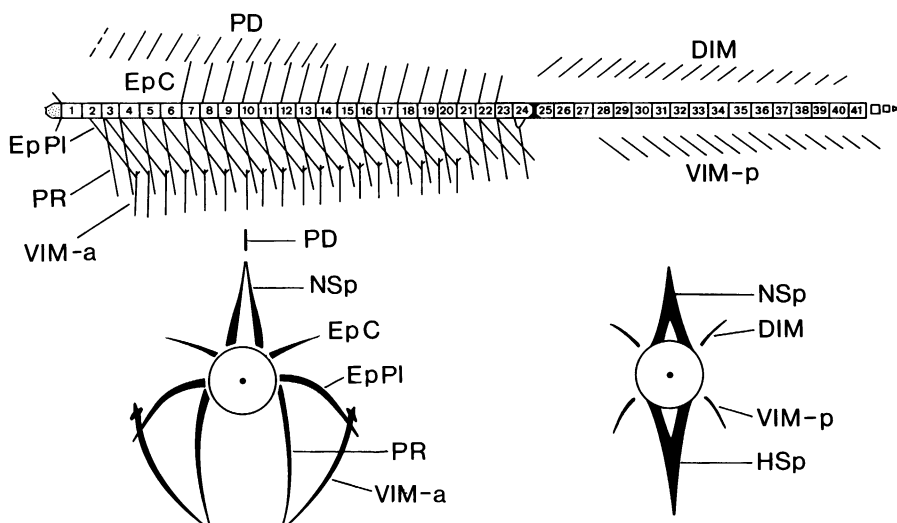The paired *hemal spines* (HSp) begin on about the 25th vertebra and are fully fused

FIG. 30. Vertebral column (left lateral view) showing schematic arrangement of ribs and intermuscular bones (neural and hemal arches omitted) and below, cross-sections of abdominal and caudal regions. DIM, dorsal intermuscular bones; EpC, epicentrals; EpPl, epipleurals; HSp, hemal spine; NSp, neural spine; PD, predorsal bones; PR, pleural ribs; VIM-a and p, anterior and posterior ventral intermuscular bones. Note: the presence of the 1st "half-centrum" is problematic (see p. 26).

proximally to the centrum. The 1st hemal spine is short, the two halves separate distally but bridged at about their midpoint; thereafter the two halves are always joined. Proximally, they are supported by a pad of bone
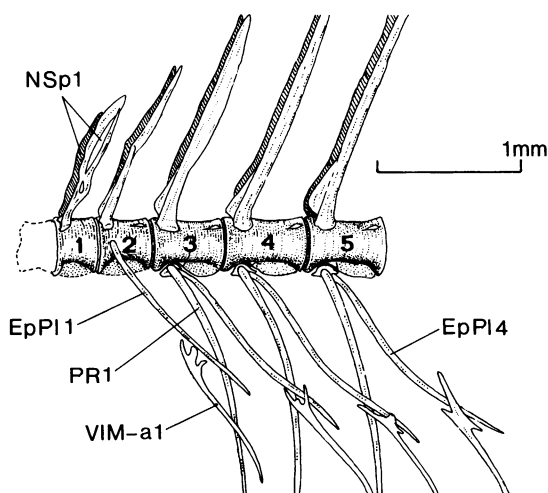

FIG. 31. Vertebrae 1–5 (left lateral view). EpPl, epipleurals 1 and 4; NSp, neural spine 1; PR, pleural rib 1; VIM-a, anterior ventral intermuscular bone 1.

apposed to the ventral surface of the centrum, but lateral to this is a distinct strut; as with the neural spines, at preural 6 the main axis of the spine moves back and its basal support is shared by the ventral plates or flanges on the centrum, with a small foramen between these anterior and posterior portions of the spine base; the parhypural, on the other hand, does not follow this pattern, but arises from a discoidal plate unfused to the centrum.

Pleural ribs (PR) are present on vertebrae 3–24. The base of the rib is not expanded, but articulates with a small bony plate which has small anterior and posterior projections; basally, this plate articulates with a small triangular projection fused to near the anterior rim of the centrum. The final rib, on the 24th vertebra, articulates with a bony stalk comprising a plate and lateral to it a small strut, thus anticipating the basal support structure of the hemal spines.

There are six distinct series of intermuscular bones: the epicentrals are attached to the centra; the epipleurals to the ribs; the anterior ventral intermusculars are attached to the epipleurals; and the predorsal bones, dorsal intermusculars, and posterior ventral intermusculars lie free between the myosepta.
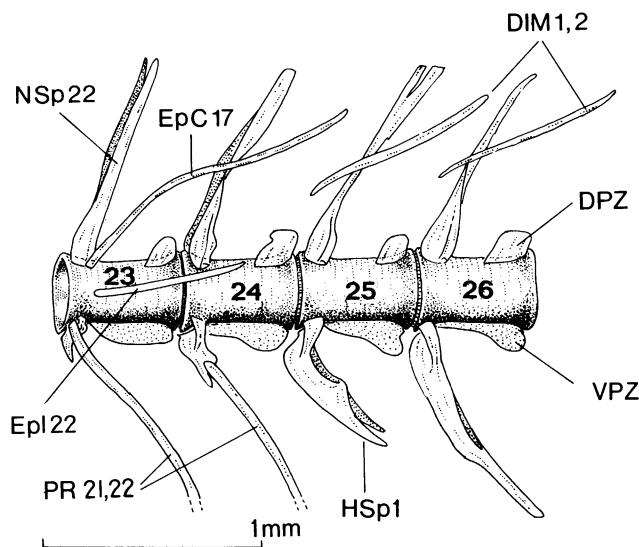
FIG. 32. Vertebrae 24–27, showing transition between abdominal and caudal vertebrae (left lateral view). **DIM1, 2,** dorsal intermuscular bones 1 and 2; **DPZ,** dorsal posterior zygapophysis; **EpC17,** epicentral 17; **EpPl21,** epipleural 21; **HSp1,** hemal spine 1; **NSp22,** neural spine 22; **PR21, 22,** pleural ribs 21 and 22; **VPZ,** ventral posterior zygapophysis.

The *epicentrals* (EpC) (epineurals of some authors) form a series of 17 slender and curved bones from the 7th to the 23rd vertebra. They arise slightly below the bases of the neural arches and they ascend at about 45° upward and backward, narrowing to fine points distally.

The *epipleurals* (EpPl) form a series of 22 slightly more robust bones, from the 2nd to the 23rd vertebra. The first arises from just below the base of the neural arch, but thereafter their origin is at the bases of the pleural ribs. The proximal tip of the epipleurals makes an increasingly sharp ventral bend in the posterior part of the series and appears to fuse without any visible line to the head of the rib. The final epipleural resembles the first in that it arises above the head of the rib. By definition, the epipleurals arise from the pleural ribs, but in the present case the first and last cannot belong to any other intermuscular series and have evidently migrated.

The *anterior ventral intermuscular bones* (VIM-a) are attached to the tips of the first 18 epipleurals (vertebrae 2–20). The head of each is expanded into a small bipartite or tripartite cartilaginous plate which is applied to the anterior face of the epipleural tip; these

intermuscular bones curve down to meet the tip of the rib and thus, together with the epipleural from the same vertebra, form a slender triangle backwardly inclined, its apex at the belly.

The *dorsal intermuscular bones* (DIM) begin at the 24th vertebra and form a series of 17 short and slender plates inclined upward, each overlapping the next in the vertical plane; the 1st is a repetition of the tip of the final epicentral, while the last three become slightly broader and are nearer to the horizontal. There is a slight break between the last epicentral and the first dorsal intermuscular bone, but it could be argued that these bones form a single series, the epineurals of authors.

The *posterior ventral intermuscular bones* (VIM-p) begin at about the 27th vertebra, thus somewhat behind the dorsal series, but they are otherwise virtually identical in shape, size, and orientation.

There are 12 slender and sigmoid *predorsal bones* (PD), the 1st behind (occasionally in front of) the 1st neural spine. We include these bones in the intermuscular series, partly for convenience and partly because they appear to serve the same function.
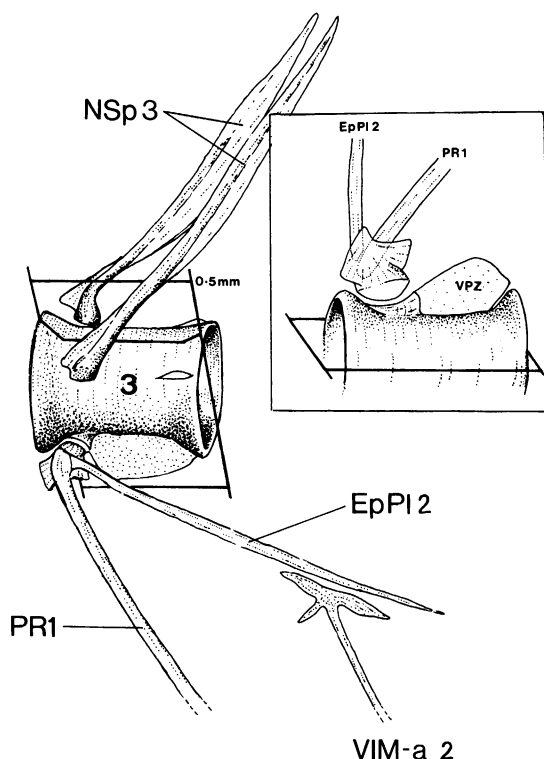
FIG. 33. Vertebra 3 (left dorsolateral view), with inset showing articulation of the epipleural and pleural rib (right anterolateral view). **EpPl2,** epipleural 2; **NSp3,** neural spine 3; **PR1,** pleural rib 1; **VIM-a2,** anterior ventral intermuscular bone 2; **VPZ,** ventral posterior zygapophysis.

FIG. 34. Vertebrae 1–3 (right anteroventral view). **EpPl1, 2,** epipleurals 1 and 2; **NSp1,** neural spine 1; **PR1,** pleural rib 1; **VIM-a2,** anterior ventral intermuscular bone 2.

CAUDAL SKELETON (figs. 20B, 36–38)

The caudal fin skeleton is essentially the same as in other clupeoid fishes. The caudal elements are supported by structures associated with three preural and three ural centra. The 1st *preural centrum* (PU1) bears an oblique and elongate neural plate with a subcylindrical stem that is firmly ankylosed to the centrum (NPU). The *parhypural* (PH), which is clearly autogenous but firmly attached to the centrum, has a laminar anterior flange and above it a short and sharply pointed posterolateral hypurapophysis (tip rounded in the SEM specimen). Of the six *hypurals,* the 1st is autogenous, with its head some distance from the centrum, the 2nd is very firmly fused to the first ural centrum, and the remainder have very well-defined articular
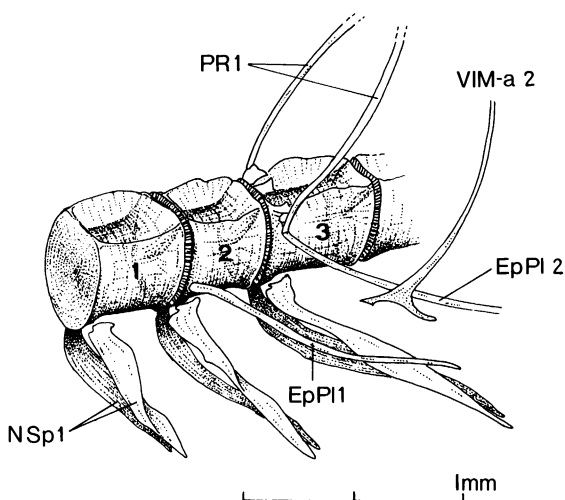
heads but are only loosely bound to the urostyle.

The *1st ural centrum* (U1), which is a little shorter than the preceding preural, is wedge-shaped and provides the rising angle of the urostyle. The *2nd ural centrum* (U2) is a barrel-shaped tubular ossification, clearly defined at its base but uniting distally with a shorter and narrower cylinder; the latter is presumably a poorly differentiated *3rd ural centrum* (U3); it is present in juvenile *Clupea* (Ramanujam, 1929, p. 412) and Hollister (1936, figs. 46, 48, 53) shows it in *Harengula, Sardinella,* and *Anchoviella.* A pair of lateral wings spread on either side of the posterior faces of these two centra. Three pairs of *uroneurals* (UN) are present, the 1st longitudinally ridged, pointed distally, and very firmly fused proximally to the hind rim of the first preural centrum; the 2nd pair of uroneurals are more slender, surpass the first distally, and at their bases abut the two ural wings; the 3rd pair is loosely and obliquely attached to the tips of the 2nd and slightly expanded distally. Two short *epurals* (EP) are present (the posterior one absent in one of the five alizarin specimens). The *notochord* (N) projects beyond the 3rd uroneurals and expands distally into a cartilaginous plate between the
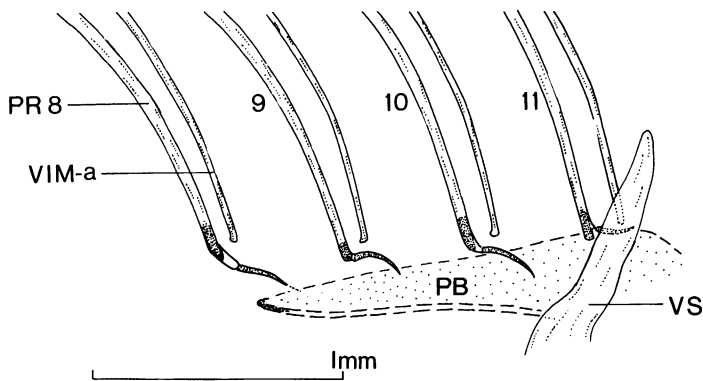
FIG. 35. Tips of pleural ribs above pelvic girdle (left lateral view). **PB,** pelvic bone; **PR,** pleural ribs 8–11; **VIM-a,** anterior ventral intermuscular bones; **VS,** pelvic scute.

last dorsal basal fulcrum and the 1st upper caudal finray (the *opisthural* of Monod, 1968).

Dorsal and ventral *basal fulcra* (BF), or procurrent rays, increase in size and inclination posteriorly and provide a slight bulge in the lateral profile between peduncle and fin; there are 10–11 upper and nine lower fulcra, of which 3–4 (and 3–4) are segmented. Preceding the 1st upper and the 1st lower fulcra is a folded scale (Sc), which takes up alcian blue stain but not alizarin.

In one alcian blue specimen a small ball of cartilage lies between the tip of the neural spine on PU2 and the tip of the 1st epural; presumably this is a *dorsal caudal radial* (DCR). In all three alcian blue specimens, there are three distinct *ventral caudal radials* (VCR), the 1st closely apposed to the tip of the hemal spine of PU2, the 2nd at the tip of the parhypural, and the 3rd at the ventral corner of the 1st hypural.

The bases of the two principal (i.e., outer and unbranched) *caudal finrays* embrace, respectively, the 6th and the 1st hypurals (and/or the parhypural). The bases of the two innermost rays embrace, respectively, the 3rd and the 2nd hypurals; these bases are much longer than those of the finrays above or below them and each has a small dorsal (or ventral) projection or knob at the point where the finray joins its hypural.

BIOLOGY

Sierrathrissa has mostly been studied in the man-made lakes Volta in Ghana and

Kainji in Nigeria, rather than in its normal riverine habitat. However, some habitat data can perhaps be accepted from authors who recorded "larval" or "unmetamorphosed" *Pellonula,* e.g., Johnels (1954) for the Gambia and Daget (1954) for the upper parts of the Niger. In fact, the juveniles are fairly eas-
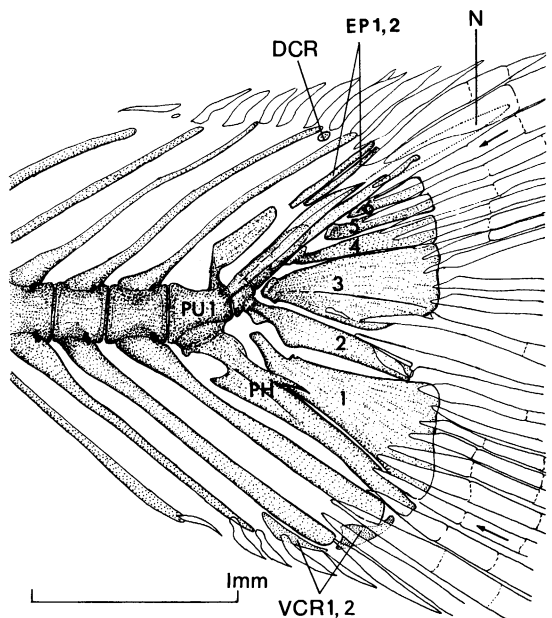

FIG. 36. Caudal skeleton (left lateral view). **DCR,** dorsal caudal radial; **EP1, 2,** epurals 1 and 2; **N,** tip of notochord; **PH,** parhypural; **PU1,** preural centrum 1; **VCR1, 2,** ventral caudal radials 1 and 2. Hypurals labeled 1–6; principal caudal finrays shown by arrows.
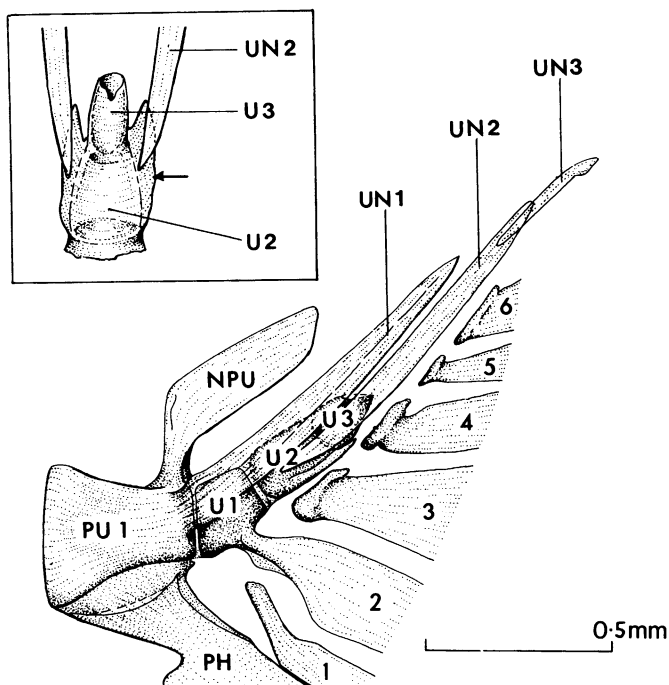
FIG. 37. Caudal skeleton (left lateral view), with inset showing final ural centra (dorsal view, enlarged). **NPU,** neural spine on 1st preural centrum; **PH,** parhypural; **PU1,** preural centrum 1; **U1, 2, 3,** ural centra 1–3; **UN1, 2, 3,** uroneurals 1–3. Hypurals labeled 1–6; epurals omitted; arrow shows right lateral wing of ural 2.

ily distinguished by the position of the dorsal fin (fig. 39).

Habitat: Lelek (1973) reported *Sierrathrissa* throughout Lake Kainji, finding it present at all stations in the open lake and over depths of 10–32 m; generally, it was most abundant where the banks sloped sharply into the lake and less abundant where the slopes were
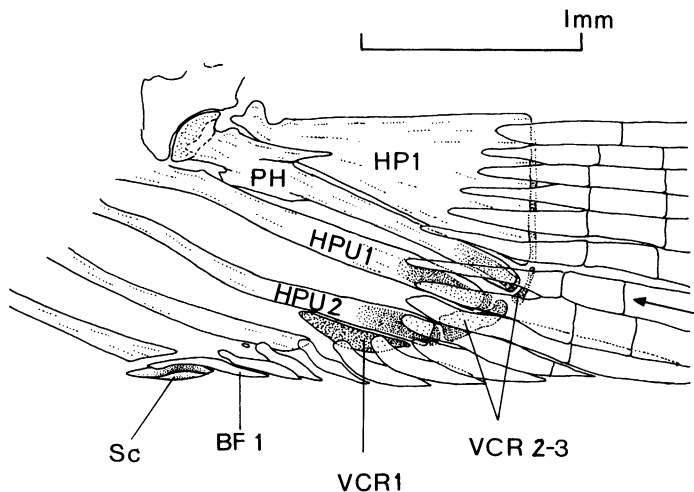

FIG. 38. Caudal skeleton, lower part (left lateral view). **BF1,** basal fulcrum 1; **HP1,** hypural 1; **HPU,** hemal spines of preural centra 1 and 2; **PH,** parhypural; **Sc,** scale; **VCR1, 2-3,** ventral caudal radials.
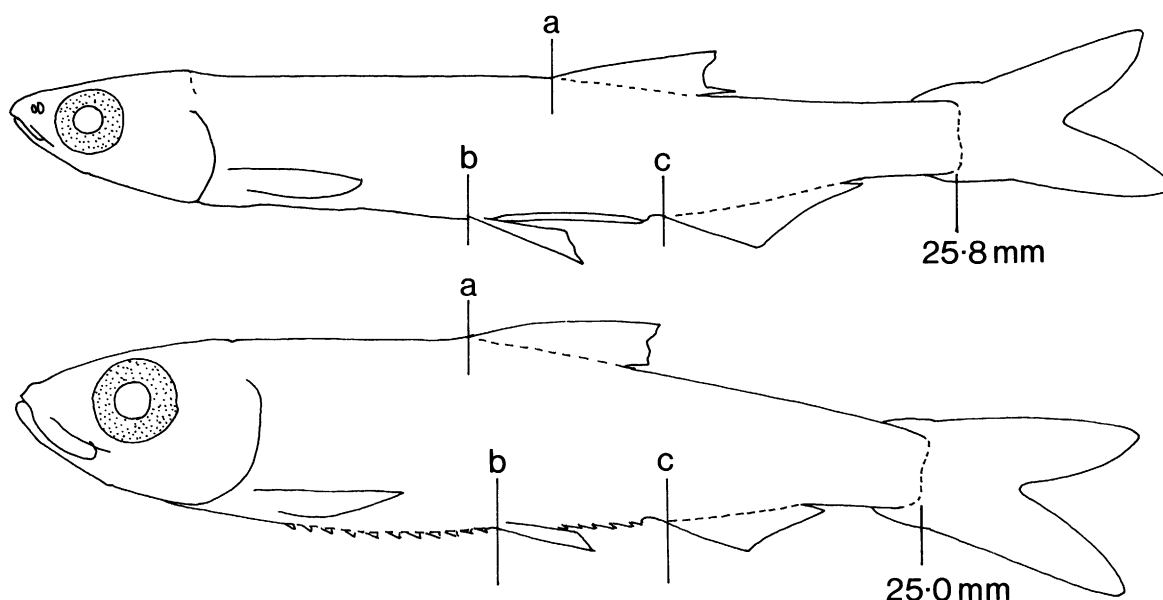
FIG. 39. Comparison between adult *Sierrathrissa leonensis* (above) and juvenile *Pellonula afzeliusi* (below), both from the Gambia River (part of syntypical series of *P. afzeliusi*).

gentle. Sagua and Otobo (1974) and Otobo (1978) recorded the species especially in the shallow waters of Lake Kainji and noted its preference in the open waters for the upper part of the water column (2–8 m), although depth varied with the seasonal differences in water clarity. Loiselle (*in litt.*, 11 November 1970) noted that in Lake Volta the fish "frequently swims just below the surface of the water. It is a rather slow swimmer and moves in a most distinctive manner. It employs an attenuated sinusoidal lateral motion, very similar to that employed by *Denticeps clupeoides*. Like *D. clupeoides*, it appears to depend principally upon its movements through the water for buoyancy—dead fish sink like a stone." When observed with a light at night, Loiselle found *Sierrathrissa*, together with larval clupeids and *Aplocheilichthys normani*, to occupy the top 30 cm, whereas below this he found *Pellonula*, as well as *Eutropius*, *Micralestes*, etc.; those in the lower layer would dart up to snatch prey from the upper layer.

Feeding: In Lake Kainji, Adeniji (1975) reported *Sierrathrissa* as almost exclusively planktivorous, feeding especially on cladocera (*Bosminopsis dietersi* formed 95% of the gut contents in his samples). In the same lake, Otobo (1979b) identified zooplankton as the main food element (*B. dietersi* and *Bosmina longirostris* in particular). In fact, Lewis (1974b) attributed the general success of clupeids in Lake Kainji to the great abundance of zooplankton (mainly *Bosminopsis*, *Diaphonosoma*, and *Thermocyclops*). *Sierrathrissa* has probably been opportunistic in these man-made lakes. Its riverine diet is not recorded, but probably it is a facultative feeder on whatever zooplankton is seasonally available and small enough to be taken. Most likely, it competes with small *Pellonula* (among others).

Breeding: The most detailed studies are those made by Otobo (1976, 1978) in Lake Kainji. Males were mature at about 18 mm SL and females at about 19 mm; males predominated (sex ratio 1:1.8); fecundity ranged from 94 to 2595 eggs; and mature gonads were recorded throughout the year, with peaks of activity in February/March and again in October/November. In museum samples we have usually found that the smallest males and the largest females exceed the range of the opposite sex, suggesting that sexual size dimorphism is also a feature of riverine pop-

ulations. As noted above (see p. 10), the testes are paired but there is a single (left) ovary only: in a female of 23 mm SL we estimated 200 eggs, mostly 0.2 mm in diameter; males have a small but distinct genital papilla.

Migrations: It is not recorded whether *Sierrathrissa* moves seasonally from the main river into the floodwater pools, but this is such a general pattern among small riverine fishes in Africa that *Sierrathrissa* probably adopts it. Reynolds (1969) described several types of clupeid migration in Lake Volta, of which the most striking was a diurnal vertical migration, subsequently to be recorded also in Lake Kainji (Otobo, 1978). At about 1730 hours the fishes, apparently including *Sierrathrissa,* ascend the water column and around 0500 hours they descend again. In Lake Kainji, there is also a seasonal cycle of such vertical movements, at least with the crustacean zooplankton, which comes up from the deoxygenated hypolimnion to the oxygenated thermocline or hypolimnion during periods of stratification (Adeniji, 1975); zooplanktivors like *Sierrathrissa* (and its predators) presumably follow this trend.

DISTRIBUTION (fig. 40)

Because of its small size and the rather frequent assumption that it was merely a juvenile, *Sierrathrissa* has been recorded from relatively few localities. Originally described from Sierra Leone coastal rivers (Thys van den Audenaerde, 1969), it is now known to occur from the Senegal River eastward to the Wouri River in Cameroon, not only in the lower and middle reaches of rivers but, at least in the Niger, far up as well. It seems to have thrived in man-made lakes (Volta and Kainji), thus perhaps also in natural lakes.

DISCUSSION

In his stimulating review of heterochrony in developmental processes, as a means to explore connections between ontogeny and phylogeny, Gould (1977) drew the valuable distinction between two methods of achieving paedomorphosis. Youthful-looking adults can arise through an accelerated rate of sexual development (relative to the rate of somatic development), to provide a short generation time and usually small adults (*progenesis*); or

such adults can arise through a retarded rate of somatic development to give a long generation time and usually large adults (*neoteny*). In these terms, *Sierrathrissa* is clearly progenetic, achieving sexual maturity at a size (thus presumably at an age) when "normal" clupeoids are in larval or early juvenile stages.

The selectional advantages of either rapid maturation or small size—or both combined—can only be hazarded. Gould (1977) postulated progenesis as a response to uncrowded but ephemeral conditions. Such conditions exist in the temporary floodwater pools of African rivers, which provide spawning sites for some riverine fishes (e.g., *Labeo victorianus*—see Fryer and Whitehead, 1959). However, such fishes exploit the temporary conditions not by a short generation time, but by very rapid embryonic development (about 24 hours), thus ensuring that well-grown juveniles can escape back into the river before the pools are cut off and desiccate. *Sierrathrissa,* on the other hand, if its somatic development proceeds as fast as that of other small African fishes, must have a generation time of only two or three months, which is far too frequent to coincide with flood conditions. The fact that adults with mature gonads are found throughout the year (at least in Lake Kainji) implies that the advantages of fast maturation are not wasted and that there is an extremely high reproduction rate.

Since size generally increases up any food chain (while numbers decrease) and thus mortality from predators is greatest in early ontogenetic stages, it would seem that progenesis merely increases predation risks. If this is exactly balanced by the higher reproductive rate, then the overall achievement in selectional terms will be energy saving. Is this sufficient to account for the evolution of a pygmy species successful enough to have spread its riverine populations across more than 2000 km of West Africa? Perhaps other selectional strategies have been at work. For example, *Sierrathrissa* may merely have taken advantage, at its small size, of an underexploited zooplankton resource (e.g., the cladocerans of Lake Kainji), although it can be argued that the development of a few more gillrakers would have served the same end (but perhaps with loss of growth efficiency).
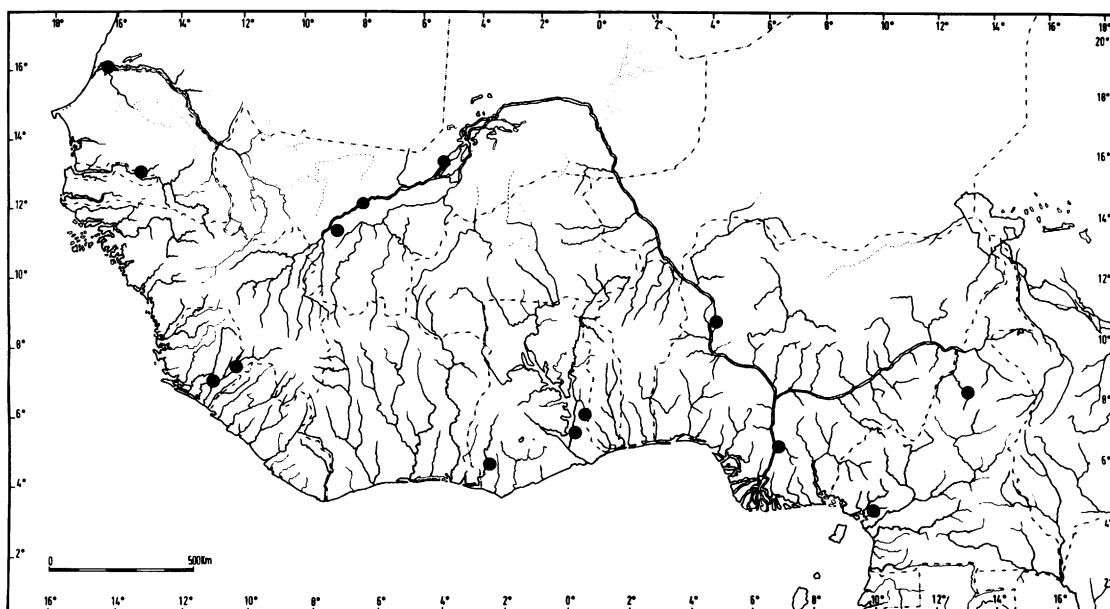
FIG. 40. Records of *Sierrathrissa leonensis* from West African rivers (Senegal River eastward to Wouri River).

Again, like most clupeoids, *Sierrathrissa* is a schooling fish and thus fecundity, generation time, and school size must have a fairly exact relationship to mortality rates from predation (assuming that the school is basically a defense strategy). A progenetic species, by decreasing generation time, may tip the balance just a fraction in its favor, even at the cost of its obligatory sacrifice in fecundity (due to small size). Finally, it seems that *Sierrathrissa* rather often occurs with *Pellonula,* judging by museum collections. Perhaps it has adopted a "shared risk" strategy with juvenile *Pellonula,* either because it is itself unable to generate schools large enough to ensure adequate protection, or because its own pre- and postpredatory avoidance techniques are inferior (the sinusoidal swimming movements observed by Loiselle suggest slow reactions). Erlich and Erlich (1973) have pointed to the defensive advantages of such heterotypic schooling. In this way, *Sierrathrissa* would also have rendered itself immune from one major predator—*Pellonula,* which presumably does not attack schools of its own juveniles. One must bear in mind, however, Loiselle's further observation (see under Biology) that adult *Pellonula* in Lake

Kainji were schooling at a lower level and came up to feed on the shallower *Sierrathrissa*; also, Lelek (1973) found *Sierrathrissa* throughout Lake Kainji to outnumber *Pellonula* by 85:15.

The excellent review of small size in fishes and its selectional advantages in various ecotypes by Miller (1979; small and pygmy clupeoids not dealt with, however) does not take the question further as regards *Sierrathrissa,* for which much more biological and physiological data are needed before hypotheses about progenesis can be usefully discussed.

The relationship of *Sierrathrissa* to other clupeids is also problematic. It seems reasonable to suppose that its closest living relative must be among the other 20 or so freshwater African pellonulines. However, many of the characters described here for *Sierrathrissa* can be subsumed under a single (apomorphic?) feature, progenesis. Such characters may not carry much phylogenetic information, being obligatory juvenile features which for purely developmental reasons could not progress beyond particular ontogenetic points. The failure of certain bones to ossify, or the premature halt in the forward migration of the dorsal fin, may be among

these. Thus, cartilaginous gill elements may ensure a necessary elasticity which might not be achieved by a more rigidly ossified gill basket at this small size; a more posterior dorsal fin is so generally found in clupeoids before metamorphosis that it may be mechanically essential (presumably for sudden bursts of speed before body size allows more sustained fast swimming).

The pellonulines are small fishes, usually not more than about 60–100 mm SL, although the predatory piscivors *Cynothrissa* and *Odaxothrissa* reach 130 mm SL. All of them show three apparently paedomorphic characters: absence of a 1st (anterior) supramaxilla, retention of the posterior frontal fontanelles, and only i7 pelvic finrays (but only i6 in *Sierrathrissa*). The anterior supramaxilla ossifies later than the posterior one; the roofing of the posterior frontal fontanelles may not be completed until quite late in ontogeny (at 50–90 mm SL in some clupeoids), and there is some evidence from the clupeine *Opisthonema* that the final pelvic finray appears later than the rest (Richards, Miller, and Houde, 1974, p. 1131). Further "loss" characters occur among the pellonulines (posterior supramaxilla highly reduced or absent, scutes reduced or absent, branchiostegal rays reduced; see Introduction, p. 2). In fact, if the subfamily Pellonulinae is indeed monophyletic, then the dominant trend has been reduction in size and a truncated development of certain body parts. To find the closest relative of *Sierrathrissa* in this context requires comparative studies of the larval stages of other pellonulines.

LIST OF STUDY MATERIALS

Holotype, 25.5 mm SL, Waanje-Ferry near Pujehun, Sierra Leone (7°24′N, 11°45′W); coll. D. Thys van den Audenaerde; 15.IV.1969; MRAC 174610.

40 fishes, *paratypes*, 16.5–28.5 mm SL, same data as the holotype; MRAC 174611-652.

43 fishes, *paratypes*, 15.5–21.0 mm SL, Moa River, Majihun near Kenema, Sierra Leone (7°52′N, 11°07′W); coll. D. Thys van den Audenaerde; 24.IV.1969; MRAC 174653-701 (3 specimens stained with alizarin).

5 fishes 18.2–25.2 mm SL, Tondé, River Sandje, Wouri system Cameroon (4°13′N, 9°50′E); coll.

D. Thys van den Audenaerde; 27.III–4.IV.1970; MRAC 73-29-P-2049-2107.

77 fishes 12.5–30.4 mm SL, Lake Kainji, Nigeria (10°20′N, 4°28′E); coll. F. Otobo; 2.IX.1972/ 14.II.1974/29.IV.1974/15.V.1974/17.VI.1974/ 29.VIII.1974/18.IX.1974/12.X.1974; MRAC 73-44-P-1-52; MRAC 75-36-P-969-1695; MRAC 76-45-P-1249-3879; MRAC 76-45-P-3922-3929; MRAC 76-45-P-3960-3990 (several specimens stained with alizarin).

20 fishes 16.4–18.4 mm SL, Lake Kainji, Nigeria (10°20′N, 4°28′E); coll. D. S. C. Lewis; 6.IX.1972; BMNH 1973.11.13.11–32 (3 fishes stained with alizarin and alcian blue).

19 fishes 21.5–25.3 mm SL, Lake Kainji, Nigeria (10°20′N, 4°28′E); coll. A. Lelek; 27.VIII.1970; BMNH 1971.11.26.1–12 (3 used for SEM photography at MacQuarie University).

8 fishes 21.5–24.8 mm SL, near Onitscha on Niger/Anambra, Nigeria (6°10′N, 6°47′E); coll. J. B. E. Awashie; BMNH 1984.4.24.1–8 (male 24.8 mm SL dissected, basis for figs. 6–8).

48 fishes 18.0–25.4 mm SL, Aklor, Volta Lake, Ghana (6°00′–9°00′N, 1°30′W–0°30′E); coll. P. Loiselle and D. Blair; 20.II.1968; BMNH 1970.9.24.177–216 (7 specimens stained with alizarin).

49 fishes 19.3–28.7 mm SL, Aklor, Lake Volta, Ghana (6°00′–9°00′N, 1°30′W–0°30′E); coll. P. Loiselle and D. Blair; 20.II.1968; BMNH 1984.4.24.9–55.

7 fishes 13.3–17.0 mm SL, Adomi Bridge, Volta River, Ghana (6°51′N, 0°17′E); coll. A. Hopson; 9.X.1961; BMNH 1970.4.24.63–69.

3 fishes 21.2–22.8 mm SL, Yeji, Volta Lake, Ghana (8°13′N, 0°39′W); coll. D. L. Kramer; 12.I.1973; BMNH 1984.4.24.56–58.

6 fishes 20.6–26.5 mm SL, Elubo, Tano River, Ghana (5°17′N, 2°46′W); coll. T. Roberts; SU 64621.

8 fishes 22.0–24.2 mm SL, Elubo, Tano River, Ghana (5°17′N, 2°46′W); coll. T. Roberts; 2.III.1964; SU 64620.

2 fishes 15.5–18.4 mm SL, Dode, opposite mouth of Afram River, Volta River, Ghana (6°30′N, 0°10′W); coll. T. Roberts; SU 64647.

12 fishes 26.0–27.6 mm SL, Alenda Wharf, Tano River, Ghana (5°07′N, 2°44′W); coll. T. Roberts; SU 64626.

102 fishes 14.0–26.1 mm SL, Senchi Ferry, Volta River, Ghana (6°12′N, 0°05′E); coll. T. Roberts; SU 64664.

1 fish 20.1 mm SL, River Sankarami, ±20 km before its confluence with the Niger, Mali (11°50′N, 8°14′W); coll. A. Lelek; 14.IX.1978; MRAC 78-35-P-1.

5 fishes 18.2–25.8 mm SL, Bansang, Gambia Riv-

er, Gambia (13°26'N, 14°39'W); coll. Svenska Expedition; 29.VIII.1950; BMNH 1977.11.29.10–14; syntypes of *Pellonula afzeliusi* Johnels, 1954; donated by A. Johnels.

5 fishes 14.6–28.4 mm SL, Bansang, Gambia River, Gambia (13°26'N, 14°39'W); coll. Svenska Expedition; 23.VIII.1950; BMNH 1977.11.29.5–9; syntypes of *Pellonula afzeliusi* Johnels, 1954; donated by A. Johnels.

About a thousand fishes 11.0–28.0 mm SL, Georgetown, Gambia River, Gambia (13°31'N, 14°45'W); coll. D. Thys van den Audenaerde; 28.III.1966; MRAC 73-5-P-284.

5 fishes 9.8–20.8 mm SL, Boundoum River, Gorom, Senegal (16°24'N, 16°04'W); coll. C. Reizer; 25.IX.1969; MRAC 77-1-P-490-494.

24 fishes 17.1–22.1 mm SL, Bamako, Sudan (=Mali) (12°40'N, 7°59'W); coll. Thomas; MNHN 1925-179; paratypes of *Microthrissa miri* Daget, 1954.

33 fishes 19.3–23.0 mm SL, Diafarabé, Sudan (=Mali) (14°09'N, 5°01'W); coll. Daget; 19.XII.1950; MNHN 1960-402; paratypes of *Microthrissa miri* Daget, 1954.

162 fishes 7.5–15.4 mm SL, Diafarabé, Sudan (=Mali) (14°09'N, 5°01'W); coll. Sissoko; 14.XII.1950; MNHN 1960-403; paratypes of *Microthrissa miri* Daget, 1954.

2 fishes 23.0–23.5 mm SL, Diafarabé, Sudan (=Mali) (14°09'N, 5°01'W); coll. Sissoko; 23.XII.1952; MNHN 1960-405; paratypes of *Microthrissa miri* Daget, 1954.

1 fish 26.5 mm SL, Lakdo, Benué River, Cameroon (±8°N, 13°E); coll. Stauch; II.1960; MNHN 1962-546.

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