Swim Bladder and Posterior Lateral Line Nerve of the Nurseryfish, *Kurtus gulliveri* (Perciformes: Kurtidae)

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ABSTRACT The morphology of the swim bladder and inner ear of the nurseryfish, *Kurtus gulliveri*, appear adapted for enhanced pressure wave reception. The saccule is enlarged and surrounded by very thin bone and two large fontanelles that would present reduced resistance to pressure waves. The swim bladder is elaborate, with six dorsolaterally projecting pairs of lobes that are tightly encased in ribs and an additional caudally projecting pair of lobes encased in the first hemal spine. The ribs and musculature surrounding the swim bladder laterally are very thin, so that four or five "rib windows" are readily apparent on back-lit specimens. This swim bladder–rib configuration would also present reduced resistance to pressure waves to enhance function as a peripheral auditory structure. However, high-resolution X-ray computed tomography and dissection reveal no anterior projections of the swim bladder that could serve as a mechanical coupling to the inner ear. The posterior lateral line nerve is well developed and lies directly over the tips of the ribs encasing the swim bladder lobes. This nerve is not, however, associated with a lateral line canal and a lateral line canal is absent on most of the body. We hypothesize that the posterior lateral line nerve transmits mechanosensory information from the swim bladder. J. Morphol. 260: 193–200, 2004. © 2004 Wiley-Liss, Inc.

KEY WORDS: swim bladder; posterior lateral line nerve; nurseryfish; mechanosensory; peripheral auditory structure

In addition to its role in buoyancy, the swim bladder is generally accepted as a simple resonating device and an accessory auditory organ in many fishes (Schellart and Wubbels, 1998). Gas in a swim bladder is compressible and the density difference between gas and fluids presumably allows the swim bladder to serve as an acoustic transformer capable of amplifying particle motion over a wide frequency range (Hawkins, 1993). The swim bladder has been shown to enhance mechanosensory function either by coupling with the lateral line (Webb, 1998) or the inner ear. The inner ear of fishes detects mechanical stimuli either by simple transmission of pressure waves through the braincase or with the aid of peripheral auditory structures. Schellart and Wubbels (1998) classify fishes that utilize specialized mechanical coupling devices between the swim bladder and the inner ear as hearing "specialists." They suggest that even without mechanical coupling the swim bladder can enhance hearing for "nonspecialists." Yan et al. (2000), however, found no experimental evidence for enhanced hearing in nonspecialist fishes and suggested that the swim bladder may not serve as an accessory auditory organ in teleosts that lack mechanical coupling with the inner ear.

Hearing specializations help define several major teleostean lineages and are also found independently in widely divergent taxonomic groups. A series of modified vertebrae that physically couples the swim bladder to the inner ear forms the Weberian apparatus, which is a synapomorphy of otophysan fishes. This is thought to be a major factor in the evolutionary success of this speciose clade of primarily freshwater fishes that includes the Orders Cypriniformes (carps, minnows, loaches), Characiformes (characins), Siluriformes (catfishes), and Gymnotiformes (knifefishes). Auditory sensory enhancement presumably is important in freshwater habitats where turbidity impairs vision. Another common form of hearing specialization in fishes is a rostral extension of the swim bladder toward the inner ear (Popper and Fay, 1999). A form of this otophysic connection helps define the Clupeomorpha (herrings and anchovies). This mechanosensory specialization potentially replaces the function of the lateral line, which is lacking on the body of most clupeomorph fishes. Rostral extensions of the swim bladder also occur in euteleostean fishes including

nocturnal squirrel fishes. These holocentrids have varying degrees of contact between the swim bladder and the otic capsule and species with increased contact typically have a greater behavioral response from an auditory stimulus (Coombs and Popper, 1979).

The typical habitat of nurseryfish is turbid coastal rivers. In fishes found in this type of habitat the lateral line is often well developed, presumably to augment vision as a form of sensory input. In the nurseryfish, however, the lateral line canal is restricted to the anterior part of the body just above the pectoral fin. The posteriormost extent of the lateral line canal ends at a vertical near the origin of the dorsal fin. Beaufort (1914) pointed out that the bones of the neurocranium are very thin and that the otic bulla is bordered both dorsally and laterally by fontanelles. However, he did not point out that these morphological features could theoretically facilitate direct near field mechanosensory perception of the inner ear. Beaufort (1914) also described the oddly shaped dorsolaterally projecting lobes of the swim bladder and their encasement and close connection with bizarre-shaped ribs. He did not detail the overall shape of the swim bladder or speculate on the potential auditory function of this arrangement. We hypothesized that the unique swim bladder morphology found in nurseryfish may serve as a peripheral auditory structure and could help compensate for the lack of an extensive lateral line canal on the body.

Kurtus gulliveri is found in coastal rivers of southern New Guinea and northern Australia, and its smaller congener, *K. indicus,* occurs from India to Borneo (Berra, 2001). These two species constitute the Kurtidae and the only family within the perciform suborder Kurtoidei (Nelson, 1994). *Kurtus gulliveri* is notable for its unusual mode of parental care. The male carries an egg mass attached to a supraoccipital hook. This assembly resembles a cluster of tiny grapes on the fish's head, which resulted in the common name of nurseryfish applied to this "forehead brooding" species (Balon, 1975). This remarkable system was first reported by Weber (1910, 1913). Guitel (1913) described the early-stage eggs of Weber's specimen. Beaufort (1914) diagrammed the skeleton including the unusual expanded ribs surrounding the lobed swim bladder and discussed various aspects of soft anatomy. Until recently, almost nothing has been published on the biology of this species since these 90-year-old articles. From a literature survey, Tominaga et al. (1996) listed the absence of a posterior extension of the swim bladder of *K. indicus*. Johnson (1993) noted that the pattern of "sensory papillae" on the head of the nurseryfish is similar to that found in apogonid fishes, but it was not mentioned if these sensory structures are chemosensory or mechanosensory.

Field work to investigate the life history of nurseryfish was begun in 2001 on the Adelaide River, east of Darwin, Northern Territory, Australia, by one of us (TMB). A map and description of the study area are given by Berra (2003). Berra and Wedd (2001) described the prawn, isopod, and fish diet of nurseryfish. The gross anatomy and histology of the male's hook and skin were examined by Berra and Humphrey (2002). The integument in the cleft of the hook is devoid of secretory mucus and neurosensory cells and is folded into crypts that extend into the dermis. This is considered a specialization that facilitates adhesion of the egg mass. Berra and Humphrey (2002) speculated that the highly vascularized dermis engorges with blood and helps clamp the egg mass in place. Eggs and pre- and postflexion larvae were described by Berra and Neira (2003) who noted a prominent, inflated swim bladder in post-yolk-sac young. The larvae are pelagic and hatch at about 5 mm body length. They leave the plankton at about 25 mm standard length. Berra (2003) compared the meristics and morphometrics of *Kurtus gulliveri* and *K. indicus*, remarked on the unusual "rib windows," and provided a color description and map of *K. gulliveri* distribution.

The purpose of this article is to illustrate the gross morphology of the swim bladder, to describe the association of posterior lateral line nerve (Puzdrowski, 1989) with the swim bladder, and to speculate on the mechanosensory enhancement provided by this arrangement. Our study was assisted by scanning with high-resolution X-ray computed tomography (HRCT) that revealed the structure and arrangement of the ribs, swim bladder, and otoliths.

MATERIALS AND METHODS

Nurseryfish, *Kurtus gulliveri*, were collected by gill nets from the Adelaide River during April–November 2001, placed on ice, then fixed in 10% formalin (Berra, 2003) or retained fresh for disarticulated skeletal preparations. Fixed material was preserved in 70% ethanol. Disarticulated skeletal material was prepared by leaving fresh specimens in water outside in tropical ambient temperatures for several weeks, allowing soft tissues to decay. Fixed specimens were cleared and counterstained for bone and cartilage following the method of Dingerkus and Uhler (1977). Opercular bones and the pectoral girdle were removed from cleared and stained specimens on the right side to expose the area between the swim bladder and the neurocranium. Soft tissue was viewed in cleared and stained specimens by reimmersing the specimen in 70% ethanol. Soft tissues were also viewed in whole preserved specimens by dissecting away opercular bones, the pectoral girdle, lateral musculature, and associated peritoneum. Osteology and swim bladder morphology were also examined on whole specimens using HRCT. The specimens were scanned at the HRCT Facility at the University of Texas at Austin, which is described in Ketcham and Carlson (2001). The actual wall of the swim bladder is not distinguishable from other tissues by X-ray attenuation. Therefore, it was necessary to scan the specimen with the swim bladder empty of fluid so that an endocast could be constructed using the contrast created by the completely "transparent" air inside the bladder. Unfortunately, it was not possible to completely drain all alcohol from the specimen prior to scanning. Therefore, we scanned the specimen twice, once with the head up and once with the head down. Swim bladder visualizations produced for this article will have two seams where the data from the scans are "stitched" together. The specimen was scanned on the ultrahigh-resolution subsystem for a total of 899 slices with an interslice spacing of 0.0891 mm and image resolu-
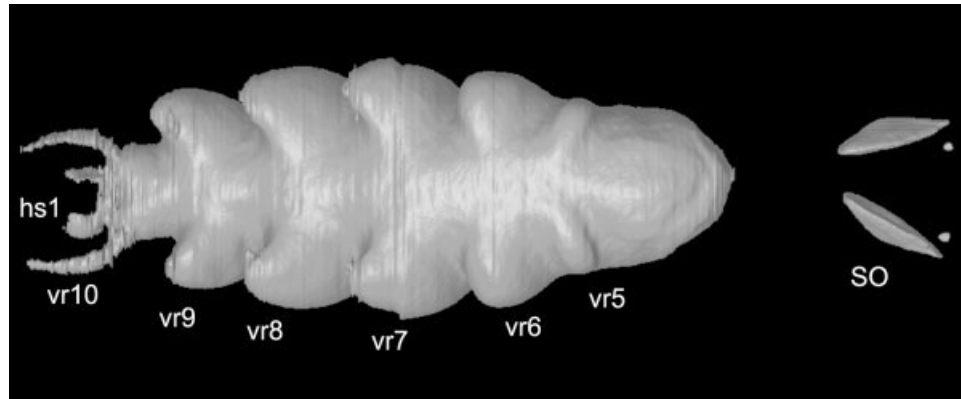
Fig. 1. High-resolution X-ray computed tomographic data showing dorsal view of the swim bladder in relation to saccular otolith (SO) of 126-mm standard length *Kurtus gulliveri* male. Dorsolateral swim bladder lobes are encased in ribs associated with the fifth (vr5), sixth (vr6), seventh (vr7), eight (vr8), ninth (vr9), and tenth (vr10) vertebral elements and the posteriormost lobes are encased in the first hemal spine (hs1). The surface inconsistency apparent on the lobe associated with the rib of the seventh vertebra (vr7) is due to a graphical seam from two data sets "stitched" together.

tion in the slice plane of 0.07 mm/pixel. The rescan had identical parameters, but only included the 290 slices comprising the bladder. Data were visualized with Amira® and VGStudio Max®. Both volumetric rendering (for osteological views) and surface modeling (for the swim bladder endocast) were employed.

Materials examined and their museum numbers were as follows (CS designates specimen cleared and stained, S designates whole skeletal preparation, D designates whole specimen dissection, CT designates whole specimen HRCT-scanned, W designates whole specimen, ODU designates the Old Dominion University fish collection museum, TMB designates a specimen in the collection of the second author, all sizes are in standard length): ODU 3149, 280 mm S; ODU 3150, 224 mm S; ODU 3152 275 mm S; ODU 3153 225 mm S; ODU 3154 54 mm CS; ODU 3156 108 mm CS; ODU 3157 CS; ODU 3158 192 mm, 224 mm D; ODU 3162 126 mm CT; TMB01-32 120 mm W.

RESULTS
Swim Bladder and Rib Configuration

The swim bladder of *Kurtus gulliveri* has six dorsolaterally extended lobes on each side (Figs. 1, 2) that cradle precaudal vertebrae (Fig. 3). The caudalmost of these lobes is the narrowest and most dorsally extended (Figs. 1, 2). All these dorsolaterally extended lobes are encased and tightly bound to dorsally extended lobes of the ribs associated with the fifth to tenth vertebrae (Figs. 3, 4). The bone, integument, and lateral musculature overlying these rib extensions are also very thin, so that light is easily transmitted through both preserved and fresh specimens, resulting in four or five apparent "rib windows" (Fig. 5; Berra, 2003). In addition to the six pairs of dorsolateral lobes, a pair of lobes extends caudally (Fig. 1) and is encased by the first hemal spine, which is expanded laterally and caudally and is hollow to receive this swim bladder extension. This additional pair of posterior swim bladder lobes was not mentioned by Beaufort (1914) or Tominaga et al. (1996). There are no anterior lobes of the swim bladder that could articulate with the neurocranium and inner ear (Figs. 1–3). The rostral end of the swim bladder is heavily vascularized to form a gas gland. The space between the rostral end of the swim bladder and the neurocranium is tightly packed with viscera, including kidney and liver. The ventral projection of the swim
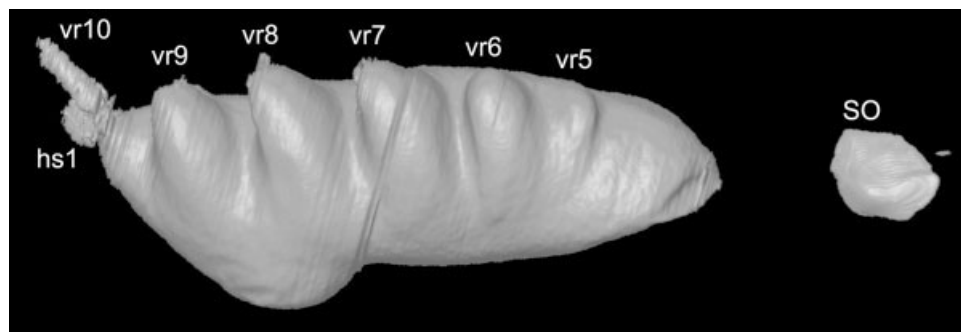

Fig. 2. High-resolution X-ray computed tomographic data showing right lateral view of the swim bladder in relation to the saccular otolith (SO) of 126-mm standard length *Kurtus gulliveri* male. Dorsolateral swim bladder lobes are encased in ribs associated with the fifth (vr5), sixth (vr6), seventh (vr7), eight (vr8), ninth (vr9), and tenth (vr10) vertebral elements and the posteriormost lobes are encased in the first hemal spine (hs1). The surface inconsistency apparent on the lobe associated with the rib of the seventh vertebra (vr7) is due to a graphical seam from two data sets "stitched" together.
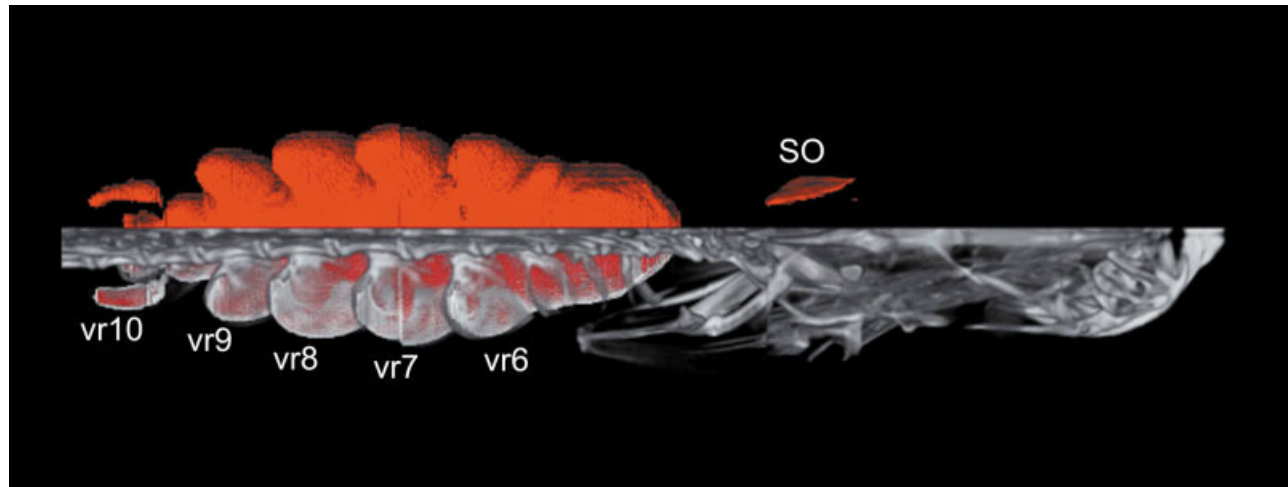
Fig. 3.   High-resolution X-ray computed tomographic data showing dorsal view of swim bladder in relation to saccular otolith (SO) and skeletal elements of right side of 126-mm standard length *Kurtus gulliveri* male. Dorsolateral swim bladder lobes are encased in ribs associated with the fifth (vr5), sixth (vr6), seventh (vr7), eight (vr8), ninth (vr9), and tenth (vr10) vertebral elements. The surface inconsistency apparent on the lobe associated with the rib of the seventh vertebra (vr7) is due to a graphical seam from two data sets "stitched" together.

bladder (Fig. 2) is the site of the oval gland. The surface of the swim bladder is very thin under the rib lobes and thickened in spaces between the ribs (Fig. 4) and ventrally.

Association of the Posterior Lateral Line Nerve With the Swim Bladder and Inner Ear

In most fishes the posterior lateral line nerve is associated with mechanosensory neuromasts enclosed in a lateral line canal or free superficial neuromasts of the trunk (e.g., Puzdrowski, 1989). The posterior lateral line nerve in nurseryfish is very well developed along the sides but is not associated with a lateral line canal. A preliminary examination of microstructure reveals apparent superficial neuromasts (A.F. Mensinger, pers. commun.) on the head (apparently the "sensory papillae" of Johnson, 1993) and body, including many of these neuromasts over the ribs (V.R. Townsend Jr. and A.H. Savitzky, pers. commun.). The posterior lateral line nerve presumably serves as an afferent pathway for these neuromasts but the innervation and distribution of these neuromasts are still under investigation. The posterior lateral line nerve lies over and is in close contact with the distalmost part of the ribs that encases the six dorsolaterally projecting tips of the lobes of the swim bladder (Fig. 6). The posterior lateral line nerve extends over the caudal vertebrae where it gradually attenuates in size, passing over the caudal peduncle. It lies close to the skin and is clearly visible on swimming fish held in captivity and on fresh and preserved specimens (Fig. 5). The posterior lateral line nerve and "rib windows" are also clearly visible in the museum specimens of *Kurtus indicus* illustrated by Berra (2003, fig. 6). Super-

ficially, the posterior lateral line nerve appears as a horizontal septum separating epaxial from hypaxial myotomes. Rostral to the fifth vertebra, the posterior lateral line nerve loses contact with the ribs and runs proximal to the supracleithrum, cleithrum, and operculum toward the exoccipital (Fig. 6). It is joined by branches of the glossopharyngeal nerve and enters the neurocranium through the glossopharyngeal foramen on the exoccipital near the angle of the basioccipital and exoccipital condyles (Fig. 7). In the nurseryfish, this foramen lies just distal to the lagena and caudal to the saccule. The foramen does not communicate directly with the lagenar alcove of the exoccipital but instead is separated from the lagena by a laminar projection that forms the roof of the lagenar alcove and the foramen appears to communicate more directly toward the saccule. The saccule is large and exposed both laterally by a vestibular fontanelle and dorsally by a large fontanelle (Fig. 7; Berra and Humphrey, 2002, fig. 3) bordered by the parietal, epiotic, pterotic, and exocciptial. The vestibular fontanelle is bordered by the prootic, intercalar (opisthotic), basioccipital, and parasphenoid. All bones surrounding the inner ear are very thin.

DISCUSSION

The ecology of the nurseryfish suggests that it must rely mostly on a nonvision sensory system. The coastal riverine habitats of the nurseryfish are typically very turbid and heavily populated with piscivorous crocodiles, sharks, sawfish, and barramundi (Berra and Wedd, 2001). Nurseryfish feed mostly on small mobile prey such as crustaceans and small fish. Freshwater fish that inhabit turbid waters typically rely on electrosensory systems or some means of enhanced mechanosensory input through
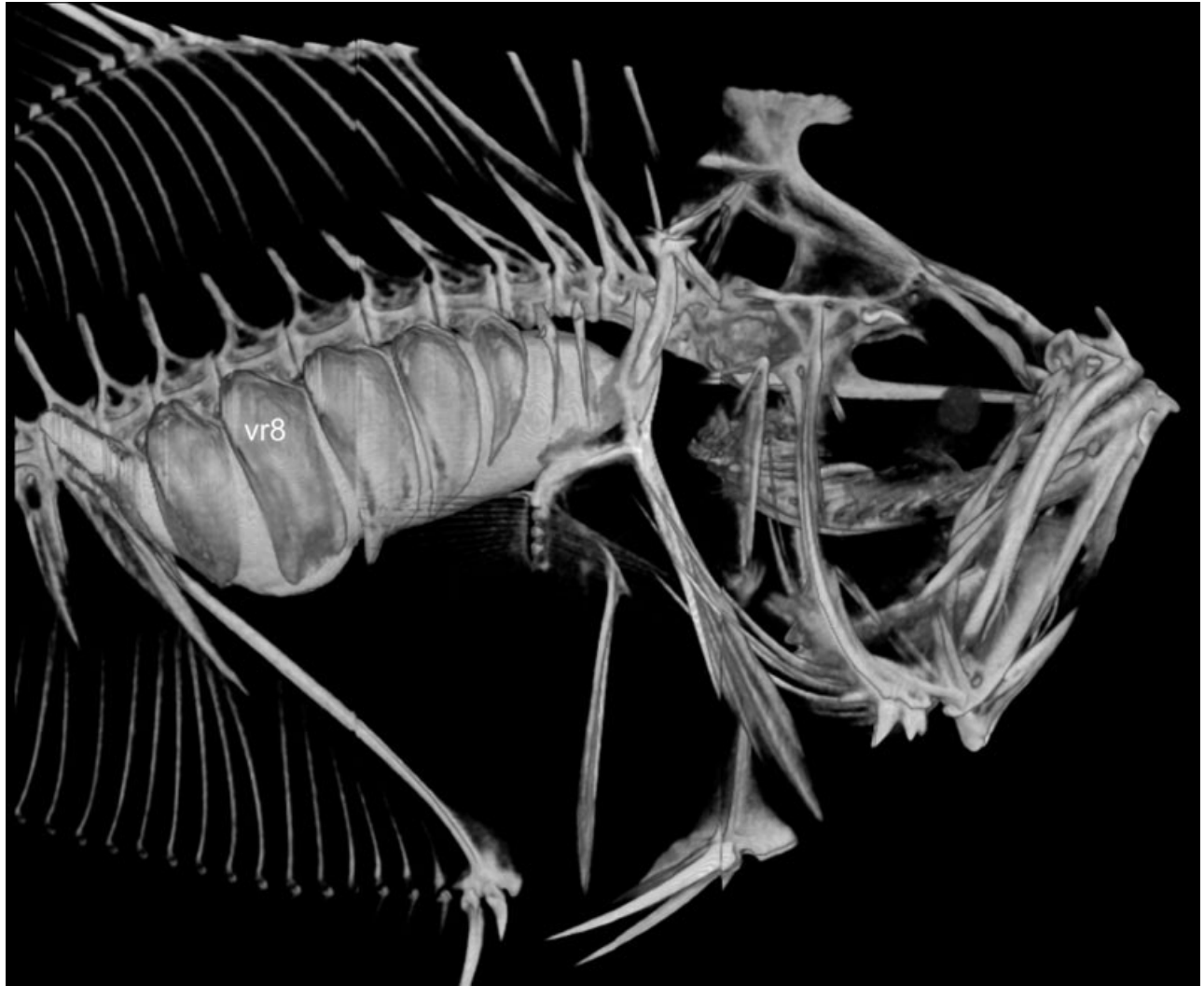
Fig. 4. High-resolution X-ray computed tomographic data showing lateral view of skeleton and associated swim bladder of 126-mm standard length *Kurtus gulliveri* male. The rib associated with the eighth (vr8) is labeled for orientation relative to other figures. The surface inconsistency apparent on the lobe associated with the rib of the seventh vertebra is due to a graphical seam from two data sets "stitched" together.

peripheral auditory structures or well-developed lateral lines.

Nurseryfish appear to rely on two different mechanosensory means in addition to superficial neuromasts and the limited lateral line canal. These are direct perception by the inner ear and some form of mechanosensory perception facilitated by the swim bladder. Although direct otolithic sound perception has only been proven for a few fish (Canfield and Rose, 1996), the enlarged saccule and associated dorsal and lateral neurocranial otic fenestra of the nurseryfish would theoretically enable enhanced perception of direct or near-field particle motion in a low-frequency range. The mechanism for this requires only the different density of the otolith and specialized macular tissue.

The swim bladder can pulsate through stimuli both from near-field, low-frequency particle motion, and from far-field sound over a range of higher fre-

quencies (Schellart and Wubbels, 1998). Although indirect perception of swim bladder pulsation by the inner ear is theoretically possible, this perception may not be possible without some means of direct coupling of the inner ear to the swim bladder (Yan et al., 2000). In the nurseryfish, indirect perception of swim bladder pulses would be dampened by the soft liver and kidney tissue that intervenes between the anterior part of the swim bladder and the neurocranium. We hypothesize that the posterior lateral line nerve provides some form of mechanosensory perception through its close association with the swim bladder. However, it is not yet clear if the lateral line serves as a mechanical link to the inner ear or strictly as a neural pathway for superficial neuromasts on the body. Webb (1998) hypothesized that pressure detection of the lateral line could be enhanced due to proximity to an extension of the gas bladder in butterflyfishes of the family Chaetodon-

Fig. 5. Right lateral view of 120-mm standard length *Kurtus gulliveri* male with pectoral fin folded forward showing externally visible posterior lateral line nerve (LL) in relation to "rib windows." The "rib windows," including the one associated with the rib of the eight vertebra (vr8), appear as four or five dark bars on sides behind the operculum and are translucent.
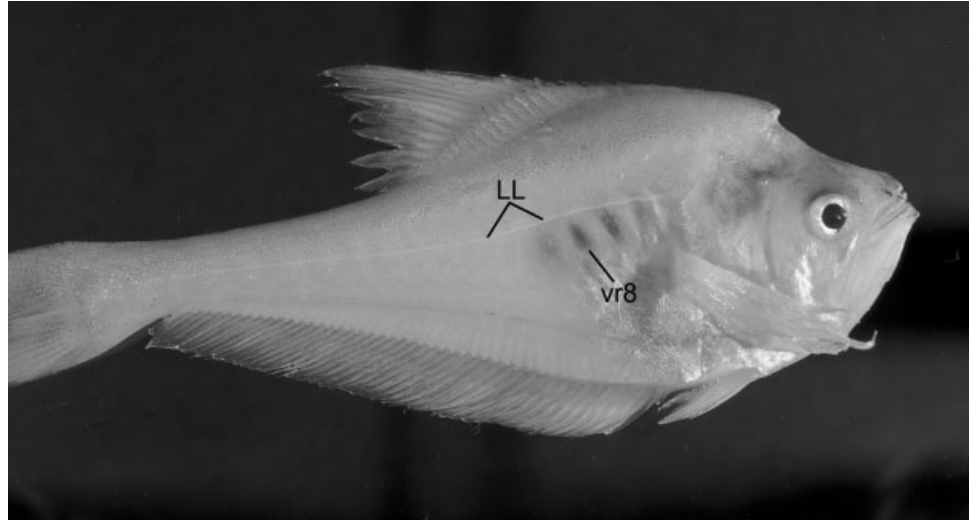
tidae. Similarly, mechanosensory perception of the superficial neuromasts or as-yet undetected free neuromasts may somehow be enhanced by vibra-tions transformed by the swim bladder in the nurseryfish. If the posterior lateral line nerve serves strictly as an afferent pathway for free or superficial
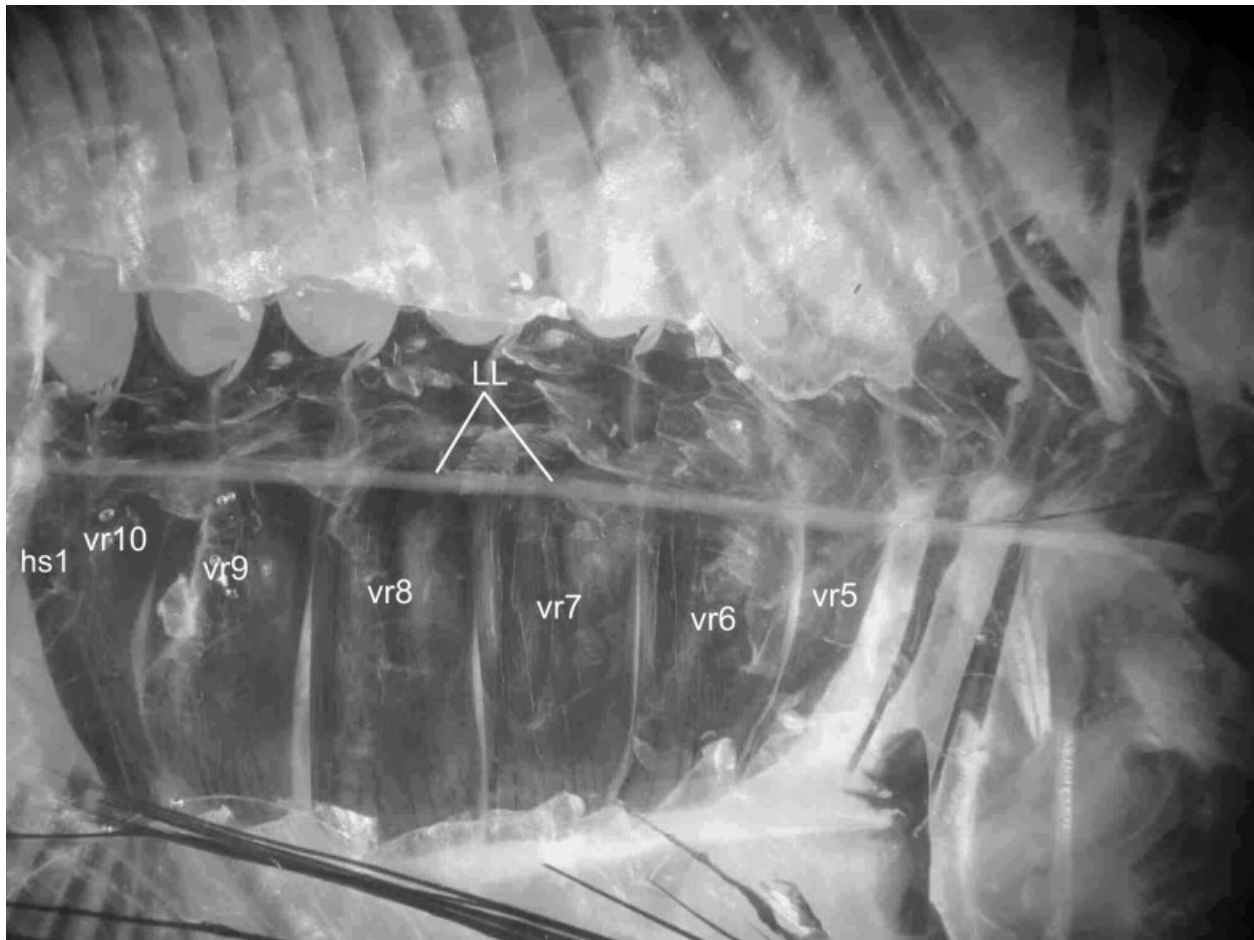

Fig. 6. Lateral view of right side of 43-mm standard length cleared and stained *Kurtus gulliveri* specimen with opercular bones, pectoral girdle, and overlying skin dissected away to expose the path of the posterior lateral line nerve (LL) over the dorsolateral lobes of the ribs. Dorsolateral swim bladder lobes are encased in ribs associated with the sixth (vr6), seventh (vr7), eight (vr8), ninth (vr9), and tenth (vr10) vertebral elements and the posteriormost lobes are encased in the first hemal spine (hs1).
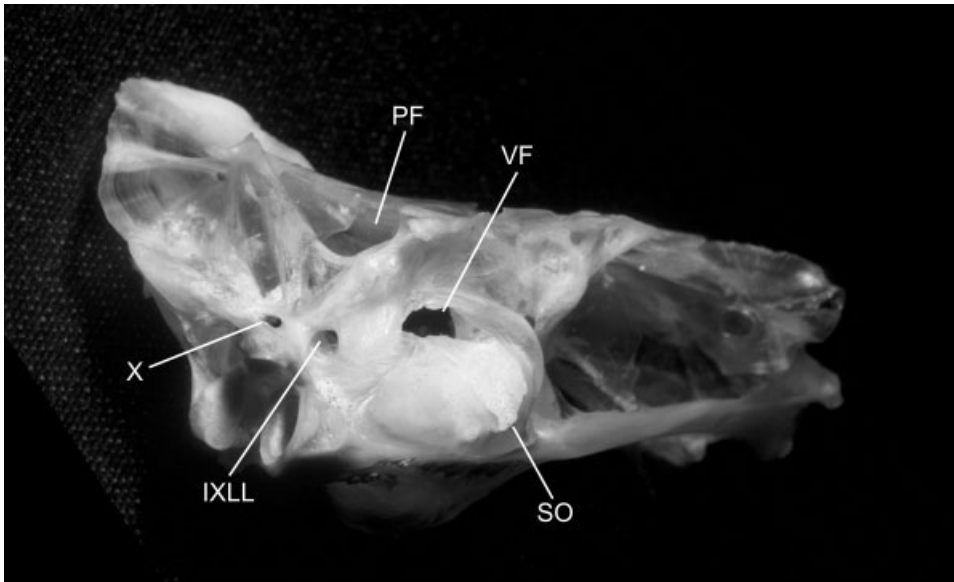
Fig. 7. Oblique ventrolateral view of neurocranium of 275-mm standard length *Kurtus gulliveri* female. The combined glossopharyngeal and posterior lateral line nerve enters a foramen (IXLL) just anteroventral to the vagus foramen (X). The saccular otolith is exposed laterally by the vestibular fontanelle (VF) and dorsally by a large fontanelle (PF) bordered by the parietal, epiotic, pterotic, and exocciptial.

neuromasts, then its physical association with the swim bladder is merely incidental. However, the path of the posterior lateral line nerve over the tips of swim bladder lobes and its entrance into the neurocranium at the site of the pars inferior indicate a potential mechanical coupling if a direct contact with some part of the membranous inner ear can be demonstrated. The posterior lateral line nerve in the nurseryfish is solid nerve tissue and a mechanism of coupling is unclear. The nerve may function similar to a "string and cup" means of vibration transmission. It appears to be taut in whole preserved specimens. Some dampening of pulses may be expected as it passes through soft tissue. The anterior position of the gas gland and ventral position of the oval glands do not appear to interfere with potential vibration transmission along the posterior lateral line nerve. Swimming through sinusoidal body movement would be expected to cause varying tension along the nerve. However, observations of swimming behavior of nurseryfish in an aquarium indicate that they normally remain motionless and typically use sinusoidal body swimming after prey items are detected (Berra and Wedd, 2001). Videotape of *Kurtus gulliveri* swimming in a 5,000-liter aquarium at the Territory Wildlife Park outside of Darwin shows that nurseryfish spend most of their time hovering placidly in mid-water. They maintain their position by gentle movements of the pectoral and caudal fins, which move simultaneously. They are capable of brief bursts of speed to engulf prey items by movement of the caudal fin, but the overall impression is of a fish suspended in the water column. Confirmation of this swimming behavior in situ has not been practical because of turbid water and the presence of numerous saltwater crocodiles. Remaining mostly motionless is a strategy of many freshwater fish that rely on electrosensory means. This interferes less with electrosensory fields sur-

rounding the fish. There is no evidence of electroreceptors in the nurseryfish. Remaining mostly motionless may interfere less with the function of the posterior lateral line nerve in the nurseryfish since it not only overlies the tips of the dorsolateral swim bladder lobes, but also extends along the sides and attenuates near the caudal fin. Experimental evidence suggests that far-field indirect sound may serve to elicit an alert response, whereas direct near-field sound may serve more for directional hearing (Canfield and Rose, 1996). The posterior lateral line nerve may therefore serve primarily to transmit indirect sound while motionless. While swimming, the transmission of direct sound to otoliths may be more important. Microstructure and experimental evidence are required to elucidate the nature of vibration transmission and the role of free superficial neuromasts in relation to the swim bladder for direct neural stimulation.

We speculate that the "rib windows," rib morphology, and bizarre swim bladder shape all enhance acoustic reception. The tissue of the dorsolateral lobes of the swim bladder is thin. Overlying the tips of these lobes there is very sparse ossification of the encasing rib, greatly reduced musculature, and a thin integument. This translucent configuration that gives the "rib windows" appearance would present reduced resistance to transmission of sound and particle displacement. This reduced resistance is similar to the thin neurocranium and otic fontanelles that could facilitate direct otolithic stimulation.

In addition to facilitating sound transmission, the configuration of the dorsolateral swim bladder lobes and associated ribs may also enhance selective frequency stimulation. These lobes are all different sizes, in particular the slender and elongate sixth lobe associated with the rib of the tenth vertebra. The gas in the different lobes would resonate at

different frequencies and this may allow perception of different frequencies over a wide range. A rich variety of hair cells associated with the saccule, particularly in hearing specialists, may help extract selective frequencies from a stimulus (Popper and Fay, 1999). However, how this is done in fishes and the details of frequency reception are mostly speculative (Fritzsch, 2000).

Beaufort (1914) concluded his comprehensive anatomical study of *Kurtus gulliveri* by returning to the unique and strange shape of the gas bladder and its encasement by ribs. He attempted to interpret this arrangement in terms of buoyancy and concluded that the rigid ribs would interfere with the expansion and contraction of gas with depth and remained puzzled by its functional significance: "Ich muss hierauf die Antwort schuldig bleiben" (I have to owe you an answer). Microstructure and experimental evidence are needed (and such studies are in progress) to confirm that the swim bladder functions primarily as a means of acoustic transformation to enhance hearing and to determine if vibrations are mediated directly by the posterior lateral line nerve or indirectly by superficial neuromasts. Either form of swim bladder mediated enhanced acoustic perception would be unique.

ACKNOWLEDGMENTS

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