New Interpretation of the 3-D Configuration of Lateral Line Scales and the Lateral Line Canal Contained within Them

Authors: Webb, Jacqueline F., and Ramsay, Jason B.

Source: Copeia, 105(2) : 339-347

Published By: The American Society of Ichthyologists and Herpetologists

URL: https://doi.org/10.1643/CG-17-601
New Interpretation of the 3-D Configuration of Lateral Line Scales and the Lateral Line Canal Contained within Them

Jacqueline F. Webb1,2 and Jason B. Ramsay1,3

The lateral line scales are important features of bony fishes, but the three-dimensional configuration of the scales and the lateral line canal segments contained within them have been illustrated inaccurately in the literature. The lateral line scales of ten percomorph species (in Embiotocidae, Pomacentridae, and Pleuronectiformes [Bothidae, Pleuronectidae]) were studied histologically and in cleared and stained material. Canal diameter and the degree of overlap between adjacent lateral line scales appears to vary among species, but the lateral line scales are consistently oriented at a shallow angle, the cylindrical canal segments form a continuous canal that runs roughly parallel to the skin surface, and canal pores (when present) are perforations of the epithelium between adjacent lateral line scales. A new figure illustrates this anatomical configuration, which is in stark contrast to that portrayed in textbooks and in the primary literature, but is likely common among bony fishes. This work provides a new interpretation of a fundamental feature of bony fishes and highlights the ease with which inaccurate figures are disseminated and thus the need to verify the accuracy of anatomical illustrations.

The mechanosensory lateral line system was named for the “lateral line” or the “trunk canal” that typically runs from the margin of the operculum to the caudal peduncle on the lateral flank of bony fishes (reviewed in Webb, 2014). The number of lateral line scales is an important meristic character for species identification of different populations within species, as noted in a myriad of identification keys and related resources. The lateral line system of bony fishes is composed of neuromast receptor organs found, not only in a canal on the trunk, but also in canals on the head, and on the skin of the head and trunk. It detects unidirectional and oscillatory water flows, which is critical for prey detection, predator avoidance, navigation, and communication (reviewed in Webb et al., 2008; Montgomery et al., 2014). The accurate description of sensory anatomy plays an important role in understanding sensory function, which has critical implications for fish behavior and ecology.

The trunk canal is composed of tubular canal segments found within a horizontal series of overlapping scales, the “lateral line scales.” These generally form a single scale row that starts at the caudal margin of the skull and extends to the caudal peduncle (Fig. 1). Among bony fishes, eight patterns describe the number, course, and extent of development of the lateral line canals on the trunk (Webb, 1989a). The lateral line scales themselves demonstrate a good deal of interspecific variation (Voronina, 2007; Voronina and Hughes, 2017), some of which can be explained by changes in developmental timing (Voronina and Hughes, 2013). Furthermore, morphological variation is found between scales in the rostral and caudal portions of the trunk canal in some taxa (e.g., labrids; Webb, 1990), among the multiple trunk canals in Hexagrammos (Wonssettler and Webb, 1997) and Xiphister (Clardy et al., 2015), and between the trunk canals on the eyes versus the blind side of the body in flatfishes (e.g., Voronina, 2009a, 2009b).

Like all of the scales that typically cover the body of bony fishes, the lateral line scales are found within the dermis (deep to the epidermis, basement membrane, and dermal pigment cells), but superficial to the stratum compactum (the fibrous collagenous component of the dermal connective tissue) and the trunk musculature. The lateral line scales form an overlapping series in which the exposed caudal edge of one scale lies over the rostral portion of the scale caudal to it. There is typically some overlap between the lateral line scales and the rows of scales dorsal and ventral to them (Fig. 1). The way in which the tubular canal segments within adjacent, overlapping scales align to form a continuous canal is a function of the morphology of the scales and the canal segments contained within them. An anterior suprascalare pore and a posterior infrascalare pore (Coombs et al., 1988) represent the rostral and caudal ends of the short tubular canal segment in each lateral line scale, respectively, and link the lumens of the canal segments in adjacent scales (Fig. 1C). One or more perforations in the wall of the canal segment in each scale, if present, represent additional pores that connect the canal lumen to the environment (Webb, 1990; Voronina and Hughes, 2013). One canal neuromast is typically found in the epithelial lining in the floor of each canal segment (one neuromast per lateral line scale; e.g., Allis, 1889; Jollie, 1984; Webb, 1989b; Wonssettler and Webb, 1997; Webb and Shirley, 2003; Bird and Webb, 2014; Webb et al., 2014). The floor of each canal segment may be pierced by a nerve foramen through which a branch of the posterior lateral line nerve extends to innervate the hair cells that compose the canal neuromast (e.g., Wonssettler and Webb, 1997). However, a nerve foramen is not reported for all types of lateral line scales (Voronina and Hughes, 2013; Wada et al., 2014), so in these cases, the course that a branch of the lateral line nerve takes to innervate a neuromast is unclear.

Papers that have described individual lateral line scales in a range of teleost taxa (e.g., Delamater and Courtenay, 1973; Lippitsch, 1990; Voronina, 2007, 2009a, 2009b; Voronina and Hughes, 2013, 2017) typically provide little or no information about how individual lateral line scales are configured to compose the continuous trunk canal. An illustration of this feature of lateral line anatomy was published more than a century ago (Allis, 1889). Nevertheless, the basic features of the trunk canal contained in the lateral line scales—the relationships between the lateral line canal segments, the...
lateral line scales in which they are contained, the location of the canal neuromasts, and the nature of the canal pores that link the lumen of the fluid-filled lateral line canal to the external environment—have been inconsistently and inaccurately illustrated in ichthyology and comparative vertebrate anatomy textbooks (Fig. 2).

For instance, in Figure 2A (Romer and Parsons, 1977 [after Goodrich, 1930]; also published in Wolff, 1991; based on *Perca*), the lateral line canal is parallel to the skin surface and passes through the overlapping lateral line scales, which are oriented at a 45° angle to the skin surface. Canal neuromasts are positioned periodically within the canal, but do not appear to be associated with each canal segment in the lateral line scales. Elongated tubules appear to extend within each of the lateral line scales and have terminal pores at the skin surface, and the canal perforates the base of each scale as it extends down the body. The lateral line nerve is below both the canal and the scales, and nerve branches travel between adjacent scales to innervate each neuromast. In Figure 2B (Barton, 2007), the lateral line canal is parallel to the skin surface, and a tubule extends, within a scale, to the skin surface ending in a pore. The canal appears to pass through sequential scales, and the nerve branches extend up between scales to innervate each neuromast. In Figure 2C (Helfman et al., 1997, 2009, adapted from Hildebrand, 1988; based on a minnow), the canal is parallel to the skin surface, with short tubules that lead to the skin surface in the soft tissue between scales. The neuromasts are found in the canal in the vicinity of each scale. In Figure 2D (Weichert, 1958), the scales overlap only slightly and lie at a very shallow angle. The canal is parallel to the skin surface, but is deep to the scales, but nevertheless contains neuromasts whose positions are in register with each scale. Canal tubules pierce each of the scales between the locations of adjacent neuromasts and extend to the skin surface. The lateral line nerve runs deep to both the scales and the canal. In Figure 2E (Walker and Liem, 1994), the scales are at a 45° angle, the lateral line canal is parallel to the skin surface, but lies deep to the scales, and neuromast locations are not in register with either the scales or the tubules that extend to the skin’s surface. In Figure 2F (Moyle and Cech, 1982), the canal is parallel to the skin surface, the roof and base of the scales are represented quite schematically, with no indication of any overlap, and periodic pores pierce the skin between adjacent canal neuromasts, suggesting that one neuromast is located in the canal within each scale. This figure was borrowed from Dijkgraaf (1962), the pioneer in the study of the behavioral roles of the lateral line system.

In addition to the way in which the anatomy is portrayed, the provenance of figures can be quite complicated, making it difficult to identify their original source or assess their anatomical accuracy. For instance, Weber and Schiewe (1976), in their study of the effect of gas-bubble disease on lateral line physiology of steelhead trout, present a figure depicting a sagittal section through the trunk canal, which was then reproduced in at least two papers in the lateral line literature (Coombs et al., 1988; Kroese and Schellart, 1992; Fig. 3A). Weber and Schiewe (1976) state that “[d]escriptions of lateral line systems of salmonids are found in reports by Vladykov (1926) and Disler (1960)”, but neither of these sources include figures of the 3-D configuration of the trunk canal in a series of lateral line scales. Thus, it is assumed that Weber and Schiewe’s (1976) figure is original. They indicate that they “expand[ed] on Vladykov’s (1926) observations of

---

**Fig. 1.** Lateral line scales composing the trunk canal. (A) Trunk canal in a damselfish (based on *Pristotis obtusirostris*). (B) Cleared and stained lateral line scales of *P. obtusirostris* (=*P. jerdoni*, MCZ 54084, 80 mm SL) in the position of the box in A. (C) Lateral line scale from *Chromis lepidolepis* (MCZ uncat., 58 mm SL) showing the suprascalar pore (solid line) on the scale surface and the infrascalar pore (dotted line) on the underside of the scale. The suprascal and infrascalar pores represent the anterior and posterior ends (respectively) of the short tubular canal segment within a lateral line scale, which link the canal lumen in adjacent overlapping scales. Abbreviations: isp, infrascalar pore; llc, lateral line canal; ssp, suprascalar pore. B and C © President and Fellows of Harvard College.
the trunk lateral line [in a trout, *Trutta fario* L.], and present the general morphology” in their figure. A translation of Vladykov (1926; in Czech) provided by the US National Marine Fisheries Service was used by Weber. That translation includes captions for figures 1 and 2 (which depict the head and trunk canals in a trout according to the caption) and a footnote indicating that “[u]nfortunately, these diagrams were lost while in print”, presumably meaning that they were lost in transit or during production. Thus, in the absence of an actual figure, Weber and Schiewe (1976) could have only used Vladykov’s written description of lateral line scale and trunk canal anatomy (e.g., translation p. 15) and dissection of specimens to construct their original figure. It is interesting to note, however, that Vladykov (1926) used terminology concerning lateral line canals based on Shimkevitch (1921), whose figure of a sagittal section through the trunk canal (his fig. 302) is cited as “Nach Allis aus R. Wiedersheim”. Wiedersheim’s (1907) figure (his fig. 184) is cited as “after Maurer” (1895). However, Maurer included no such figure, but the figure published by Wiedersheim (1907) is indeed the one originally published by Allis (1889; see Fig. 3B) in his monograph on the lateral line system of the bowfin, *Amia calva*.

The variation in the portrayal of the configuration of the lateral line scales and the trunk canal and the complex histories of published figures demanded that the anatomy of this fundamental feature of fishes be re-examined. To address this, histological material prepared from ten species of percomorph fishes (embiotocids, pomacentrids, pleuronectiforms [Bothidae, Pleuronectidae]) was studied in detail. All of these species have a single, complete trunk canal composed of relatively unspecialized lateral line scales, which represent the most common lateral line scale type found among teleost fishes (Voronina and Hughes, 2017). This suggests that these taxa are good representatives of percomorph fishes, and perhaps of teleost fishes more generally. Additional cleared and stained material was also used to document the 3-D relationships of the lateral line scales and tubular lateral line

---

**Fig. 2.** Sample of figures from ichthyology and comparative anatomy textbooks depicting the configuration of the lateral line scales and the trunk canal contained within them in sagittal section (rostral to the left). Figures have been redrawn to provide uniform labeling. See text for additional explanation. (A) From Romer and Parsons, 1977 based on *Perca* sp.; (B) from Barton, 2007; (C) from Helfman et al., 2009; (D) from Weichert, 1958; (E) from Walker and Liem, 1994; (F) from Moyle and Cech, 1982 (originally published by Dijkgraaf, 1962), without indication of the lateral line nerve. Abbreviations: llc, lateral line canal; n, canal neuromast; p, pore (dotted line); plln, posterior lateral line nerve; s, scale; sn, superficial neuromast.
canal segments contained within them as well as the location of both the canal neuromasts and the canal pores that link the canal lumen to the external environment.

MATERIALS AND METHODS

Material from one small adult individual in each of ten species was prepared histologically (see Material Examined, below). Fish collected by JFW in Mission Bay (CA) and off San Juan Island (WA) had been fixed in 10% formalin in seawater for several years. Specimens in the collection of the Museum of Comparative Zoology (MCZ, Harvard University, accession numbers provided) had been fixed in 10% formalin in seawater and stored in 70% ethanol. Tissue containing a portion of the rostral trunk canal and underlying muscle tissue was dissected from the right side of each specimen, decalcified in Cal-Ex (Thermo Fisher Scientific) for eight hours, rinsed in running tap water, dehydrated in an ascending series of ethanol solutions (70%–100%), infiltrated overnight in JB-4 (Polysciences), and embedded. Sagittal sections (10 μm thickness) of the canal were cut with a tungsten carbide knife on a Leica motorized retracting microtome. Every other section was mounted out of water on clean glass slides (yielding a 20 μm inter-section interval), dried overnight at 60°C, stained with 0.5% cresyl violet, and rinsed with tap water. Slides were then air dried overnight and coverslipped with Entellan (Electron Microscopy Sciences). Images were captured digitally using Spot Software (v. 5; Diagnostic Instruments) and a Spot digital camera (Model 25.22, Mp Color Mosaic) on an Olympus BH-2 compound microscope. Tracings of images of histological sections were made using Microsoft PowerPoint. They were enhanced to highlight different tissues (epithelium, scale, neuromasts, connective tissue, nerves), the three dimensionality of the lateral line canal segments, the spatial relationships of the lateral line scales, and the location of the canal neuromasts and canal pores.

In addition, strips of tissue containing lateral line scales with underlying muscle were dissected from the rostral portion of the trunk canal of seven species (including some of the same species from which tissue was prepared histologically, see Material Examined), enzymatically cleared and stained for bone with alizarin red, and stored in glycerin (as per Potthoff, 1984). This material was used to visualize the configuration of the lateral line scales in situ and to confirm observations and interpretations derived from the analysis of histological material.

RESULTS

The lateral line scales in all ten species examined were situated within the dermis, deep to the epidermis and basement membrane, but superficial to the collagenous stratum compactum (dermal connective tissue) and the trunk musculature that lies beneath it. Adjacent lateral line scales were found to overlap to different degrees among species, but in all cases, scales were oriented at a very shallow angle so that the lateral line canal segments within them were opposed end to end, forming a continuous lateral line canal running roughly parallel to the skin surface. One neuromast was typically found in the canal segment in each of the tubed lateral line scales.

Sections through the trunk canal and lateral line scales were difficult to interpret at first due to the assumption that each canal segment was a cylinder with flat ends. However, careful study revealed that the lateral line scales in the embiotocids (Figs. 4, 5) and pomacentrids (Fig. 6) are in the...
form of a cantilever, with a posterior extension of the roof of the canal of one scale overlapping the base and the anterior edge of the roof of the next, more caudal, scale in the series. Each scale had a rather short, central cylindrical canal segment in which a neuromast was found, but the length and diameter of the canal segments appeared to vary among species (Figs. 5, 6). In all cases, canal pores were represented only by a perforation in the skin between scales, and short tubules extended from the canal to the skin surface in the embiotocids and pomacentrids examined.

Fig. 4. Sagittal section through the trunk canal of the embiotocid Embiotoca jacksoni showing the location of canal neuromasts (n) in the canal segments contained in the lateral line scales (s). Rostral to left. The scales sit within the dermis and beneath the epidermis; the lumen of the canal (llc) is lined by epithelium. The thin dotted line drawn between opposing tips of what appears to be one scale would suggest that the scales sit at a 45° angle within the dermis (see Fig. 2). However, the thicker dashed lines indicate the ends of the tubular canal segment (out of plane of section), which connect the base and roof of each canal segment. Scale bar: 500 μm. Abbreviations: dct, dermal connective tissue; llc, lateral line canal; m, trunk muscle; n, canal neuromast; p, pore; s, scale.

Fig. 5. Sections of the trunk canal in embiotocids with semi-diagrammatic representations. (A, B) Embiotoca jacksoni; (C, D) Micrometrus minimus; (E, F) Phanerodon furcatus; (G, H) Cymatogaster aggregata. Rostral to left. Diagrams drawn by tracing histological sections (B, D, F, H) highlight key anatomical features including the location of each neuromast (n, with domed cupula) and a 3-D representation of one tubular canal segment in a scale. Dotted lines denote the anterior suprascalar pore and the posterior infrascalar pore of the canal segment. Scales are located in the dermis and covered by an epidermis (gray); canal lumen is lined with epithelium (gray). Curvature of the scale roof and/or base (black) and separation of tissue layers are preparation artifacts. Scale bars: 500 μm.
The pleuronectiforms also appeared to demonstrate interspecific variation in the relative diameter of the canal segments (Fig. 7). However, in contrast to the embiotocids and pomacentrids, the lateral line scales on the eyed side in the bothid and pleuronectids showed little if any overlap (also reported by Voronina and Hughes, 2013). Interestingly, a neuromast was only present in association with every other scale in *Glyptocephalus zachirus*. Quite unexpectedly, lateral line canal pores could not be detected in serial histological sections in any of the pleuronectiform species examined.

**DISCUSSION**

This analysis of the 3-D configuration of the lateral line scales reveals anatomy that is in stark contrast to that portrayed in the primary literature and in ichthyology and comparative anatomy textbooks. Some of the variation in the relationship of the lateral line scales and the trunk canal portrayed in published figures might be due to interspecific differences, but with few exceptions (e.g., Allis, 1889; Romer and Parsons, 1977), the species depicted are not identified.

This study has revealed common features of the configuration of the lateral line scales and the lateral line canal found among ten species in three percomorph taxa (Fig. 8). The lateral line scales sit at a very shallow angle within the dermis. Tubular lateral line canal segments are located within the lateral line scales and form a continuous canal lumen that runs parallel to the skin surface, without significant undulations along its course (see Figs. 2A, C, 3). Each lateral line scale is in the form of a cantilever formed by the rostral extension of the scale plate and the caudal extension of the dorsal roof of the lateral line canal segment, which is like the scales reported in hexagrammids ("Scorpaeniformes," Wonsettler and Webb, 1997). When viewed from above, these scales appear to be Type UTS I or II lateral line scales (Voronina and Hughes, 2017), which are common among percomorph fishes, and among bony fishes more generally (Voronina and Hughes, 2017). The pores that link the fluid within the canal to the water in the external environment are simple perforations in the skin located between scales (see also Fig. 7). Additional tubules that terminate in multiple pores in some fishes (e.g., in labrids, Webb, 1990; the ossified "canaliculi" of Voronina and Hughes, 2013) are not depicted here. Furthermore, one canal neuromast is found in the epithelial lining of each canal segment (e.g., in each lateral line scale), and a nerve foramen perforates the scale plate beneath each neuromast. The posterior lateral line nerve runs rostro-caudally, superficial to the trunk musculature, but within the dermal connective tissue beneath the scales. It should be noted that in the three pleuronectiform fishes examined, the lateral line scales are simple tubes (without a cantilever), do not overlap, and pores in the skin are absent (Fig. 7). This feature, noted by Voronina (2009b), appears to be unusual among fishes, but may have functional significance, which warrants further consideration.

Allis’ (1889) illustration of a sagittal section through the trunk canal of *Amia calva* (Fig. 3B) is based on a histological section. Its overall similarity to the anatomy in percomorphs revealed in this study (Fig. 8) is striking, and is in contrast to the anatomy portrayed in papers and textbooks (Figs. 2, 3A). We can conclude that the morphological features that define the 3-D configuration of the lateral line scales and trunk canal identified in this study are likely common among bony fishes more generally. This study provides a starting point for
an assessment of sources of variation in the 3-D configuration of the trunk canal that may be correlated with differences in lateral line scale types (Voronina and Hughes, 2017). It also provides a new baseline for the functional analysis of the trunk canal in bony fishes, and for the growing field of lateral line biomimetics, which has a goal of designing hydrodynamic sensors inspired by the mechanosensory lateral line system.
Dissemination of anatomical data—A caveat.—The dissemination of anatomical data has a long history and is now facilitated by the ease with which images are reproduced and modified electronically. However, published figures are considered a trusted and reliable source of accurate anatomical data, which are routinely re-published in primary papers and review papers, as well as in broadly accessible electronic resources (e.g., Wikipedia, http://en.wikipedia.org/wiki/Lateral_line; Encyclopedia Britannica, http://www.britannica.com/EBchecked/topic/331503/lateral-line-system).

The current study discusses only one example of what is likely a broader issue concerning the reproduction of inaccurate anatomical data. Researchers need to continue to publish accurate illustrations of fundamental features of anatomy directly from the organism, using the capabilities of an expanding range of visualization methods and digital technologies. Regardless of the method used to generate images, more comprehensive descriptions and figure captions must clearly explain anatomical details, specify what taxon is being represented, and indicate whether a figure is semi-diagrammatic, diagrammatic, or is a literal representation of anatomical structure. Finally, our understanding of fundamental, and seemingly simple, anatomical features must be periodically re-assessed as published figures are adapted, schematized, or simplified for use in the scientific literature and in publicly accessible online resources.

MATERIAL EXAMINED

HISTOLOGY

Family Bothidae

Citharichthys sordidus: uncatalogued, 1, 89 mm SL, off San Juan Island, WA.

Family Embiotocidae

Cymatogaster aggregata: uncatalogued, 1, 75 mm SL, Mission Bay, CA.

Embiotoca jacksoni: uncatalogued, 1, 66 mm SL, Mission Bay, CA.

Micrometrus minimus: uncatalogued, 1, 73 mm SL, Mission Bay, CA.

Phanerodon furcatus: uncatalogued, 1, 76 mm SL, Mission Bay, CA.

Family Pleuronectidae

Glyptocephalus zachirus: uncatalogued, 1, adult.

Family Pomacentridae

Abudealuf taurus: (=A. torus) MCZ 43097.

Chromis lepidolepis: MCZ 64373, 58 mm SL.

C. tertatensis: MCZ uncat., 65 mm SL.

Pomacentrus lepidogenus: MCZ 64376, 61 mm SL.

Pristotis obtusirostris: (=P. jerdoni) MCZ 54084.

ACKNOWLEDGMENTS

We thank K. Hartel (Ichthyology Department, MCZ, Harvard University) who graciously provided access to specimens. D. Khosla prepared the histological material used in this analysis as part of her 1998 undergraduate honors thesis at Villanova University. JFW acknowledges funding from the George and Barbara Young Endowment at University of Rhode Island.

LITERATURE CITED


Vladykov, V. 1926. Postranni system u Eeledi Salmonidae. Dil. 1. Topografie a histologie postrannih systemu u pstruhu obecního (Trutta fario L.), [Lateral line system in Salmonidae. Part I. Topography and histology of lateral system in common trout (Trutta fario L.)]. Spisy Vydavane Pfiridovgdeckou Fakcultou Karlovy University, No. 57. [In Czechoslovakian. Translation available NMFS Foreign Fish (Translations), Washington, D.C.]


