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Morphology of the mechanosensory lateral line system in elasmobranch fishes: ecological and behavioral considerations

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Synopsis

The relationship between morphology of the mechanosensory lateral line system and behavior is essentially unknown in elasmobranch fishes. Gross anatomy and spatial distribution of different peripheral lateral line components were examined in several batoids (*Raja eglanteria*, *Narcine brasiliensis*, *Gymnura micrura*, and *Dasyatis sabina*) and a bonnethead shark, *Sphyrna tiburo*, and are interpreted to infer possible behavioral functions for superficial neuromasts, canals, and vesicles of Savi in these species. *Narcine brasiliensis* has canals on the dorsal surface with 1 pore per tubule branch, lacks a ventral canal system, and has 8–10 vesicles of Savi in bilateral rows on the dorsal rostrum and numerous vesicles ($\bar{x} = 65 \pm 6$ SD per side) on the ventral rostrum. *Raja eglanteria* has superficial neuromasts in bilateral rows along the dorsal body midline and tail, a pair anterior to each endolymphatic pore, and a row of 5–6 between the infraorbital canal and eye. *Raja eglanteria* also has dorsal canals with 1 pore per tubule branch, pored and non-pored canals on the ventral surface, and lacks a ventral subpleural loop. *Gymnura micrura* has a pored dorsal canal system with extensive branch patterns, a pored ventral hyomandibular canal, and non-pored canal sections around the mouth. *Dasyatis sabina* has more canal pores on the dorsal body surface, but more canal neuromasts and greater diameter canals on the ventral surface. *Sphyrna tiburo* has primarily pored canals on both the dorsal and ventral surfaces of the head, as well as the posterior lateral line canal along the lateral body surface. Based upon these morphological data, pored canals on the dorsal body and tail of elasmobranchs are best positioned to detect water movements across the body surface generated by currents, predators, conspecifics, or distortions in the animal's flow field while swimming. In addition, pored canals on the ventral surface likely also detect water movements generated by prey. Superficial neuromasts are protected from stimulation caused by forward swimming motion by their position at the base of papillar grooves, and may detect water flow produced by currents, prey, predators, or conspecifics. Ventral non-pored canals and vesicles of Savi, which are found in benthic batoids, likely function as tactile or vibration receptors that encode displacements of the skin surface caused by prey, the substrate, or conspecifics. This mechanotactile mechanism is supported by the presence of compliant canal walls, neuromasts that are enclosed in wide diameter canals, and the presence of hair cells in neuromasts that are polarized both parallel to and nearly perpendicular to the canal axis in *D. sabina*. The mechanotactile, schooling, and mechanosensory parallel processing hypotheses are proposed as future directions to address the relationships between morphology and physiology of the mechanosensory lateral line system and behavior in elasmobranch fishes.

Introduction

The mechanosensory lateral line system is present in all fishes and aquatic amphibians (Dijkgraaf 1962, Lannoo 1987, Northcutt 1992), and detects near field water movements relative to the skin surface (Harris & Van Bergejik 1962, Kalmijn 1989, Coombs 1994). The functional unit of the lateral line system is the

neuromast receptor organ, which consists of sensory hair cells and support cells covered by a gelatinous cupula. Displacement of the cupula by viscous drag due to water movements causes modulation of the spontaneous primary afferent discharges sent to the mechanosensory processing centers in the hindbrain (Hoagland 1933, Münz 1985, Denton & Gray 1988).

Chondrichthyan fishes (holocephalans and elasmobranchs) have several types of mechanosensory lateral line end organs that are classified by morphology and location. Superficial neuromasts (or pit organs) are located on the skin surface either in grooves (batoids) or between modified scales (sharks) with their cupulae directly exposed to the water (Figure 1). In contrast, canal neuromasts are situated in sub-epidermal canals that are either in contact with the external environment via tubules that terminate in pores, or are isolated from the environment in non-pored canals. In chimaerid fishes, canal neuromasts are also located within a system of open grooves (Cole 1896, Ekström von Lubitz 1981). Vesicles of Savi consist of neuromasts enclosed in sub-epidermal pouches found primarily on the ventral surface of some torpedinid, narcinid, and dasyatid batoids (Savi 1844, Nickel & Fuchs 1974, Chu & Wen 1979). Spiracular organs are located in diverticula of the first visceral pouch in several fish taxa including elasmobranchs, and are stimulated by flexion of the cranial-hyomandibular joint (Barry et al. 1988a,b, Barry & Bennett 1989). The morphology and spatial distribution of these mechanoreceptors determines the distance range of the lateral line system, extent of the receptive field, frequency response properties, and which component of water motion is encoded (Denton & Gray 1983, 1988, Hoekstra & Janssen 1986, Münz 1989, Kroese & Schellart 1992). Elasmobranchs are among the few fish taxa to possess multiple types of mechanosensory receptors, and therefore provide an excellent opportunity to study structure-function-behavior relationships of different mechanoreceptors within a single group of fishes.

The mechanosensory lateral line system shows considerable morphological diversity among chondrichthyan species, but the functional significance of this diversity has received little attention. Current knowledge of lateral line function is based primarily on behavioral and physiological studies in a limited number of amphibian and teleost species, which do not possess many of the morphological specializations found in chondrichthyan taxa. Therefore, in the absence of these types of experiments in chondrichthyans, comparative studies on the peripheral organization and morphology of the lateral line system can provide valuable data to infer behavioral functions for the lateral line system in this group of fishes. For example, neuromast morphology determines which type of information (e.g. velocity, acceleration, or displacement) is encoded (Kroese & Schellart 1992), spatial distributions of lateral line components define the receptive field of the system (Denton & Gray 1983), and position of lateral line mechanoreceptors on the head and body can have behavioral implications. Therefore, the purpose of this study is to integrate data on the morphology and peripheral organization of the lateral line system in several elasmobranch species (*Narcine brasiliensis*,

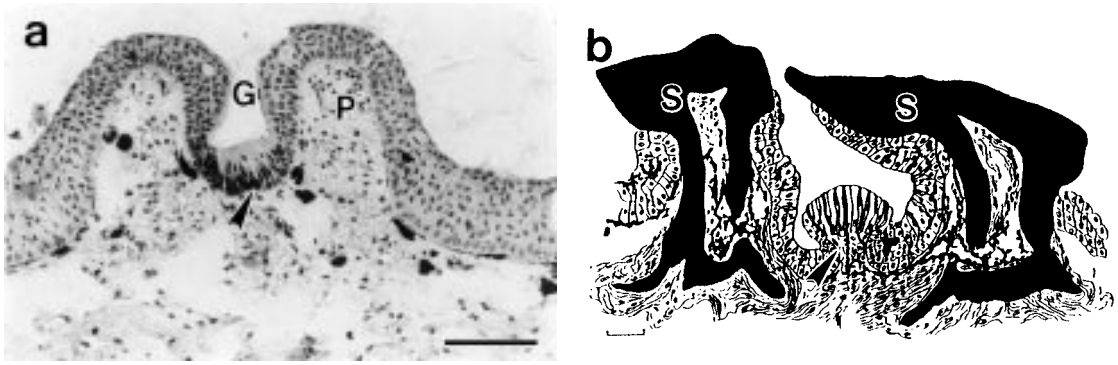

Figure 1. Morphology of superficial neuromasts in batoids and sharks. a– Transverse section of a single superficial neuromast papilla in the skate, *Raja eglanteria*. Superficial neuromasts are located on raised papillae (P) on the skin surface with a sensory epithelium (arrowhead) positioned at the base of a central groove (G). Scale bar = 100 μm. b– Schematic transverse section of a single superficial neuromast in the nurse shark, *Ginglymostoma cirratum*. Sensory epithelia (arrowhead) of shark superficial neuromasts are located between the bases of modified scales (S). Scale bar = 50 μm. Cupulae are not shown (modified from Budker 1958).

Raja eglanteria, *Gymnura micrura*, *Dasyatis sabina*, and *Sphyrna tiburo*) with their known ecology and behavior to infer possible biological functions for different mechanoreceptor types.

Past studies

The lateral line canal system was first discovered in chondrichthyans in the 1600's and was originally thought to be a mucus-producing organ in all fishes (Stenonis 1664). Direct histological evidence of the sensory nature of the lateral line canal neuromasts was provided by Leydig (1850), and subsequent physiological studies in teleost fishes determined that the lateral line was capable of detecting water movements at a range of approximately 1–2 body lengths (Hofer 1908, Hoagland 1933, Dijkgraaf 1934). Despite the number of studies on lateral line structure and function in teleost fishes and amphibians (Flock 1965a,b, Coombs et al. 1988, Coombs & Janssen 1989, Münz 1989, Görner & Mohr 1989), relatively few examine the system in cartilaginous fishes.

General morphology and organization of the canal portion of the lateral line system received the most attention from early anatomists, who used detailed descriptive terminology to label each section of the canal system based on anatomical landmarks and innervation patterns (e.g. Garman 1888, Johnson 1917). However, in subsequent years much of this comprehensive terminology was simplified so that only several canals (e.g. hyomandibular, infraorbital, supraorbital, mandibular, and posterior lateral line) are now recognized. The holocephalan fishes have a lateral line canal system that consists of canals and open grooves, which were suggested to represent an intermediate morphology between the free neuromasts of cyclostomes and the sub-epidermal canals of elasmobranchs and teleosts (Cole 1896, Garman 1888, Ekström von Lubitz 1981). Early studies in elasmobranch fishes described the lateral line canal system as a series of sub-epidermal canals that contained neuromasts arranged in an almost continuous sensory epithelium (Ewart 1892, Ewart & Mitchell 1892, Garman 1888, Johnson 1917). In addition to pure descriptions of canal distribution, several studies also provided data on the innervation and histology of the lateral line system in species such as the Greenland shark, *Somniosus microcephalus* (Ewart 1892), the skate, *Raja batis* (Ewart & Mitchell 1892), and others (Johnson 1917). These studies were followed by several other anatomical, histological, and finally ultrastructural examinations of elasmobranch lateral line canal systems (Tester & Kendall 1969, Roberts & Ryan 1971, Hama & Yamada 1977, Boord & Campbell 1977, Chu & Wen 1979), but references to its biological function in these fishes were few.

Many of these studies on the morphology and spatial distributions of elasmobranch lateral line systems also showed that the canal system in elasmobranchs differed from that of bony fishes, and therefore may have different response properties and biological functions. For example, elasmobranch lateral line systems differ from that in bony fishes due to the presence of non-pored canals, which contain innervated neuromasts. Early researchers had observed non-pored canals in elasmobranch fishes, but the functional or behavioral significance of these canals was not discussed (Garman 1888, Ewart & Mitchell 1892). Further, unlike the canals in most bony fishes (Webb & Northcutt 1997), pored lateral line canals in elasmobranchs contain multiple neuromasts between adjacent pores and the sensory epithelium is nearly continuous (Johnson 1917, Tester & Kendall 1969, Hama & Yamada 1977). This is the pattern present in many adult elasmobranch species, as well as in the primary canals of the ratfish *Chimaera monstrosa* (Ekström von Lubitz 1981), but its functional significance also remains unknown.

Distribution, innervation and morphology of elasmobranch superficial neuromasts (or pit organs) were first described in the skate *R. batis* (Ewart & Mitchell 1892). Elasmobranch pit organs were initially thought to function as chemoreceptors because of their structural similarity to taste buds and their sensitivity to monovalent cations such as potassium and sodium (Katsuki & Hashimoto 1969, Katsuki et al. 1969). However, other studies demonstrated that pit organs contain sensory hair cells, an overlying cupula, and are innervated by branches of lateral line nerves (Ewart & Mitchell 1892, Tester & Kendall 1967, Tester & Nelson 1969, Maruska & Tricas 1998). Therefore, pit organs in elasmobranchs are now considered to be mechanoreceptors comparable to the superficial (or free) neuromasts of teleost fishes.

Vesicles of Savi are another type of elasmobranch mechanoreceptor, which were first described in torpedo rays (Savi 1844). Subsequent morphological studies on the vesicles of Savi in *Torpedo* and *Narcine* revealed their close association with cartilaginous

skeletal elements, the lack of connection with the external environment, their innervation by branches of lateral line nerves, and the presence of one large central and two smaller peripheral neuromasts within each vesicular pouch (Norris 1932, Nickel & Fuchs 1974, Barry & Bennett 1989). To date, vesicles of Savi are found only in some species of torpedinid, narcinid, and dasyatid batoids (Norris 1932, Nickel & Fuchs, 1974, Chu & Wen 1979, Barry & Bennett 1989, Maruska & Tricas 1998), but the function of these mechanoreceptors remains to be unequivocally demonstrated.

Thus, past studies on the morphology and distribution of lateral line canals and mechanoreceptors in chondrichthyan taxa are largely descriptive, and generally do not include complete descriptions of the entire mechanosensory system (e.g. canals, canal neuromasts, superficial neuromasts, vesicles of Savi) within a single species. More importantly, the majority of past studies fail to integrate morphological data with the ecology and behavior of each species in order to infer biological functions of the lateral line system in chondrichthyan fishes.

Materials and methods

General organization, distribution, and morphology of the mechanosensory lateral line system was examined in the lesser electric ray, *Narcine brasiliensis*, clearnose skate, *Raja eglanteria*, butterfly ray, *Gymnura micrura*, Atlantic stingray, *Dasyatis sabina*, and the bonnethead shark, *Sphyrna tiburo*. These species are all common inshore or estuarine elasmobranchs along the southeastern United States that feed in part on benthic invertebrate or teleost prey, and represent a range of body shapes. Canal and neuromast distributions were examined by gross dissection and standard histological techniques. Spiracular organs were not examined in this study and will not be discussed. Morphology and spatial distribution of the lateral line system was integrated with known ecology and behavior of each species in order to propose biological functions of different receptor types in these elasmobranch fishes.

Peripheral organization of the lateral line system

Adult and juvenile *R. eglanteria*, *G. micrura*, *N. brasiliensis* and *S. tiburo* of both sexes were collected in near shore waters off Cape Canaveral, Florida by bottom otter trawl at a depth of approximately 15 m. Adult *D. sabina* were collected by dip or seine net in the shallow waters (0.2–1 m) of the Banana River estuary, Florida. Atlantic stingrays were used as a representative batoid to quantify differences between dorsal and ventral lateral line canal systems, and for scanning electron microscopy (see below). All specimens were euthanized on ice, fixed in 10% formalin in seawater, and stored in 50% isopropyl alcohol. The distribution of canals on the dorsal and ventral surface was mapped following pressure injection of an aqueous 0.5% methylene blue or a 0.5% toluidine blue solution (in 20% isopropyl alcohol) into the canals and visualized with a dissecting microscope. Multiple injections were performed at different locations and then overlying or underlying epidermal tissue was removed to visualize and map the distribution of all of the canals and tubules on the head and body in each species. Tubules are defined as extensions of the main canal which lack sensory neuromasts, and terminate in pores at the skin surface. A total of at least five individuals of each species were used to determine canal distributions. Terminology for classification of lateral line canals as hyomandibular (including the subpleural loop), infraorbital, supraorbital, scapular, and mandibular follows that of Ewart & Mitchell (1892), Tester & Kendall (1969), Chu & Wen (1979), and Maruska & Tricas (1998). The term ‘posterior lateral line’ which is based on innervation of this canal by the posterior lateral line nerve is used instead of ‘lateral canal’ used by earlier researchers (e.g. Ewart & Mitchell 1892, Tester & Kendall 1969, Chu & Wen 1979). Distribution of the vesicles of Savi in *N. brasiliensis* was determined by removal of epidermal tissue, application of an aqueous 0.5% methylene blue solution, and subsequent dissection to expose the neuromasts within the vesicular pouches. The number of vesicles of Savi on the dorsal and ventral surfaces was also counted in 6 individuals (disk widths 9.0–13.0 cm).

The distribution of superficial neuromasts was examined only in the clearnose skate, *R. eglanteria*. Superficial neuromasts in batoids are located on raised papillae that contain a central groove with a sensory epithelium at the base of this groove. These papillae were easily visualized with a dissecting microscope in freshly euthanized animals. All superficial neuromasts were marked with colored latex paint to map their distribution. The orientation of grooves that contain superficial neuromasts were recorded as the angular deviation from the rostrocaudal body axis and midsagittal plane.

Canal neuromasts, superficial neuromasts and vesicles of Savi along with surrounding tissue were

removed from 10% formalin-fixed, isopropyl alcohol preserved specimens and prepared for histological analysis. Tissue was dehydrated in a graded ethanol series, cleared in toluene, and infiltrated with and embedded in paraffin (Paraplast®). Tissue was sectioned in the transverse or sagittal plane at 10 μm, mounted on chrom-alum coated slides, and stained with Mayer's or Ehrlich's hematoxylin and eosin (Presnell & Schreibman 1997). The anatomy of the canal neuromasts, superficial neuromasts and vesicles of Savi was examined with a compound microscope.

The morphology of the lateral line canals on the dorsal and ventral surface was quantitatively compared in a representative batoid species, *D. sabina*. Lateral line canal pores were marked with toluidine blue solution or latex paint and viewed with a dissecting microscope to perform counts. In addition, each lateral line canal was injected with a 0.5% toluidine blue solution in order to stain the cupulae and neuromasts. The canals were then cut open and individual neuromasts were counted. The total number of lateral line canal pores and canal neuromasts was counted on the left side of each ray and doubled (assuming bilateral symmetry) on both the dorsal and ventral surface of five individuals (disk width 22–26 cm). Enumeration did not include the portion of the posterior lateral line canal on the tail. Diameter of the pored hyomandibular canal on the dorsal surface and non-pored hyomandibular canal on the ventral surface was also measured (neuromast base to canal roof) with an ocular micrometer from transverse histological sections in five stingrays (disk width 22–26 cm). Number of pores, neuromasts, and canal diameters were compared between the dorsal and ventral surface with an unpaired Student's t-test.

Hair cell morphology

Neuromasts from the non-pored hyomandibular and infraorbital canals on the ventral surface of *Dasyatis sabina* were examined with scanning electron microscopy (SEM) to describe neuromast and hair cell morphology and to determine hair cell polarity. The hyomandibular canal lateral to the gill slits or infraorbital canal near the mouth was dissected open in freshly euthanized rays to expose the canal neuromasts. Cupulae were then mechanically removed with a water jet. A 1.0–1.5 cm section of canal including neuromasts was removed, fixed in 2% glutaraldehyde in Millonig's buffer, rinsed in Millonig's buffer, rinsed in 0.1 M phosphate buffer, post-fixed in 1% osmium tetroxide, rinsed in 0.1 M phosphate buffer, and dehydrated in an ethanol series. Tissue was dried in an LADD critical point dryer with carbon dioxide as a transitional fluid and sputter coated with gold-palladium alloy. Neuromasts were viewed with a Hitachi S-2700 SEM at an accelerating voltage of 8–10 kV and images were recorded on VHS tape for analysis. Each hair cell has many stereocilia in a stepwise arrangement of increasing height towards a single kinocilium. The polarity of each hair cell was measured as the angular deviation of the axis of maximum excitation of the hair cell (towards the stepwise stereocilia and single kinocilium) from the longitudinal axis of the canal. Therefore, 0° and 180° represent hair cells oriented in opposite directions along the longitudinal canal axis. Measurement error was estimated to be ±15°. Hair cell polarities were determined for 150 randomly selected hair cells from 15 neuromasts in the hyomandibular canal in 6 stingrays (disk width 22–26 cm).

Results

Peripheral organization of the lateral line system

The mechanosensory lateral line system of elasmobranch fishes consists of superficial neuromasts on the skin surface, a sub-epidermal canal system, and the sub-epidermal vesicles of Savi. The presence, number and distribution of each mechanoreceptor type varies among species. Therefore, the peripheral organization of the lateral line system in *Narcine brasiliensis*, *Raja eglanteria*, *Gymnura micrura*, *Dasyatis sabina* and *Sphyrna tiburo* will be described separately below. Several morphological features of the lateral line system in each species are summarized in Table 1.

Narcine brasiliensis (Batoidea: Narcinidae)
The lesser electric ray, *N. brasiliensis*, has both vesicles of Savi and a lateral line canal system on the dorsal surface (Figure 2). Vesicles of Savi are located in bilateral rows on the rostrum from the anterior edge of the eye to the edge of the rostrum. There are approximately 8–10 vesicles in each row just lateral to the rostral cartilage. Vesicle pouches are oval with their long axis oriented approximately 45° to the rostrocaudal body axis. Vesicles within a rostrocaudal row have a common orientation.

All canals on the dorsal body surface have pores except for a short section of the hyomandibular that

Table 1. Summary of morphological features of the lateral line system in *Narcine, Raja, Gymnura, Dasyatis*, and *Sphyrna*.

Species	Surface	SN location (#)	VS location (#)	Pored canals	# pores per tubule branch*	Non-pored canals
Narcine brasiliensis	Dorsal	ND	Bilateral rows along rostrum midline (8–10 per row)	HYO, IO, SO, PLL	1	None
	Ventral	ND	Rostrum and anterior to electric organs ($\bar{x} = 65 \pm 6$ SD per side)	None	NA	None
Raja eglanteria	Dorsal	Bilateral medial rows to end of tail, anterior to EP (2), between IO canal and eye (5–6)	None	HYO, IO, SO, PLL	1	SO
	Ventral	None	None	HYO, IO (SPL absent)	1	IO, MAN, SO
Gymnura micrura	Dorsal	ND	None	HYO, IO, SO, PLL	1–35	SO
	Ventral	ND	None	HYO, IO (SPL present)	1–3	HYO, IO, MAN, SO
*Dasyatis sabina***	Dorsal	Bilateral medial rows to end of tail (~100 per side)	None	HYO, IO, SO, PLL	1–10	SO
	Ventral	None	Bilateral rows along rostrum midline (6–10 per row)	HYO, MAN (SPL present)	1	HYO, IO, SO
Sphyrna tiburo	Dorsal	Lateral along PLL and on dorsolateral body (> 400 per side), anterior to EP (2)†	None	HYO, IO, SO, PLL	1–20	IO, HYO
	Ventral	Mandibular row, umbilical row†	None	HYO, IO, SO (SPL NA)	1–20	IO, MAN

Some canals contain pored and non-pored sections and are listed under both categories. *numbers represent the range of average values from all canals; **from Maruska & Tricas (1998); †from Tester & Nelson (1969); EP = endolymphatic pore, HYO = hyomandibular, IO = infraorbital, MAN = mandibular, ND = not determined, NA = not applicable, SO = supraorbital, SPL = subpleural loop, SN = superficial neuromast, VS = vesicles of Savi.

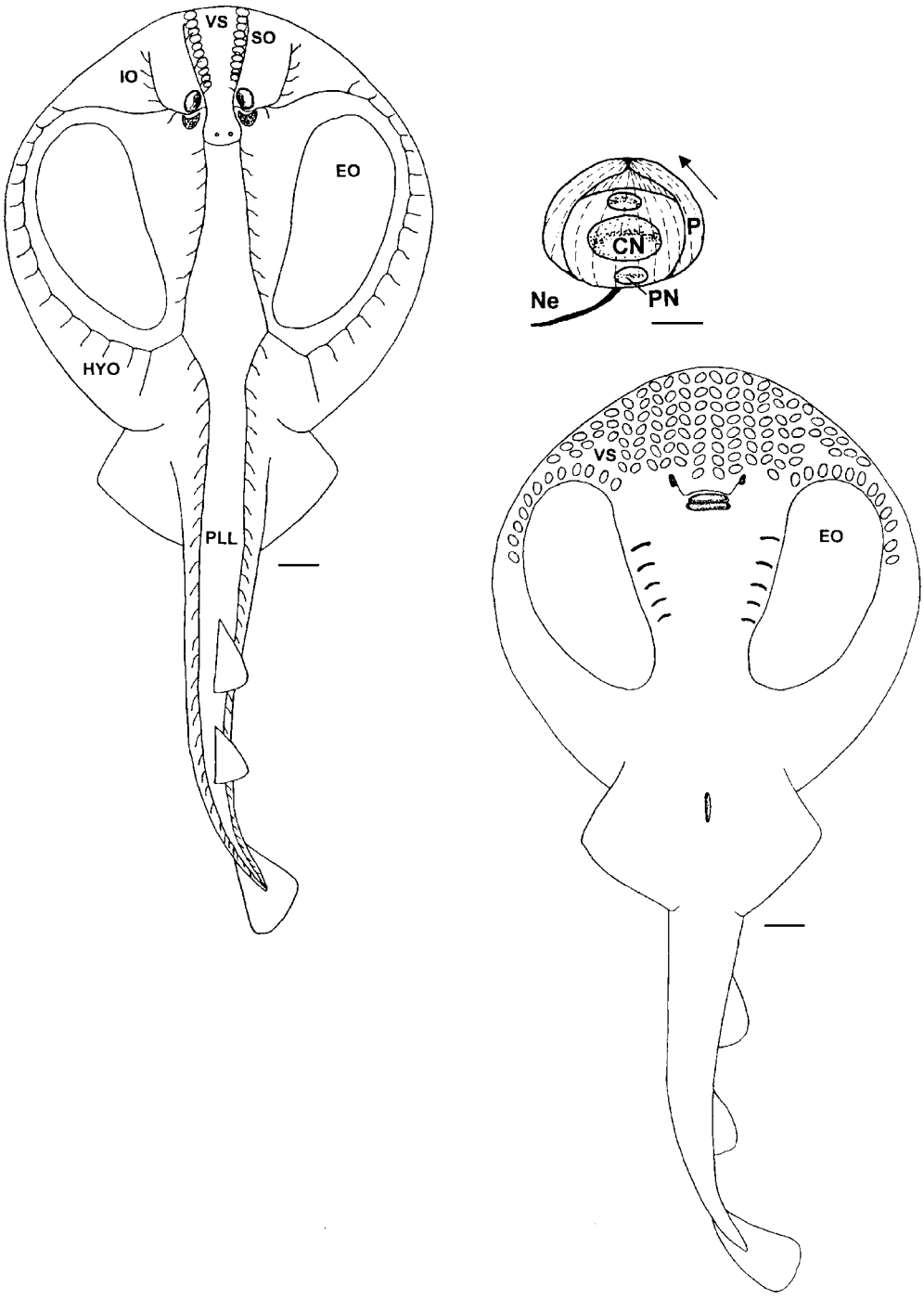

Figure 2. Distribution of the lateral line canal system and vesicles of Savi on the dorsal (upper) and ventral (lower) surface of the lesser electric ray, *Narcine brasiliensis*. Canals on the dorsal surface are bilateral, interconnected and pored, while the ventral surface lacks a canal system. Vesicles of Savi (VS) are arranged in a single row just medial to the supraorbital canal (SO) on the dorsal surface, and in several rows on the rostrum and along the anterior edge of the electric organ (EO) on the ventral surface. Scale bars = 1 cm. Schematic diagram of a single vesicle of Savi in *N. brasiliensis* (upper right). Each vesicle contains a large central neuromast (CN) and two smaller peripheral neuromasts (PN) covered by separate cupulae (not shown) all enclosed in a thin-walled pouch (dashed lines). A connective tissue pedicle (P) supports the vesicle on either side of the neuromasts. Arrow lies along the rostrocaudal body axis. Scale bar = 400 μm (HYO = hyomandibular canal, IO = infraorbital canal, Ne = nerve, PLL = posterior lateral line canal).

is connected to the infraorbital canal just anterior to the electric organ (Figure 2). The main hyomandibular canal extends from the infraorbital canal near the spiracle, to the disk margin where it then caudally circumscribes the electric organ. This canal then joins the posterior lateral line canal near the midline. The hyomandibular canal has lateral tubules (0.5–1.5 cm in length) that terminate in single pores near the disk margin. Tubules, which lack sensory neuromasts, are extensions of the main canal that terminate in pores at the skin surface. The dorsal infraorbital canal extends from the supraorbital canal on the head, between the eye and spiracle, and then terminates near the disk margin. The dorsal supraorbital canal is located on the cranium and extends from near the endolymphatic pores, where it is connected across the midline by a commissural canal, to the rostrum tip just lateral to the vesicles of Savi. Several (3–5) short tubules extend medially from the supraorbital canal and terminate in pores directly dorsal to the vesicles of Savi. The posterior lateral line canal begins at the supraorbital canal near the endolymphatic pores along the cranium. This canal extends to the tip of the tail and has numerous lateral tubules that terminate in pores ventral to the main canal along its entire length.

The ventral lateral line system completely lacks canals, but has a complex of vesicles of Savi (Figure 2). Vesicles of Savi are located on the ventral rostrum anterior and lateral to the mouth, and along the anterior edge of the electric organs. Vesicles on the rostrum are arranged in 6–7 rostrocaudal rows per side, each of which contains 7–10 vesicles. Each side of the ventral body surface contains approximately 65 vesicles ($\bar{x} = 65 \pm 6$ SD, $n = 6$). Each vesicle is oval in shape and oriented approximately 45° to the rostrocaudal body axis. All vesicles within an individual row have a common orientation, but are oriented orthogonal to vesicles in the adjacent row. Individual vesicles of Savi have no connection to the external environment and are located in pouches approximately 0.5–2.0 mm below compliant epidermal, dermal and connective tissue layers (Figure 3a–d). In addition, there is no evidence that the compartments of adjacent vesicles are contiguous. Each vesicle consists of a large central neuromast and two smaller adjacent neuromasts, all three of which are innervated (Figure 3b). The cupula of the central neuromast appears more dense than the cupulae of the smaller adjacent neuromasts (observed in fresh tissue). The walls of each individual pouch are thin and the roof over the large central neuromast is supported by an arch formed by connective tissue pedicles that extend from the floor of the vesicle (Figure 2). The vesicles are also attached at their bases to a connective tissue band, which is closely associated with the overlying cartilage (Figure 3c).

Raja eglanteria (Batoidea: Rajidae)

The clearnose skate, *R. eglanteria*, has superficial neuromasts located on raised papillae with the sensory neuromast at the base of a central groove. The sensory epithelium is likely covered by a cupula that is in contact with the external environment, but cupulae were not observed in this species possibly because this structure is often lost during histological processing. Superficial neuromasts occur in bilateral rows along the dorsal midline from the suprabranchial region to the caudal fin, and are located on the dorsolateral surface of the tail near the median spines (Figure 4). In addition, a group of 5–6 superficial neuromasts are found between the infraorbital canal and the eye, and a single pair of superficial neuromasts is located anterior to each endolymphatic pore. Superficial neuromasts near the eye have a central groove oriented almost parallel to the rostrocaudal body axis while those anterior to the endolymphatic pores are oriented approximately 135° to the rostrocaudal body axis. Central grooves located on the body and tail are oriented between 90° and 135° to the rostrocaudal body axis in the transverse plane.

The canals on the dorsal surface of *R. eglanteria* are bilateral, interconnected and independently penetrate the disk to join the canals on the ventral surface (Figure 5). The hyomandibular canal extends caudally and laterally from the infraorbital canal on the rostrum, along the pectoral fin margin where it then extends medially to join the anterior branch of the scapular canal. A posterior branch of the scapular canal extends from the posterior lateral line canal to the caudal disk edge several centimeters posterior to the anterior branch of the scapular canal. The hyomandibular and scapular canals contain straight tubules, which extend anteriorly to terminate in single pores. The infraorbital canal is contiguous with the supraorbital canal between the eye and spiracle, and extends rostrally to the edge where it penetrates the disk to join the infraorbital canal on the ventral surface. The infraorbital canal also contains short tubules that extend laterally or rostrally from the main canal. The supraorbital canal on the head extends anteriorly to the tip of the rostrum where it joins the supraorbital canal on the ventral surface. A deep commissural canal posterior to the endolymphatic

pores connects the dorsal supraorbital canals on the left and right sides of the body. Several tubules extend laterally from the supraorbital canal and terminate in single pores in the region rostral to the eyes. However, there is a section of supraorbital canal on the rostrum that is non-pored. The posterior lateral line canal begins near the endolymphatic pores and extends along the midline to the tip of the tail. Tubules extend ventral to the posterior lateral line canal from the scapular canal junction to the caudal edge of the pelvic fins, and both dorsal and ventral to the posterior lateral line canal from the pelvic fins to the tip of the tail.

The canals on the ventral surface are also interconnected (except mandibular) and independently penetrate the disk to join the canals on the dorsal surface (Figure 5). The hyomandibular canal extends rostrally from near the caudal edge of the pectoral fin, around the gill slits, where it joins the infraorbital canal just lateral to the nares. Several tubules extend laterally from this canal in the vicinity of the gill slits, and medially in the area caudal to the gill slits to terminate in single pores. The clearnose skate has no subpleural loop of the ventral hyomandibular canal as seen in most other batoid species (Chu & Wen 1979). The infraorbital canal extends from the hyomandibular canal, medially to the posterior edge of the naris and along the rostrum midline. There is a single pore in the canal section between the hyomandibular canal and naris, while the infraorbital canal that extends along the midline of the rostrum contains several tubules that terminate in single pores medially. Another section of infraorbital canal is contiguous with the hyomandibular canal lateral to the naris, and extends to the anterior pectoral fin margin where it penetrates the disk to join the infraorbital canal on the dorsal surface. The ventral infraorbital canals are joined across the midline by a commissural connection anterior to the mouth. The ventral supraorbital canal extends from the infraorbital canal just anterior to the infraorbital–hyomandibular canal junction, extends to the anterior disk margin just lateral to the infraorbital canal, and penetrates the disk at the rostrum tip to join the supraorbital canal on the dorsal surface. A short mandibular canal is located posterior to the lower jaw and extends across the midline as a single canal that lacks pores. Vesicles of Savi were not observed in this species.

Gymnura micrura (Batoidea: Gymnuridae)

The canal system on the dorsal surface of the butterfly ray, *G. micrura*, consists of the same main canal pattern found in other batoid species. However, this species differs due to the profuse number of tubules that terminate in pores over the entire body surface (Figure 6). The hyomandibular canal begins at the rostrum, extends along the entire disk margin, and joins the posterior lateral line canal near the caudal edge of the pectoral fin. Tubules extend from this canal, often branch several times, and terminate in approximately 1–10 pores near the disk margin. The dorsal infraorbital canal is contiguous with the supraorbital canal on the head, extends between the eye and spiracle, and then bifurcates into two divisions just below the eye. The caudal division branches extensively in the mid-disk region, whereas the anterior division branches over the anterior disk and then penetrates the rostrum to join the infraorbital canal on the ventral surface. The dorsal supraorbital canal is located on top of the cranium and has numerous tubules that are medial and caudal to the eye and spiracle. The supraorbital canal then extends anteriorly to the tip of the rostrum where it penetrates the disk to join the supraorbital canal on the ventral surface. The posterior lateral line canal extends from the supraorbital canal on the head, along the dorsal midline, to the tip of the short tail. A scapular canal loop is also present in the mid-disk region near the dorsal midline. All the canals on the dorsal surface have numerous tubules that terminate in multiple pores per tubule over the entire body surface, with the exception of a short segment of the supraorbital canal on the rostrum that lacks pores.

The lateral line system on the ventral surface consists of both pored and non-pored canals that are bilateral, interconnected (except mandibular) and independently penetrate the disk to join the canals on the dorsal surface (Figure 6). The pored hyomandibular canal extends laterally along the pectoral fin margin from the midline of the rostrum to the widest point of the pectoral fin, where it then extends medially. The hyomandibular canal then shows a caudal change in position before transition to the non-pored section of this canal on the caudal region of the pectoral fin. Many tubules extend from this canal and terminate in pores at the disk margin. Each hyomandibular canal tubule on the anterior disk generally branches at a point several millimeters from the disk edge and terminates in 2–3 pores. In contrast, each tubule on the caudal portion of the subpleural loop of the hyomandibular canal generally terminates in only a single pore. The non-pored hyomandibular canal section then extends anteriorly from the caudal region of the pectoral fin along the

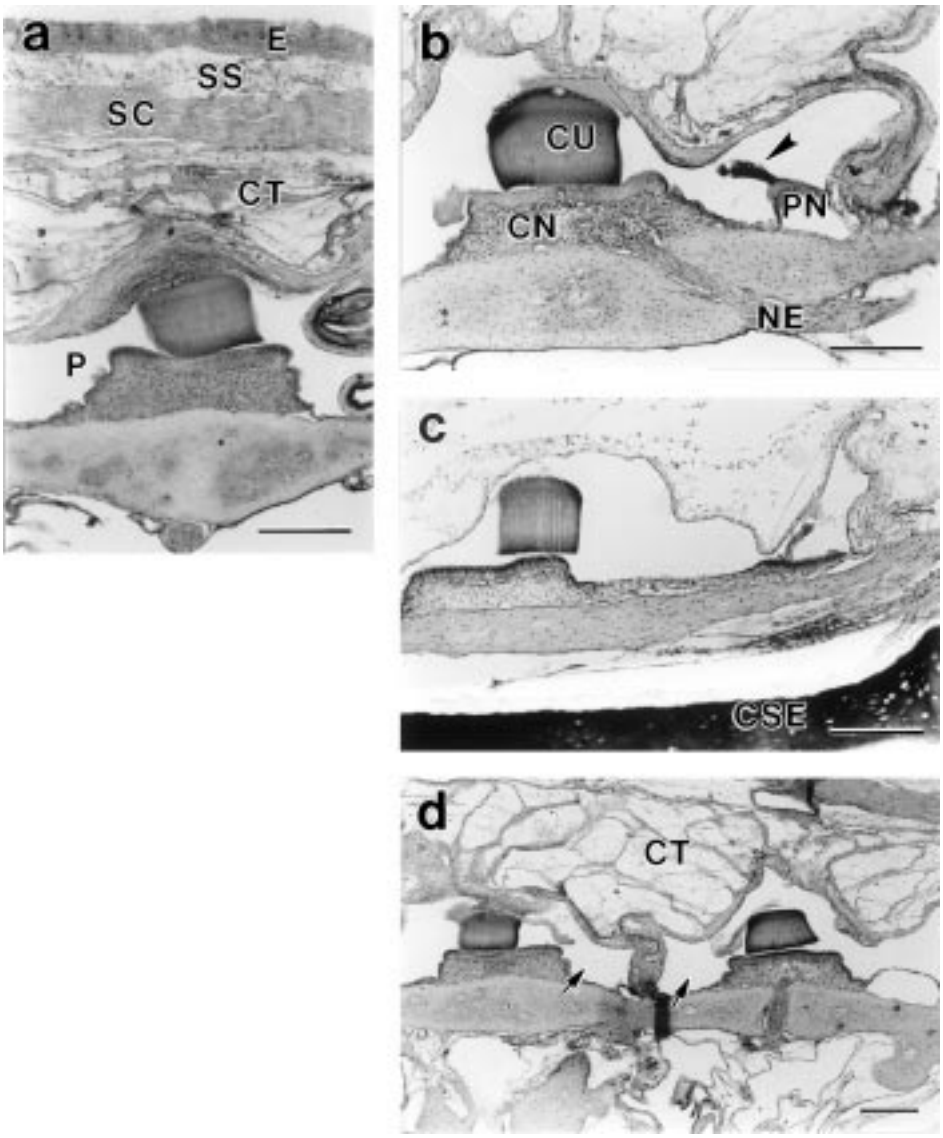

Figure 3. Histological sections of the vesicles of Savi on the ventral surface of the lesser electric ray, *Narcine brasiliensis*. a – Vesicles of Savi are located in sub-epidermal pouches (P) below epidermal (E), stratum spongiosum (SS), stratum compactum (SC) and loose connective tissue (CT) skin layers. Scale bar = 200 μm. b – Each vesicle of Savi consists of a large central neuromast (CN) and two smaller peripheral neuromasts (PN), all innervated by nerve fibers (NE). The cupula (CU) of the central neuromast is dense with a striated appearance, while the cupula (arrowhead) of the smaller peripheral neuromasts is gelatinous and similar in structure to canal neuromast cupulae. Scale bar = 200 μm. c – Vesicles of Savi are closely associated with cartilaginous skeletal elements (CSE) at their base. Scale bar = 200 μm. d – Vesicles of Savi are located in distinct rows along the ventral rostrum. Lumina of adjacent vesicles (arrows) do not appear connected but lie approximately 100 μm apart below loose connective tissue (CT). Scale bar = 200 μm. Ventral side is up.

midline just lateral to the gill slits, where it joins the non-pored sections of the infraorbital and supraorbital canals near the mouth. The infraorbital canal extends laterally from this point to form a large loop that contains straight tubules, which overlie the hyomandibular canal tubules along the disk margin. The infraorbital canal also extends medially and penetrates the disk adjacent to the hyomandibular canal on the rostrum

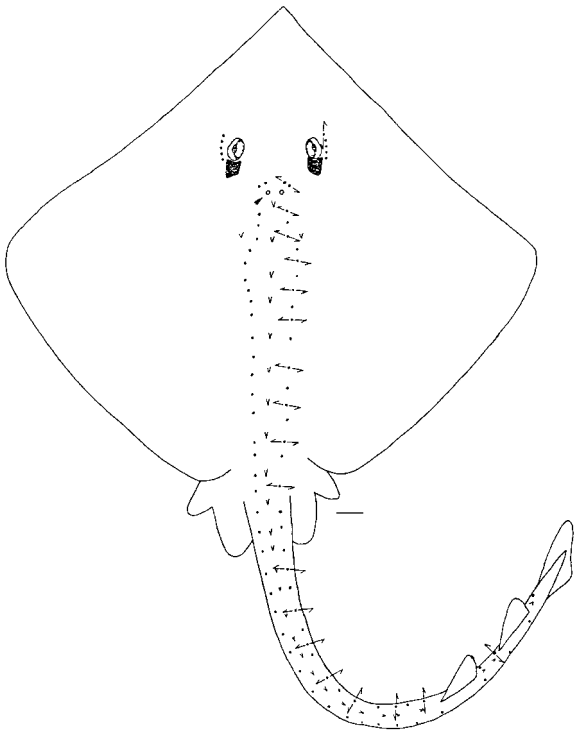

Figure 4. Distribution of superficial neuromasts on the dorsal surface of the clearnose skate, *Raja eglanteria*. Each dot represents a single superficial neuromast papilla and arrows (right side) show the groove orientation on every other neuromast. A single pair of superficial neuromasts is located anterior to each endolymphatic pore (arrowhead), a row of 5–6 neuromasts is positioned beneath each eye within the infraorbital canal, and the remainder of superficial neuromasts extend from the suprabranchial region along the midline to the end of the tail. Superficial neuromast grooves near the endolymphatic pores are positioned at approximately 135°, grooves beneath the eye at 0° (parallel), and grooves along the midline at 90°–135° to the rostrocaudal body axis. Scale bar = 1 cm.

to join the infraorbital canal on the dorsal surface. The supraorbital canal also extends rostrally from this point, forms a small non-pored loop, and then shows a medial change in position to join an additional section of the supraorbital canal on the rostrum. A short mandibular canal is located posterior to the lower jaw and extends across the midline as a single non-pored canal. Vesicles of Savi were not observed in this species.

Dasyatis sabina (Batoidea: Dasyatidae)

The distribution of lateral line canals, superficial neuromasts, and vesicles of Savi in the Atlantic stingray, *D. sabina*, was previously described in detail by Maruska & Tricas (1998). Dorsal canals are primarily pored and include the supraorbital on the cranium, infraorbital beneath the eye, hyomandibular on the pectoral fins, scapular loop on the caudal trunk and posterior lateral line along the dorsal midline and tail (Figure 7). The ventral lateral line system of the stingray consists of both pored and non-pored canals as well as vesicles of Savi. Vesicles of Savi are located in bilateral rows along the midline of the rostrum and are contiguous with the ventral supraorbital canal. Non-pored canals on the ventral surface include the supraorbital and infraorbital around the mouth, nares and rostrum, and a section of hyomandibular canal along the midline just lateral to the gill slits. Pored canals on the ventral surface include the hyomandibular canal that forms the subpleural loop, and the short mandibular canal posterior to the lower jaw.

The total number of canal pores and neuromasts was counted on both the dorsal and ventral surface, and the diameter of the dorsal pored hyomandibular and ventral non-pored hyomandibular canal was measured in the stingray to quantitatively compare dorsal and ventral canal organization. There are over 250 pores on the dorsal surface and less than 90 on the ventral surface (Figure 8a) of the stingray. However, there are about twice as many neuromasts on the ventral surface ($\bar{x} = 1028 \pm 51$ SE) than on the dorsal surface ($\bar{x} = 570 \pm 32$ SE) (Figure 8b). The diameter of the non-pored hyomandibular canal on the ventral surface is on average 2.5 times larger than the diameter of the hyomandibular canal on the dorsal surface (Figure 8c). There is a difference between the dorsal and ventral surface in *D. sabina* for all comparisons tested (unpaired t-test, $p < 0.001$). Although not quantitatively examined, these relative differences between dorsal and ventral lateral line systems are also present in *R. eglanteria*, *N. brasiliensis* and *G. micrura*. In addition, the morphology and structure of the canal system on the ventral surface differs from the dorsal in all batoids examined. Generally, ventral canals are large in diameter, have compliant canal walls, and lie deep to loose, pliable dermal and connective tissue layers (Figure 9a–c). In contrast, the dorsal canals are smaller in diameter, have rigid canal walls, and lie deep to dense dermal and connective tissue layers (Figure 9d). However, further quantitative histological evaluations of the skin and canal wall structures are needed to confirm relative stiffness of the canals on the dorsal versus ventral surface in batoids.

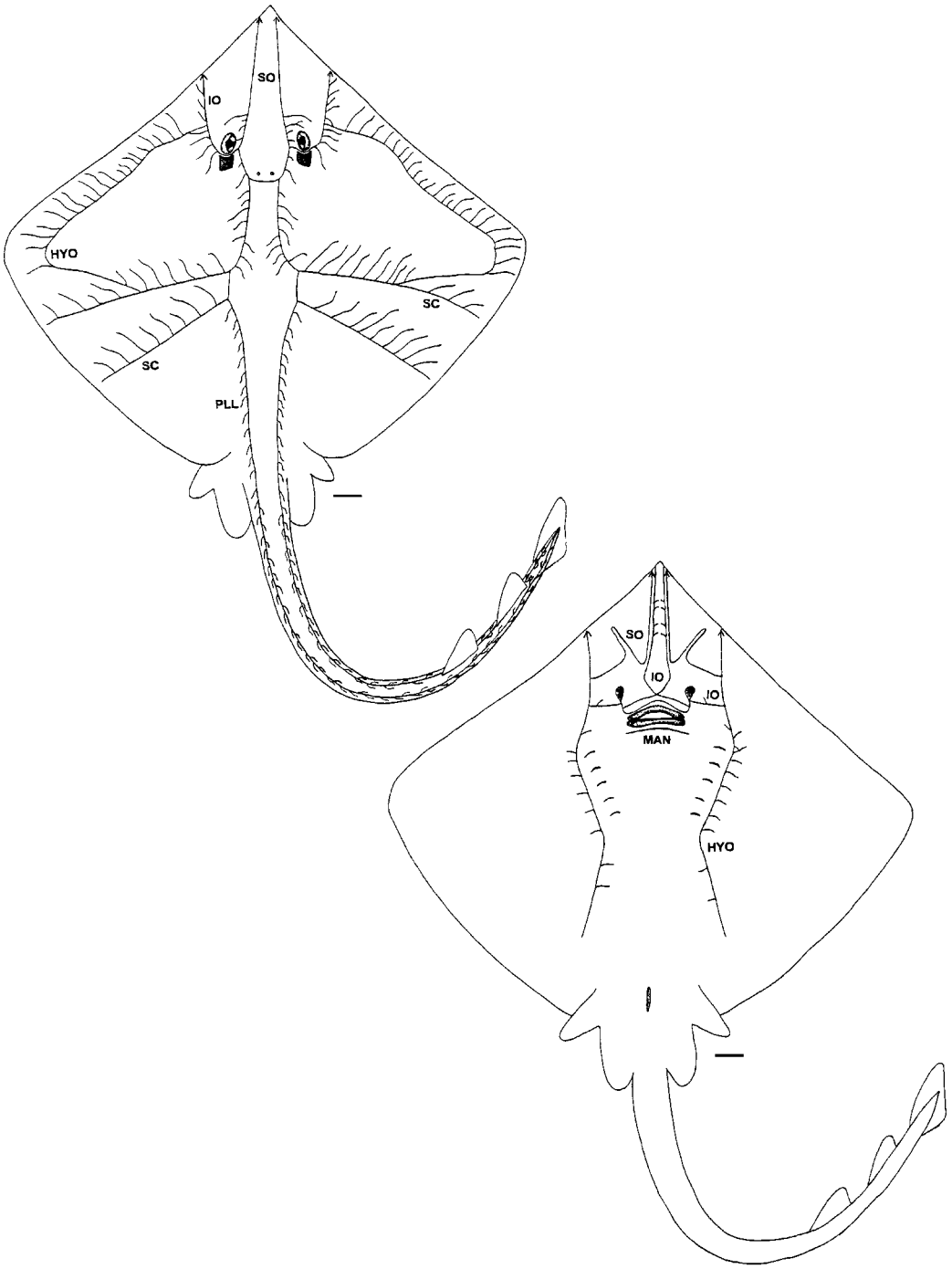

Figure 5. Distribution of the lateral line canal system on the dorsal (upper) and ventral (lower) surface of the clearnose skate, *Raja eglanteria*. All canals (except mandibular) are interconnected both among and within sides. Straight tubules extend from the main canals to terminate in single pores. The ventral hyomandibular canal does not contain a subpleural loop in this species. Scale bars = 1 cm (HYO = hyomandibular canal, IO = infraorbital canal, MAN = mandibular canal, PLL = posterior lateral line canal, SC = scapular canal, SO = supraorbital canal).

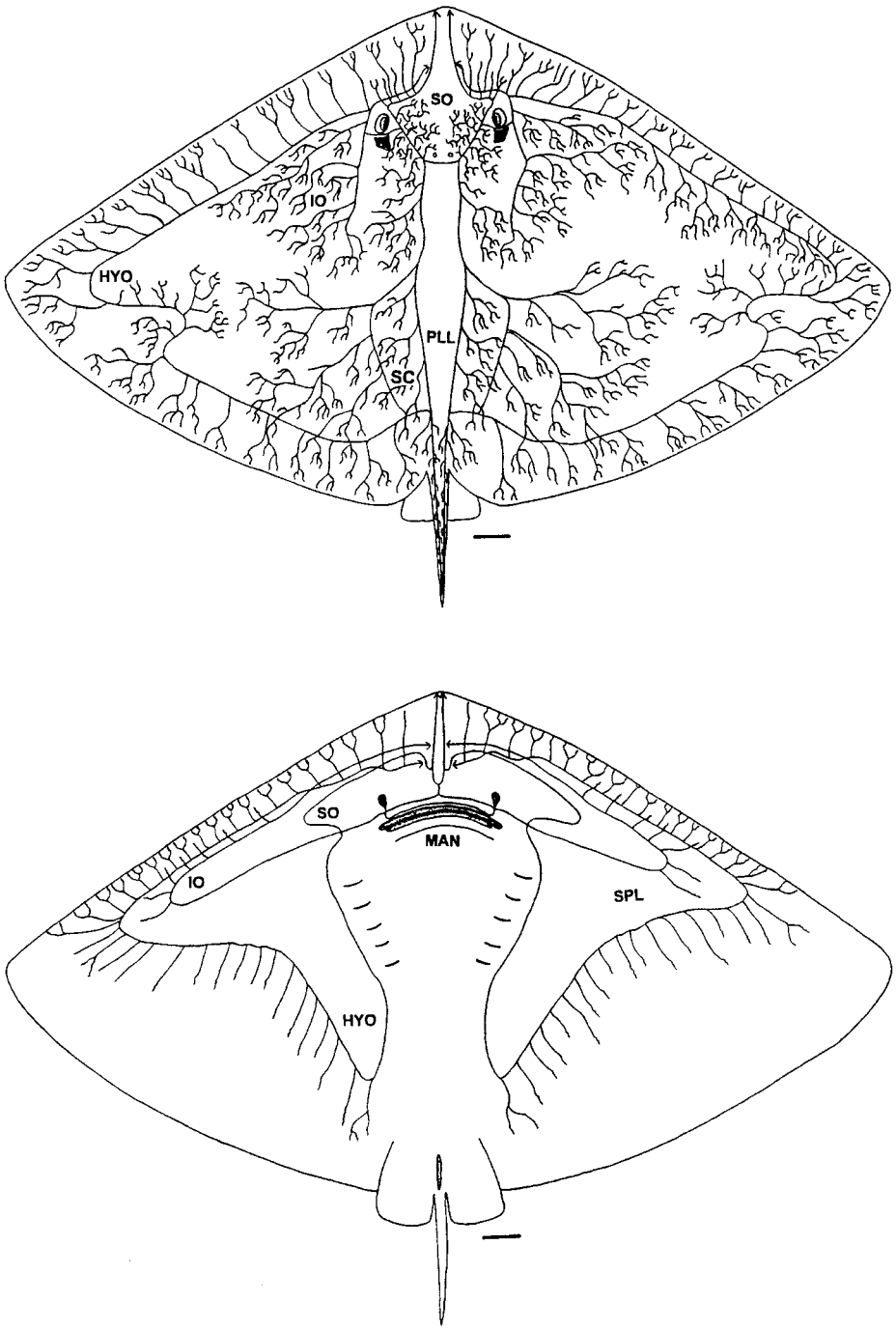

Figure 6. Distribution of the lateral line canal system on the dorsal (upper) and ventral (lower) surface of the butterfly ray, *Gymnura micrura*. All canals (except mandibular) are interconnected both among and within sides with extensive tubule branching on the dorsal surface. The ventral system consists of both pored canals, and non-pored canals along the midline and around the mouth. Scale bars = 1 cm (HYO = hyomandibular canal, IO = infraorbital canal, MAN = mandibular canal, PLL = posterior lateral line canal, SC = scapular canal, SO = supraorbital canal, SPL = subpleural loop).

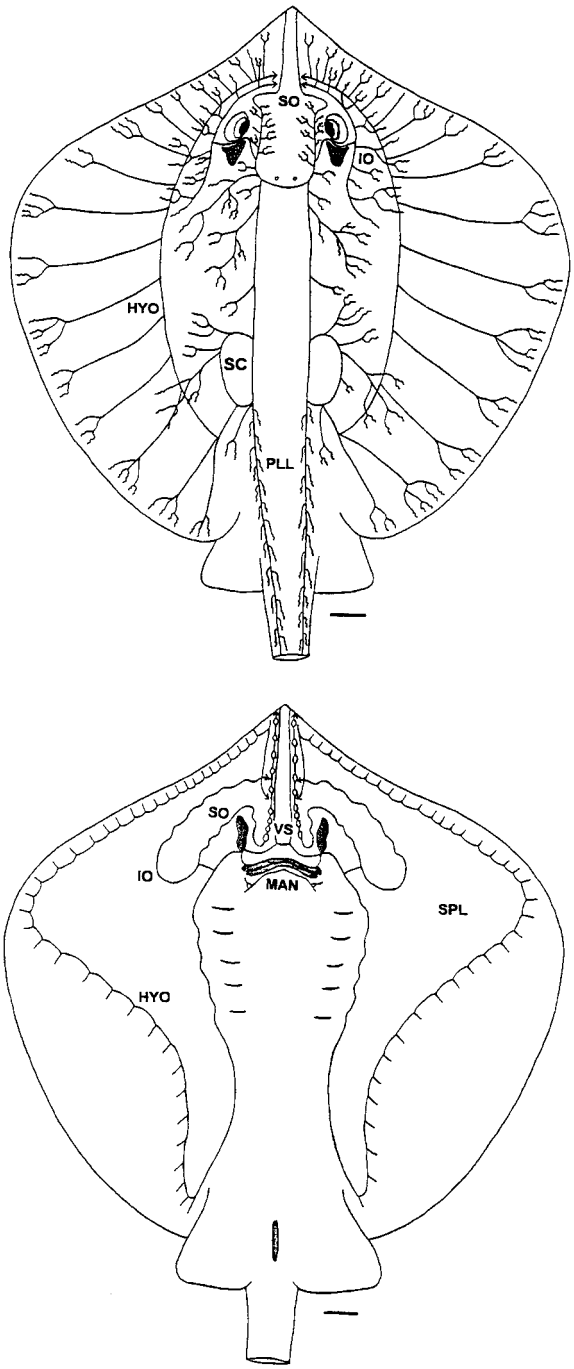

Figure 7. Distribution of the lateral line canal system and vesicles of Savi on the dorsal (upper) and ventral (lower) surface of the Atlantic stingray, *Dasyatis sabina*. Dorsal canals contain numerous lateral tubules that terminate in pores across the entire body surface. The infraorbital, supraorbital, and sections of the hyomandibular canal near the mouth, rostrum, and along the ventral midline, lack pores but do contain innervated neuromasts. Vesicles of Savi (VS) are located in bilateral rows on the ventral rostrum midline and are isolated from the surrounding water, but lumina of adjacent vesicles are connected via tubules. Scale bars = 1 cm (HYO = hyomandibular canal, IO = infraorbital canal, MAN = mandibular canal, PLL = posterior lateral line canal, SC = scapular canal, SO = supraorbital canal, SPL = subpleural loop).

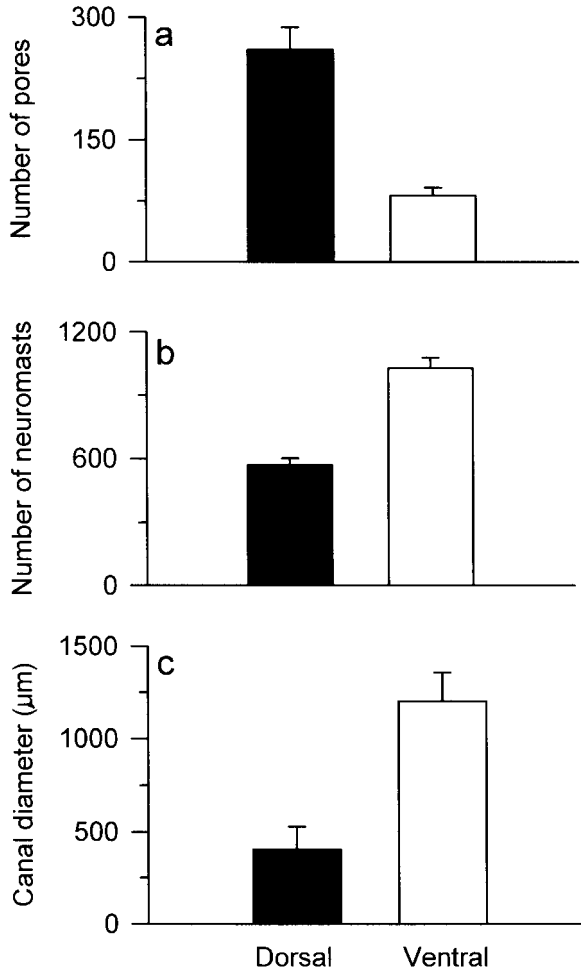

Figure 8. a – Mean number of lateral line canal pores on the entire dorsal (dark) and ventral (open) surface of adult Atlantic stingrays, *Dasyatis sabina*. There are approximately three times as many pores on the dorsal surface ($\bar{x} = 260 \pm 28$ SE) compared to the ventral surface ($\bar{x} = 82 \pm 10$ SE). b – Mean number of lateral line neuromasts on the dorsal (dark) and ventral (open) surface of *D. sabina*. There are approximately twice as many neuromasts on the ventral surface ($\bar{x} = 1028 \pm 51$ SE) compared to the dorsal surface ($\bar{x} = 570 \pm 32$ SE). c – Mean diameter of the pored dorsal hyomandibular canal (dark) and non-pored ventral hyomandibular canal (open) in *D. sabina*. The ventral non-pored canal diameter ($\bar{x} = 1200 \pm 158$ μm SE) is approximately 2.5 times greater than its dorsal counterpart ($\bar{x} = 405 \pm 125$ μm SE). The number of pores and neuromasts were counted on one side of the animal and doubled to represent the entire body. Counts do not include the portion of the posterior lateral line on the tail. Error bars represent standard error of the mean. There is a difference between the dorsal and ventral surface in all comparisons (unpaired t-test, $p < 0.001$). $n = 5$ rays, disk width = 22–26 cm.

Hair cell morphology

Canal neuromasts in the non-pored canals on the ventral surface of the Atlantic stingray, *D. sabina*, consist of a sensory epithelium surrounded by a population of large mantle cells. The sensory epithelium is a central strip, which extends along the length of the neuromast but does not span its entire width. The sensory epithelium consists of sensory hair cells interspersed with support cells that contain numerous microvilli on the apical surface (Figure 10a). Each hair cell has about 60–100 stereocilia with the typical staircase arrangement towards the single kinocilium (2–8 μm long). Some kinocilia have bulbous endings (Figure 10b) which are approximately 1.5–2.0 μm in diameter, but the percentage of hair cells with bulbous endings could not be accurately assessed due to frequent damage of kinocilia during tissue processing. Each hair cell is approximately 2–6 μm in diameter, but distances between adjacent hair cells in the sensory epithelium are variable (range = 2–25 μm) (Figure 10a). Smaller cells with only a few stereocilia of equal height and a single long kinocilium (7–10 μm long) were abundant at the ends of the sensory epithelium. However, it is unknown whether these cells are innervated, are another hair cell type, are support cells, or are precursor hair cells.

Hair cells in the neuromasts of the hyomandibular and infraorbital canals did not follow the organized arrangement of adjacent hair cells with opposite polarity oriented parallel to the canal axis (0° or 180°) commonly observed in teleosts. In the stingray, the majority (~ 76%) of individual hair cells within a neuromast were oriented within 45° of the main canal axis (Figure 11), and a small number of hair cells (~ 24%) were also oriented nearly perpendicular (90° or 270° ± 45°) to the canal axis (Figure 10a). However, it should be noted that measurement error was estimated at 15°. Adjacent hair cells of opposite polarity were observed throughout the length of the sensory epithelium, but they were interspersed with hair cells of varying polarities.

Sphyrna tiburo (Galeomorphii: Sphyrnidae)

Lateral line canals on the head of the bonnethead shark, *S. tiburo*, consist of the bilateral and interconnected hyomandibular, infraorbital, and supraorbital canals, as well as the short mandibular canals on the lower jaw, and the posterior lateral line canal found longitudinally along the trunk (Figures 12 and 13). The canal system on the dorsal surface includes numerous branched

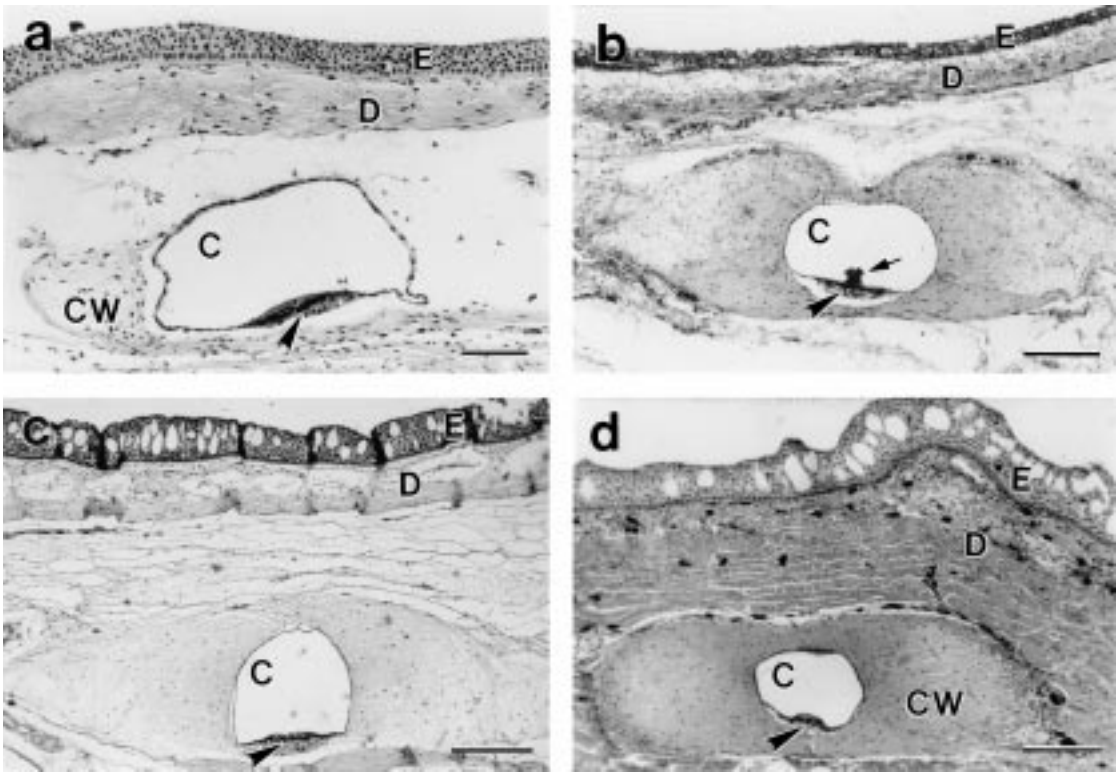

Figure 9. Histological cross sections of ventral non-pored hyomandibular lateral line canals in *Raja eglanteria* (a), *Gymnura micrura* (b), and *Dasyatis sabina* (c) and dorsal posterior lateral line canal in *Dasyatis sabina* (d) for comparison. a–c Ventral canal neuromasts (arrowheads) are located in canals (C) deep to epidermal (E) and loose, compliant dermal (D) skin layers (stratum spongiosum and compactum). Notice the large canal diameters, and loose organization of the canal walls (CW) and dermal skin layers in the ventral canals (a–c) compared to the dorsal canal (d). A portion of the cupula (arrow) is shown in (b) but is absent in a, c, d. Ventral surface of the animal is up in a, b, c and dorsal is up in d. Scale bars = (a) 100 μm, (b) 200 μm, (c) 200 μm, (d) 100 μm.

tubules that terminate in many pores primarily along the rostral edge of the head, and in a horizontal band between the eyes (infraorbital canal) (Figure 12). The hyomandibular canal on the dorsal surface of the head is reduced compared to the batoid species examined and consists of a small section that extends from the infraorbital canal medial to the eye, across the midline near the endolymphatic pores, where it joins the posterior lateral line canal. There is a deep hyomandibular canal section located lateral to the endolymphatic pores, which penetrates the head to the ventral side. The infraorbital canal consists of a loop that extends from the eye rostromedially to the dorsal midline. The most caudal portion of this loop has many small diameter tubules that branch just dorsal to the canal, while the most rostral portion of the loop has no tubules. The infraorbital canal is contiguous with the supraorbital canal near the eye. The supraorbital canal is displaced medially towards the midline of the snout, and has branched tubules that terminate in pores along the margin of the head. The supraorbital canal also penetrates the snout to join the ventral supraorbital canal near the nares. The posterior lateral line canal extends from the endolymphatic pores on the head, dorsolaterally along the body to the tip of the upper lobe of the caudal fin (Figure 13). Tubules extend in a posterior direction both dorsal to and ventral to the main canal along the entire length. However, the majority of tubules extend ventral to the posterior lateral line canal, especially on the caudal fin.

Canals on the ventral surface of the head are pored, with the exception of the mandibular canal and short sections of the infraorbital canal anterior to the mouth (Figure 12). The hyomandibular canal has numerous

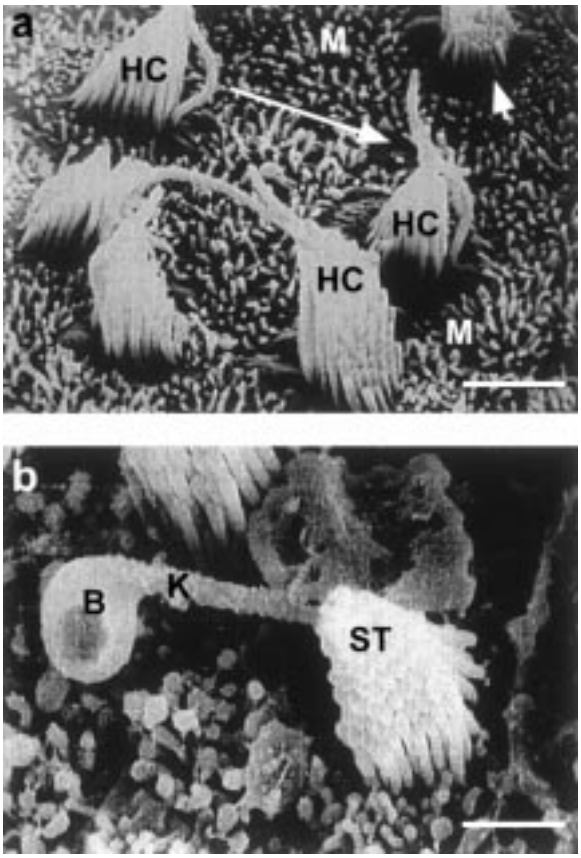

Figure 10. Scanning electron micrographs of neuromasts from the ventral non-pored hyomandibular (a) and infraorbital (b) canals in the Atlantic stingray, *Dasyatis sabina*. a – The sensory epithelium is composed of sensory hair cells (HC) and support cells with numerous microvilli (M) at the apical surface. The majority of hair cells are oriented parallel to or within 45° of the main canal axis. However, a small number of hair cells is oriented off the canal axis (small arrow). Large arrow shows the longitudinal canal axis. Scale bar = 2.0 μm. b – Individual hair cells contain 60–100 stereocilia (ST) in a staircase arrangement of increasing height towards a single kinocilium (K). Some hair cells contain kinocilia with bulbous endings (B). Scale bar = 1.0 μm.

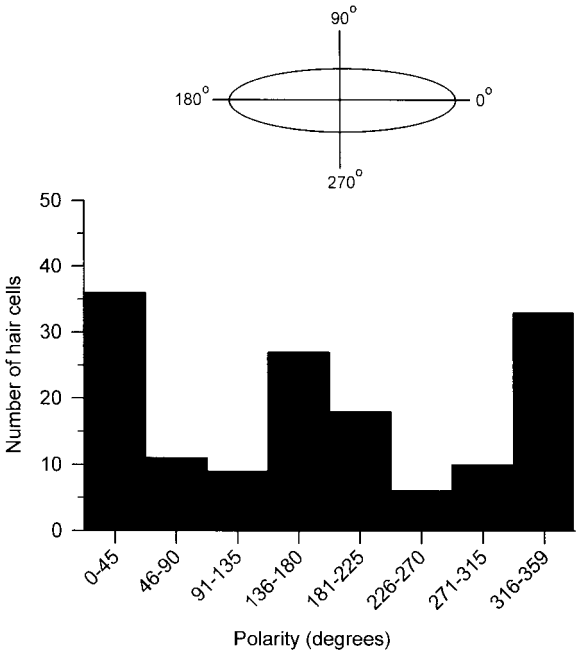

Figure 11. Frequency distribution of hair cell polarities in the neuromasts of the non-pored hyomandibular lateral line canal on the ventral surface of the Atlantic stingray, *Dasyatis sabina*. The neuromast and canal axis lies along the 0°–180° line (0° and 180° directions were chosen arbitrarily) (inset). The majority (> 75%) of hair cells are oriented within 45° of the canal axis with some oriented nearly perpendicular (90° or 270° ± 45°) to the canal axis. Bars represent a total of 150 hair cells measured from 15 neuromasts in 6 fish.

lateral tubules that terminate in pores rostral and caudal to the eye, and is connected to both the mandibular canal and the infraorbital canal. The hyomandibular canal also penetrates the head lateral to the mouth to join the dorsal canals. The infraorbital canal consists of a loop that extends from a non-pored segment of the infraorbital canal, out to the naris. Another portion of the infraorbital canal extends directly from the non-pored segment just below the loop, laterally to the edge of the head, and has numerous tubules that terminate in pores ventral to the main canal. The supraorbital canal also extends from the non-pored infraorbital canal segment and bifurcates to either side of the ventral midline. Each division extends to the edge of the snout and then caudally along the margin of the head, to the naris where it penetrates to join the supraorbital canal on the dorsal surface. The short non-pored mandibular canal joins the hyomandibular canal on either side of the lower jaw, but does not appear joined across the midline.

Discussion

This study describes the morphology and spatial distribution of the lateral line system in *Raja eglanteria*, *Narcine brasiliensis*, *Gymnura micrura*, *Dasyatis sabina*, and *Sphyrna tiburo*. Superficial neuromasts in

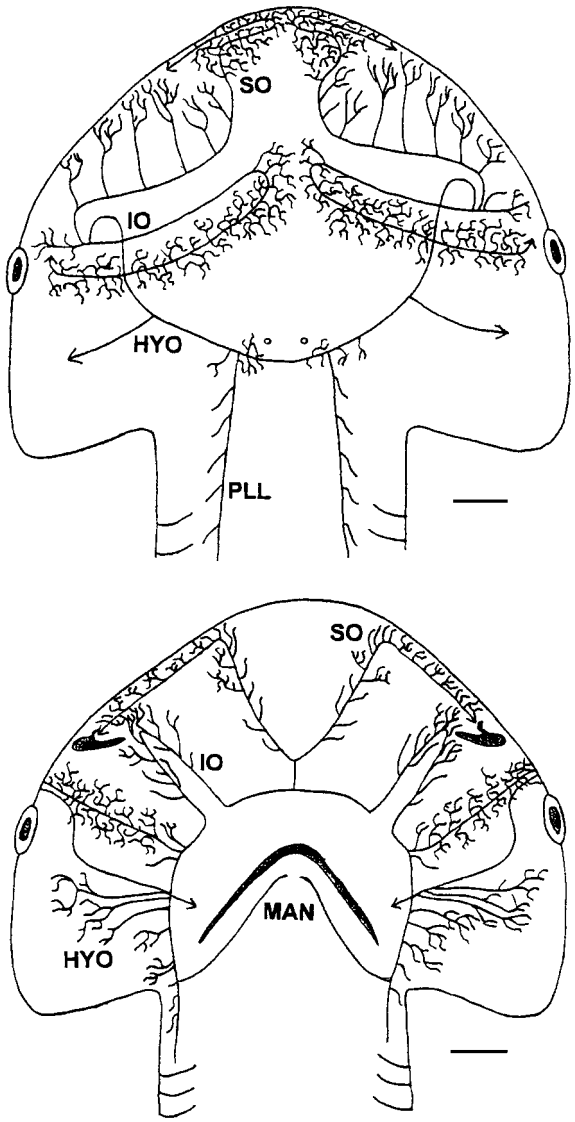

Figure 12. Distribution of the lateral line canal system on the dorsal (upper) and ventral (lower) surface of the head of the bonnethead shark, *Sphyrna tiburo*. Canals are bilateral and interconnected both among and within sides. Numerous branched tubules extend from most canals and terminate in pores at the surface. Scale bar = 0.5 cm (HYO = hyomandibular canal, IO = infraorbital canal, SO = supraorbital canal, MAN = mandibular canal, PLL = posterior lateral line canal.

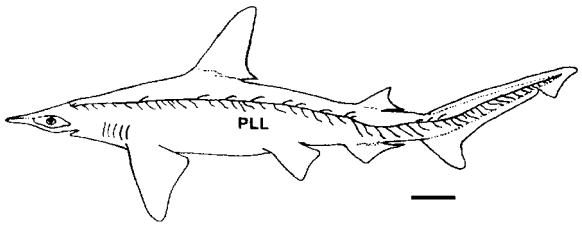

Figure 13. Distribution of the posterior lateral line canal in the bonnethead shark, *Sphyrna tiburo* (lateral view). The posterior lateral line (PLL) extends from the endolymphatic pores on the head to the tip of the upper caudal fin lobe and contains lateral tubules that terminate in pores along its length. Scale bar = 0.5 cm.

R. eglanteria are located in papillar grooves that are positioned along the dorsal midline, a pair anterior to each endolymphatic pore, and a row between the infraorbital canal and the eye. Pored canals are found on the dorsal surface of all species, but the number of pores per tubule branch increases from less (*N. brasiliensis*) to more (*G. micrura*) recently derived batoids. Pored canals are also found along the margin of the pectoral fins on the ventral surface of all species (except *N. brasiliensis*, which lacks a ventral canal system). Non-pored canals are found primarily on the ventral surface of all batoids examined (except *N. brasiliensis*) and are located on the rostrum, around the mouth, and along the midline just lateral to the gill slits. In contrast to the batoids, the bonnethead shark *S. tiburo* has primarily pored canals on both the dorsal and ventral surfaces of the head. Vesicles of Savi are found on the dorsal and ventral surface of *N. brasiliensis*, but only on the ventral surface of *D. sabina*. Quantitative comparison of the dorsal and ventral canal system in *D. sabina* shows that the ventral surface has fewer pores, but more sensory neuromasts and larger diameter canals than the dorsal surface. These morphological data are discussed below and are integrated with known ecology and behavior of elasmobranchs to propose biological functions for each mechanoreceptor type.

Superficial neuromast morphology and distribution

Morphology and distribution of superficial neuromasts is described in relatively few elasmobranch species (Ewart & Mitchell 1892, Tester & Nelson 1969, Maruska & Tricas 1998). In all batoids studied thus far, superficial neuromasts are located on papillae with sensory epithelia positioned at the base of central grooves. These papillae are raised approximately 0.3–0.5 mm above the surrounding skin and cupulae are directly exposed to the water. Superficial neuromasts in the clearnose skate, *R. eglanteria*, are located in a row

along the posterior lateral line canal, a row of about 5 between the infraorbital canal and the eye, and a pair anterior to each endolymphatic pore. This organization is very similar to that observed in the skate, *R. batis* (Ewart & Mitchell 1892), and the stingray, *D. sabina*, with the exception of the pair anterior to the endolymphatic pores and the distinct row near the eyes, which were not observed in the stingray (Maruska & Tricas 1998). The main axis of superficial neuromast grooves on the body and tail in both *R. eglanteria* and *D. sabina* range from 90°–135° to the rostrocaudal body axis. However, the orientation of superficial neuromasts near the spiracle in the stingray and endolymphatic pores in the skate is at a slightly greater degree range (100°–160°).

The orientation of superficial neuromast grooves provides insight into their possible biological functions. The position of the neuromast and cupula at the base of a well-developed groove oriented perpendicular to the rostrocaudal body axis enhances water flow parallel to the cupula especially when the animal lies motionless on the substrate, and minimizes stimulation of these receptors during forward swimming motion. This superficial neuromast morphology also indicates these receptors are directionally sensitive in elasmobranchs. This differs from most teleost fishes that have superficial neuromasts on the skin surface, which can be stimulated by water disturbances from any direction. The orientation of superficial neuromast grooves in batoids indicates a maximum response to water movements along the dorsal transverse body axis and a minimum response along the rostrocaudal body axis. However, superficial neuromasts near the eye in the skate have grooves oriented nearly parallel with the rostrocaudal body axis which indicates a maximum response to water movements along the longitudinal body axis from anterior or posterior to the eye. In addition, placement of superficial neuromasts along the dorsolateral aspect of the tail in *Raja* indicates a best response to water movements along the dorsal transverse tail axis. However, superficial neuromasts on the tail of *D. sabina* are positioned laterally which indicates a best response to vertical water movements parallel to the dorsoventral axis (Maruska & Tricas 1998). This difference in position may be explained by subtle differences in habitat and behavior of the skate compared to the stingray. For example, water movements in the dorsoventral axis along the tail would be more common for a ray swimming above the substrate than a skate that often propels itself forward with modified pelvic fins directly on the substrate. However, these proposed axes of best sensitivities are based on gross morphology and assume the hair cells are oriented parallel to the groove axis, but this requires electron microscopic confirmation.

In contrast to the batoids, superficial neuromasts in sharks generally lie between the bases of modified scales and are recessed below the skin surface. Superficial neuromasts in sharks follow the generalized plan of a line posterior to the mouth (mandibular row), a line between the pectoral fins (umbilical row), lines on the dorsolateral portion of the body and caudal fin, and a pair anterior to each endolymphatic pore (Budker 1958, Tester & Nelson 1969) (Figure 14a). Although the number and distribution of superficial neuromasts differs among species, most superficial neuromasts in sharks are associated with or positioned dorsal to the posterior lateral line canal (Tester & Nelson 1969) (Figure 14b–e). The number of superficial neuromasts in the shark species examined thus far ranges from 77 per side in the spiny dogfish, *Squalus acanthias*, to over 600 per side in the scalloped hammerhead, *Sphyrna lewini* (Tester & Nelson 1969) (Figure 14b–e).

A relationship appears to exist between the number of superficial neuromasts and the habitat and activity level of the shark species. Benthic dwelling and relatively slow swimming shark species such as the nurse shark, *Ginglymostoma cirratum*, and spiny dogfish, *Squalus acanthias*, have few superficial neuromasts with the majority located in a row just dorsal to the posterior lateral line canal along the trunk (Figure 14b,c). In contrast, more coastal-pelagic or active sharks such as the scalloped hammerhead, *S. lewini*, and bonnethead, *S. tiburo*, contain numerous superficial neuromasts distributed both dorsal to and ventral to the posterior lateral line canal along the body (Figure 14d,e). This relationship contradicts generalizations made in teleost fishes where sluggish fish or those that live in quiet waters have an increased number of superficial neuromasts, while active fish or those that live in turbulent waters have few superficial neuromasts. The position and number of superficial neuromasts in both sharks and batoids may either have some ecological significance, or represent functional specializations driven by evolution, but conclusions cannot be made until additional taxa are examined.

Based upon morphology and distribution, superficial neuromasts in both sharks and batoids likely function to detect water movements generated by predators, prey, or conspecifics, or may mediate hydrodynamic imaging

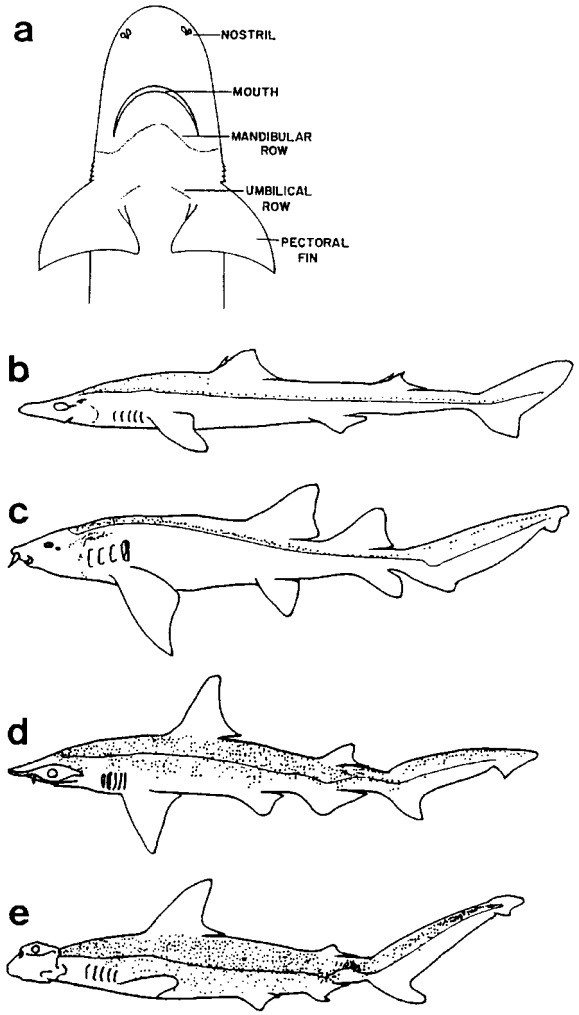

Figure 14. Distribution of superficial neuromasts (pit organs) in sharks. a – Ventral surface of the lemon shark, *Negaprion brevirostris*, shows the row of mandibular neuromasts beneath the lower jaw and the umbilical neuromasts between the pectoral fins. b – Superficial neuromasts in the spiny dogfish, *Squalus acanthias*, are few (approximately 77 per side) and located along the dorsal aspect of the posterior lateral line canal. c – Superficial neuromasts in the nurse shark, *Ginglymostoma cirratum*, are also few in number with the majority located above the posterior lateral line canal (line along dorsolateral portion of body). d – Superficial neuromasts in the bonnethead shark, *Sphyrna tiburo*, are numerous (> 400 per side) and distributed both dorsal and ventral to the posterior lateral line canal. e – Superficial neuromasts in the scalloped hammerhead, *Sphyrna lewini*, are more numerous (> 600 per side) and extend both dorsal and ventral to the posterior lateral line canal. Each dot represents a single superficial neuromast (modified from Tester & Nelson 1969).

Table 2. Summary of hypothesized behavioral functions of mechanosensory lateral line systems found in elasmobranch fishes.

Behavior	Superficial neuromasts	Vesicles of Savi*	Pored canals	Non-pored canals
Rheotaxis	+		+	
Predator avoidance	+		+	
Schooling†	+		+	
Social communication	+	+	+	+
Prey detection	+**	+	+	+
Hydrodynamic imaging	+		+	

The six general behaviors that are known to be mediated by the lateral line system in bony fishes are listed, and a + indicates a hypothesized function for each specific system in elasmobranchs. Use of each system for specific behaviors may differ between elasmobranch species (e.g. sharks versus batoids) due to both variations in lateral line systems and ecology or behaviors. *vesicles of Savi do not apply to shark species; **superficial neuromasts are likely not used for prey detection by benthic feeding batoids; †facilitation of schooling behavior would only apply to those species of sharks and batoids that are known to school.

(Table 2), but conclusions on biological function cannot be made until the adequate stimulus for these mechanoreceptors is physiologically demonstrated. In addition, superficial neuromasts in elasmobranchs may mediate rheotactic behavior (orientation to water currents) as demonstrated in teleosts (Montgomery et al. 1997), but this also remains to be tested.

Dorsal canal system morphology and organization

Differences in the spatial distribution of lateral line canals are often related to variations in body shape (Coombs et al. 1988). For example, the dorsoventrally flattened body of batoids is correlated with the extension of both the hyomandibular canal onto the enlarged pectoral fins, and the supraorbital canal onto the elongated rostrum (Chu & Wen 1979). Thus, the reduced tubule branching on the dorsal surface of *N. brasiliensis* may be related to the decreased size (width) of the disk. However, lateral line canals on the dorsal surface of both *N. brasiliensis* and *R. eglanteria* also contain only straight lateral tubules that terminate in single pores. This differs from many of the myliobatid rays, which show extensive branching of lateral tubules that terminate in many pores over the entire dorsal body surface (Chu & Wen 1979). The elaborate organization of tubule branching in the dorsoventrally flattened

G. micrura may serve to place the receptive field over the greatly expanded pectoral fins and likely increases sensitivity to water movements across the dorsal surface. However, the number and complexity of tubule branching is also greater in the more recently derived batoids such as *Rhinoptera, Aetobatus*, and *Manta* spp. (Garman 1888, Chu & Wen 1979), and may be a result of phylogeny. In addition, the number and complexity of tubule branches often increases with size of the animal which is likely an adaptation to maintain or increase sampling area as the fish grows. Thus, future examinations of lateral line characteristics across taxa should address whether differences in spatial distribution are correlated with body shape, ecology, ontogeny, or are a result of phylogenetic relationships.

Chondrichthyan lateral line canals differ from those in most bony fishes by the presence of multiple neuromasts between adjacent pores (Johnson 1917, Tester & Kendall 1969, Ekström von Lubitz 1981). The lepidosirenid lungfish, *Protopterus* (Webb & Northcutt 1997), and the oyster toadfish, *Opsanus tau* (Clapp 1898) also have multiple neuromasts between adjacent pores in their head lateral line canals. Therefore, multiple neuromasts between pores may have evolved independently in these groups of fishes. However, the presence of multiple neuromasts between pores and their organization into a nearly continuous sensory epithelium within the canal of many elasmobranch species (Johnson 1917, Tester & Kendall 1969, Boord & Campbell 1977, Maruska & Tricas 1998) indicates they likely have different response properties and possibly biological functions, but this remains to be physiologically and behaviorally tested.

The expansion of lateral line tubules and pores on the dorsal surface of all batoids examined may function to detect water movements over the disk surface and would be advantageous when a batoid lies buried or motionless on the substrate. The pored canals on the dorsal surface likely function to detect water movements across the body surface generated by predators, epifaunal prey items, or possibly conspecifics during mating (Table 2). These pored canals, as well as the superficial neuromasts, may be especially important for the detection of water movements generated by predators. Lateral line-mediated predator avoidance is likely an important behavioral response for adult and especially juvenile benthic batoids. Also, many skate species copulate on the ocean bottom, often for several hours at a time with their dorsal surface exposed to predators such as sharks. Thus, the ability to detect predators via the lateral line system while in copulo would ultimately enhance survival and reproductive success, but this hypothesis remains to be tested.

Pored canals on the dorsal surface of the head and the posterior lateral line canal on the body and tail of elasmobranchs may also serve to detect water movements generated by conspecifics to facilitate schooling behavior, and to locate objects in the environment via detection of distortions in the animal's own flow field while swimming (Table 2). Several shark (sphyrnid) and ray (myliobatid) species are known to school during certain times of the year and at certain life-history intervals (Castro 1983, Michael 1993). Therefore, the pored canals on both the dorsal and ventral surfaces of these species are likely used to detect water movements generated by conspecifics to maintain position within a school. Thus, it would be interesting to examine the correlation between schooling elasmobranch species and distribution of pored lateral line canals.

Ventral canal system morphology and organization

The lateral line canal system on the ventral surface of batoids, and ventral portion of the head of sharks generally consists of both pored and non-pored canal sections. The distribution of pored and non-pored sections of canal varies among species and this may be correlated with ecology and behavior, or explained by phylogenetic relationships among taxa. For example, the hyomandibular canal in *R. eglanteria* does not contain the subpleural loop in the mid-disk region that is characteristic of most batoids, but contains short tubules that terminate in single pores along the gill slits which is not characteristic of most other species (Garman 1888, Ewart & Mitchell 1892, Chu & Wen 1979), but is similar to the winter skate, *R. ocellata* (Garman 1888). Therefore, differences in canal structure among species within a single family (e.g. Rajidae) may be related to ecology or behavior. However, until a greater number of species are examined, conclusions on whether these differences reflect ecological correlations or phylogenetic trends cannot be made.

Neuromasts in the non-pored hyomandibular canal of *D. sabina* have sensory hair cells with numerous stereocilia in a stepwise arrangement of increasing height towards a single kinocilium. This morphology was also observed in the canal neuromasts of the spotted shark, *Mustelus manazo* (Hama & Yamada

1977) and in the vesicles of Savi of *Torpedo* spp. (Nickel & Fuchs 1974), but not in the posterior lateral line canal of the catshark, *Scyliorhinus canicula* (Roberts & Ryan 1971). Smaller cells with a single kinocilium and stereocilia of equal length were observed near the ends of the neuromast in *D. sabina*, but it is unknown whether these cells are innervated, or possibly represent a developmental interval of hair cells as described in *S. canicula* (Roberts & Ryan 1971). It is possible that these are supporting cells and that their position at the end of the neuromast and their long kinocilia both function to stabilize and support the cupula between adjacent neuromasts, but ultrastructural examination is required to test this hypothesis. In addition, many hair cells in the canal neuromasts of the stingray have kinocilia with bulbous endings similar to those observed in the lateral line system of the ratfish, *Chimaera monstrosa* (Ekström von Lubitz 1981) and saccular organ of the frog, *Rana catesbeiana* (Hillman & Lewis 1971). In the frog, the apex of this bulbous kinocilium contacts the otolithic membrane, while the base rests on a portion of the hair cell that lacks the rigid cuticular plate of the stereocilia. Movement of the stereocilia and kinocilium produces a deformation in the hair cell membrane at the base of the kinocilium. It was suggested that this specialized anatomical arrangement functions as a mechanical coupling system for the transformation of shearing motion of the otolithic membrane into a generator potential (Hillman & Lewis 1971). A similar mechanism may be operating in the stingray where bulbous kinocilia in the neuromasts of non-pored canal sections are anchored to the cupula and couple small cupular movements in any direction to hair cell stimulation. This organization may be advantageous in non-pored canals that are hypothesized to encode local displacements of the ventral skin surface in batoids (Sand 1937, Maruska & Tricas 1998). However, ultrastructural examination of the hair cell, kinocilium, and cuticular plate are needed to determine the presence or absence of a similar system in the elasmobranch lateral line.

Directional sensitivity of canal neuromasts in teleost fishes generally results from pairs of hair cells with opposite polarities oriented parallel to the longitudinal canal axis. Hair cells in canal neuromasts in some chondrichthyan species do not follow this strict arrangement of adjacent cells of opposing polarities and often contain hair cells oriented nearly perpendicular to the canal axis (Roberts 1969, Roberts & Ryan 1971, Ekström von Lubitz 1981), while other species do have this primarily parallel arrangement (Hama & Yamada 1977). However, relatively few studies examine the polarity of hair cells in cartilaginous fishes, thus the taxonomic distribution of this character is not well known. The majority of hair cells in the non-pored hyomandibular canal on the ventral surface of *D. sabina* are oriented within 45° of the main canal axis, with a small number oriented nearly perpendicular to this axis. This indicates that some hair cells will be stimulated by cupular movements in any direction. Presence of hair cells oriented at various angles within neuromasts may broaden the directionality to tactile stimuli at different locations on the skin. For example, small displacements of the skin directly beneath the ventral canals would cause displacement of the cupula inside the canal and stimulation of hair cells oriented near 0° or 180° along the canal axis. However, skin displacements at some lateral distance from the canal may also cause cupular movements and stimulation of hair cells oriented orthogonal to the longitudinal canal axis. This hypothesis is supported by the fact that these non-pored ventral canals have a large diameter which covers a greater area of underlying skin surface, and they are located above loose, compliant skin layers. Therefore, it is likely that these ventral non-pored canals function as displacement detectors (or mechanotactile receptors) rather than detectors of water movement. Further, the position of these non-pored canals around the mouth and rostrum indicates that they may be used in the detection and guidance of prey to the mouth as suggested by the mechanotactile hypothesis (Maruska & Tricas 1998). However, the functional significance of hair cell orientations both parallel and perpendicular to the canal axis in ventral non-pored canal neuromasts cannot be determined until they are compared with those of pored canal neuromasts. In addition, the response properties of these canal neuromasts should be determined and the mechanotactile receptive field on the skin surface beneath these canals requires investigation before hypotheses on biological function can be tested.

Non-pored canals on the ventral surface of elasmobranch species may also function as sensitive tactile receptors to facilitate body positioning during copulation (Table 2). Elasmobranchs have internal fertilization that often requires the male to bite the pectoral fin of the female in order to help position his body either along side, or underneath the female for insertion of the clasper (intromittent organ) into the cloaca. Therefore, the non-pored canals on the rostrum, around

the mouth, and along the midline may function as tactile receptors to facilitate body positioning between males and females during copulation. It would be interesting to examine seasonal changes in sensitivity of the neuromasts in the non-pored canals on the ventral surface in an elasmobranch species that undergoes a distinct annual reproductive cycle such as the Atlantic stingray, *D. sabina* (Maruska et al. 1996), to test the hypothesis that the lateral line plays a role in the coordination of copulatory behavior.

Vesicles of Savi

Vesicles of Savi are found primarily on the ventral surface of torpedinid, narcinid, and dasyatid batoids (Norris 1932, Szabo 1958, 1968, Nickel & Fuchs 1974, Chu & Wen 1979, Barry & Bennett 1989, Maruska & Tricas 1998), but the function of these receptors still remains unknown. *Narcine brasiliensis* has neuromasts that are located in enclosed vesicular pouches, which sit approximately 0.5–2.0 mm below a relatively compliant skin surface. Morphology of vesicles of Savi is similar in *Narcine* and *Torpedo* where each vesicle contains 3 neuromasts (one large central and 2 smaller peripheral), each of which has its own cupula and hair cells polarized parallel to the center of the neuromast (Szabo 1968, Barry & Bennett 1989). However, the cupula of the central neuromast in *N. brasiliensis* appears more dense than the cupulae of the peripheral neuromasts (observed in fresh tissue). Therefore, it is possible that the cupula of the central neuromast is weighted, and may be similar to the situation found in the otolithic organs of teleost fishes. Therefore, these electric rays may encode linear accelerations of the body in multiple directions because the vesicles of Savi are arranged in rows oriented 45° from the rostrocaudal body axis on both the dorsal and ventral surfaces. However, further analysis of cupular composition, hair cell polarization, and neuromast-cupular coupling is needed before conclusions can be made on the significance of variation in cupular density within the vesicles of Savi.

Vesicles of Savi in the dasyatid rays differ slightly in morphology and distribution from *Torpedo* and *Narcine* (Chu & Wen 1979, Maruska & Tricas 1998). In dasyatids, vesicles of Savi are located only on the ventral surface, contain only a single neuromast, are contiguous with the lumen of the supraorbital canal on the rostrum, and adjacent vesicles are connected by tubules (Maruska & Tricas 1998). Garman (1888) described a change in the subrostral canal of the batoids, *Potamotrygon* and *Paratrygon*, from a tubular structure to a row of closed rings connected by tissue, which may represent another morphological variant of the vesicles of Savi. Several researchers suggest that vesicles of Savi may represent an obsolescent canal condition, but conclusions can not be drawn until the morphological diversity of these structures is assessed. Also, the presence of vesicles of Savi only in the torpediniform and dasyatid batoids suggests that these vesicles evolved independently in these groups, but conclusions on evolutionary relationships can not be proposed until additional taxa are examined.

Vesicles of Savi are hypothesized to be receptors used to detect substrate-bourne vibrations transmitted via the skin or cartilaginous attachments in *Narcine* (Barry & Bennett 1989), or serve as specialized tactile receptors sensitive to displacement of the underlying skin caused by contact with prey, conspecifics, or the substrate (Nickel & Fuchs 1974, Maruska & Tricas 1998). Electrophysiological experiments in *Torpedo* indicate the vesicles of Savi have a peak sensitivity to vibrations of 150–200 Hz (Szabo 1968). Barry & Bennett (1989) suggest the vesicles may be high frequency vibration receptors due to their isolation and protection of the central neuromast by an arch in *Narcine*, but this remains to be experimentally tested. The concentration of vesicles on the rostrum around the mouth and their rostrocaudally arranged rows in *Narcine* puts them in an ideal location to aid in the localization and guidance of the mouth over prey items. Vesicles of Savi would not respond to pressure differences across the skin surface caused by water movements because they are not connected to the external environment, but should be sensitive to direct displacement of the compliant underlying skin. The specific orientation of the rows of vesicles (45° to the rostrocaudal axis) in *Narcine* may also provide the animal with directional information on the location of small prey items. However, comparisons of the morphology, distribution, and physiology of vesicles of Savi among batoid taxa warrants further investigation to examine the functional specialization and evolution of these mechanoreceptors.

Feeding neuroecology of the lateral line system

Feeding ecology and behavior can often be correlated with the peripheral distribution of the lateral line system

in fishes (Dijkgraaf 1962, Hensel 1978). The batoids examined in this study generally feed on infaunal or epifaunal organisms that often require excavation from the substrate and are often outside of the animal's visual field. The lesser electric ray, *N. brasiliensis*, feeds predominantly at night on burrowing polychaete worms with some amphipods, decapod shrimp, sipunculid worms, and anguilliform eels also reported in the diet (Funicelli 1975, Rudloe 1989). The clearnose skate, *R. eglanteria*, is a deep-water benthic batoid reported to feed on invertebrates such as mollusks and small crustaceans as well as the benthic tonguefish, *Symphurus plagiusa*, and other teleosts (Hildebrand & Schroeder 1928, Fitz & Daiber 1963, Schwartz 1996). Butterfly rays, *Gymnura* spp., are primarily piscivorous feeders that actively prey on teleost fishes such as spot, *Leostomous xanthurus*, and pinfish, *Lagodon rhomboides*. In addition, some crustaceans, gastropods and cephalopods were also found in the diet of smaller *Gymnura*, but teleosts become more important in the diet as the ray grows (Daiber & Booth 1960). The Atlantic stingray, *D. sabina*, feeds day and night almost exclusively on small benthic invertebrates such as amphipods, isopods, ophiuroids and polychaetes that they excavate from the substrate (Cook 1994, Bradley 1996). Integration of the feeding ecology and behavior of each of these species with the morphology and spatial distribution of the lateral line system supports the hypothesis that the lateral line system functions in predation in elasmobranch fishes.

Prey detection in elasmobranchs is mediated by multiple sensory systems, but the ventral lateral line system in batoids probably serves to locate prey and guide the mouth over it during the final stages of prey capture. The pored canal system on the ventral surface may function to detect water movements generated by locomotion, respiration, and filter-feeding activities of prey (Montgomery & Skipworth 1997), and allow the batoid to reposition its body to orient the non-pored canals and mouth directly over the prey. Non-pored canals are often located on the ventral rostrum and around the mouth, and may function as specialized tactile receptors stimulated by prey contact with the skin surface as proposed by the mechanotactile hypothesis in the stingray (Maruska & Tricas 1998). Similarly, the vesicles of Savi distributed around the mouth and on the rostrum in batoids may also serve as mechanotactile receptors involved in prey localization. The spatial separation of vesicles of Savi would allow them to serve as point source detectors when prey are just rostral or lateral to the mouth.

In addition to the correlation between peripheral lateral line organization and feeding ecology and behavior of batoids, other evidence supports the mechanotactile hypothesis of lateral line function. First, although the number of lateral line pores is greater in the canals on the dorsal surface of *D. sabina*, the canals on the ventral surface often contain twice as many sensory neuromasts. Second, the average diameter of non-pored canals on the ventral surface is 2.5× greater than that of the dorsal canals in *D. sabina*. This indicates there is a wide tactile receptive field on the ventral skin surface beneath the canal that will move canal fluid and stimulate the neuromast when it is displaced. For any given displacement of the skin surface, fluid flow inside a larger diameter canal will attenuate at shorter distances from the stimulus than in a smaller diameter canal, permitting the ray to better localize a prey item because fewer neuromasts will be stimulated. The compliant nature of the canal walls and dermal layers superficial to the ventral canal would also facilitate movement of the cupula and canal fluid in response to skin displacement. Third, cutaneous sensory endings (putative tactile receptors) in elasmobranchs are stimulated by 20 μm displacements of the skin surface (Murray 1961), but a skin displacement of less than 20 μm should stimulate the canal neuromasts of the lateral line system, making it more sensitive to tactile stimulation than the general cutaneous tactile system. Therefore, these data support the hypothesis that the non-pored canals and vesicles of Savi on the ventral surface in the stingray and other batoids function as mechanotactile receptors that likely play a role in the localization and capture of prey. However, the mechanotactile hypothesis remains to be physiologically and behaviorally tested.

The bonnethead, *S. tiburo*, was used in this study to compare the organization of the lateral line system in batoids to a shark species with similar food habits. The bonnethead is a small abundant coastal shark species that feeds primarily at night on motile invertebrates such as crabs, shrimp, bivalves, and cephalopods that often reside in seagrass beds (Cortés et al. 1996). Although the bonnethead often feeds on benthic invertebrates, it does not have the extensive non-pored canal system or vesicles of Savi present in benthic feeding batoids. Therefore, it is likely that prey localization is mediated by the detection of water motions caused by movements of prey via a pored canal system rather than a mechanotactile mechanism mediated by the non-pored canals as suggested in batoids (Maruska & Tricas 1998). However, many shark species do have sections

of non-pored canals on the head (Garman 1888, Chu & Wen 1979). Non-pored canals on the head of sharks may also serve as mechanotactile receptors to facilitate prey localization during the final stages of prey capture and handling or during copulation, or may help reduce stimulation of the canal system during forward swimming movements. However, differences in morphology and spatial distribution of the lateral line system between batoids and sharks may also result from different evolutionary selective pressures. Thus, functional or phylogenetic interpretations should be treated with caution until additional taxa are examined.

Future directions

In teleosts, the mechanosensory lateral line functions to detect water flow across the skin surface to facilitate prey detection (Hoekstra & Janssen 1985, Montgomery & Saunders 1985, Montgomery et al. 1988, Montgomery 1989, Janssen et al. 1995), social communication (Satou et al. 1991, 1994), schooling (Partridge & Pitcher 1980), predator avoidance (Blaxter & Fuiman 1990, Fuiman 1993), rheotaxis (Montgomery et al. 1997), and object localization or hydrodynamic imaging (Campenhausen et al. 1981, Hassan 1989). Several of these functions were shown behaviorally or physiologically to be mediated by a specific class of mechanoreceptor organ. For example, rheotaxis and predator avoidance in fish larvae is mediated primarily by superficial neuromasts (Montgomery et al. 1997, Blaxter & Fuiman 1990), while schooling and localization of objects is often mediated by the canal system (Partridge & Pitcher 1980, Hassan 1989). Elasmobranch lateral lines differ from teleosts by the placement of superficial neuromasts within grooves that enhance a bidirectional sensitivity, and canal neuromasts that are organized as a nearly continuous sensory epithelium with multiple neuromasts between pores. In addition, specialized non-pored canals are common in most species, and vesicles of Savi are found in some rays. Thus, it cannot be assumed that class-specific mechanoreceptor-mediated behaviors in teleosts apply to elasmobranchs. Also, the biological function of the specialized non-pored canal system and vesicles of Savi remain to be demonstrated. Testing of mechanoreceptor-specific functions requires quantitative comparisons of response properties of different mechanoreceptors as well as direct behavioral experimentation. Several of these mechanoreceptor-specific function hypotheses were mentioned in previous sections and summarized in Table 2, while a few are discussed below.

Mechanotactile hypothesis

The mechanotactile hypothesis of lateral line function in batoids states that ventral non-pored canals likely function as specialized tactile receptors used to facilitate prey capture (Maruska & Tricas 1998). Detection of weak water jets by the short-tailed stingray, which simulated water movements generated by prey, provided behavioral evidence for lateral line-mediated prey detection in elasmobranch fishes (Montgomery & Skipworth 1997). However, the relative roles of the pored and non-pored canal systems on the ventral surface of batoids during prey detection and localization is unknown. The hypothesis that non-pored canals encode displacement of the skin can be tested by electrophysiological determination of response properties of primary afferents that innervate the neuromasts in these canals. Some evidence already exists for stimulation of lateral line canals across the skin in both teleosts and elasmobranchs, but characterization of sensitivity and receptive field organization remains unknown (Sand 1937, Denton & Gray 1983, 1988). Also, the question of whether or not a natural source (e.g. prey) is able to stimulate these receptors and elicit behaviors will require behavioral testing. Many of the lateral line-mediated behaviors in teleosts were demonstrated by studies that sequentially eliminated each sensory system, including pharmacological techniques used to block lateral line receptors (e.g. cobalt chloride, gentamicin sulfate). However, elasmobranchs are often large and difficult to deal with in captivity, standard pharmacological methods (e.g. cobalt chloride blockers) do not work in salt water, and elimination of the lateral line system via surgical transection of nerves without damage to the electrosensory system is difficult. Therefore, the logistics of conducting lateral line behavioral experiments in elasmobranch fishes must be tediously resolved before conclusions on biological function can be demonstrated.

Schooling hypothesis

Teleost fishes use their lateral line systems in conjunction with vision to maintain position within a school (Partridge & Pitcher 1980). Individual fish detect short-term changes in the velocity and direction of their nearest neighbors primarily via the pored lateral

line canal along the trunk. Several elasmobranch fishes are also known to form aggregations at certain times of the year or day for reasons such as mating and parturition, feeding, or predator avoidance. These aggregations range from large schools with hundreds of individuals (e.g. *Sphyrna lewini* and *Rhinoptera bonasus*) to smaller groups of only a few individuals (e.g. *Carcharhinus amblyrhynchos*). However, relatively little is known about the organization and function of elasmobranch schools and whether the lateral line system plays a role in this behavior. Individuals within a school would detect water movements produced by swimming neighbors primarily via pored lateral line canals along the body in sharks (i.e. posterior lateral line canal) and on both the dorsal and ventral pectoral fins in batoids. Therefore, it is possible that elasmobranch species that form aggregations have lateral line specializations such as increased canal branching to expand the receptive field, increased number of pores, or increased numbers of superficial neuromasts. Morphological studies across taxa would test the hypothesis that lateral line organization is correlated with schooling behavior in elasmobranchs. In addition, behavioral experiments which measure the ability to maintain position within a school in fish with different portions of the lateral line system ablated can reveal the relative importance of the mechanosensory system in elasmobranch schooling behavior.

Mechanosensory parallel processing hypothesis

Lateral line canals on the head are innervated by the anterior lateral line nerve complex, and those of the body and tail by the posterior lateral line nerve. Both branches enter the brain and terminate somatotopically around cell plates within the medial octavolateralis nucleus of the medulla (Bodznick & Northcutt 1980, Puzdrowski & Leonard 1993). However, these nerves contain neurons that innervate both superficial and canal neuromasts. Therefore, the hypothesis that superficial neuromasts that encode lower frequency velocity information, and canal neuromasts that encode higher frequency acceleration information have separate parallel processing pathways should be tested via neuroanatomical and neurophysiological techniques. Central physiological and neuroanatomical studies in elasmobranchs have shown mechanosensory lateral line regions from the medulla to the telencephalon (Bleckmann et al. 1987, 1989, Bleckmann & Bullock 1989, Boord & Montgomery 1989), but identification of distinct cell populations that process velocity versus acceleration or displacement information received from different receptor classes has received little attention. Also, central processing of mechanosensory information from the distinct dorsal and ventral surfaces of batoids requires investigation in a behavioral context. It is currently unknown how different types of mechanosensory information are processed and integrated in the elasmobranch brain to elicit specific lateral line-mediated behaviors.

The importance of the mechanosensory lateral line system in the coordination of behaviors such as feeding, schooling, predator avoidance, hydrodynamic imaging, and courtship remain to be investigated in elasmobranch fishes. However, it is only after basic questions on lateral line structure and function are answered that more complex questions such as how the central nervous system processes and integrates lateral line information with other sensory cues to elicit behaviors can be logically approached.

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