

Lateral Line System in *Scomberomorus niphonius* (Teleostei, Perciformes, Scombridae): Recognition of 12 Groups of Superficial Neuromasts in a Rapidly-swimming Species and a Comment on Function of Highly Branched Lateral Line Canals

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Abstract The lateral line system in the Japanese Spanish mackerel *Scomberomorus niphonius* was examined in detail, being the first occasion of such in Scombridae. The canal system comprised 7 cephalic canals (supraorbital with 6 canal neuromasts, infraorbital with 9 or 10, otic with 2, preopercular with 5 or 6, mandibular with 12 or 13, postotic with 1 and supratemporal with 5 or 6) and a single trunk canal [with 3 (on head) + 234–243 neuromasts]. Although the basic topographies of these canals followed the typical teleost condition, the branching pattern of cutaneous tubes (i.e., secondary lateral line canals) on the head became extremely complex with growth. Twelve groups of superficial neuromasts, comprising 9 cephalic and 3 trunk groups, were recognized: rostral (1–4 neuromasts), nostril (10–13), cheek (6–10), opercular (7–12), preopercular (7–10), mandibular (0–3), postocular (3 or 4), supratemporal (4–6) and parietal (1–2), and predorsal (10–13), trunk accessory (36–43) and caudal fin (3–7), respectively. The presence of superficial neuromast groups on the head are reported for the first time in scombrids, and the function of the highly branched secondary lateral line canals in *S. niphonius* discussed.

Key words: sensory system, canal, neuromasts, teleosts, morphology.

Introduction

The lateral line system is a mechanosensory system in fishes and aquatic amphibians. Its morphological characteristics in teleosts (e.g., neuromast size, number and arrangement; structures that cover or flank neuromasts) are largely affected by habits and habitats of the taxa concerned (e.g., Dijkgraaf, 1963; Coombs *et al.*, 1988; Webb, 1989; Mogdans and Bleckmann, 2001; Janssen, 2004; Helfman *et al.*, 2009; Wark and Peichel, 2010; Wellenreuther *et al.*, 2010).

For example, Webb (1989) categorized four major types of cephalic lateral line canals in teleosts: simple (= narrow), branched, widened and reduced, each type being considered to have a close relationship with ecological characteristics. Although lateral line systems of several fish species have been studied in detail in recent years (e.g., Schmitz *et al.*, 2008; Wark and Peichel, 2010; Nakae and Sasaki, 2010; Wellenreuther *et al.*, 2010; Asaoka *et al.*, 2011, 2012; Nakae *et al.*, 2012a), information remains scanty, particularly

with regard to the distribution of superficial neuromasts. Descriptive accounts of parts of the lateral line system of scombrids were given by Allis (1903) (cephalic lateral line system in *Scomber scombrus* Linnaeus, 1778), Deng and Zhang (1986) [cephalic lateral line canals in *Rastrelliger kanagurta* (Cuvier, 1816)] and Ghysen *et al.* (2010) [early development in *Thunnus thynnus* (Linnaeus, 1778) and *Sarda sarda* (Bloch, 1793)], but those of whole of the system have never been given in the family.

In the present study, whole of the lateral line system (including the number of neuromasts) in *Scomberomorus niphonius* (Cuvier, 1832), a rapidly-swimming species, is described and illustrated in detail for the first time in Scombridae, as a part of the study on the morphological adaptations to the oceanic environment in scombrid fishes. Although in the teleosts, the fast swimmers have been believed to have relatively reduced lateral line system with few superficial neuromasts in general (Dijkgraaf, 1963; Janssen, 2004; Helfman *et al.*, 2009), this was not applicable to *Scomberomorus niphonius*, which appeared to have well-developed lateral line system and relatively many superficial neuromasts. The function of the highly branched secondary lateral line canals in this species is also discussed.

Materials and Methods

Thirty specimens of *Scomberomorus niphonius* (34.5–161.7 mm standard length: SL), collected from the Inland Sea of Japan and deposited at the National Museum of Nature and Science (NSMT-P), were examined. Neuromasts, lateral line canals and bones were observed on specimens stained by 2-Di-4-ASP (Nakae *et al.*, 2012b), Cyanine Blue (Akihito *et al.*, 2002) and Alizarin Red S (fixed specimens placed in 70% ethanol with a small quantity of Alizarin Red S powder for several weeks), respectively. Some neuromasts were also observed following treatment with Cyanine Blue and 1% osmium tetroxide (Jakubowski, 1963) solutions. Terminology

generally follows Webb (1989) for lateral line canals and Collette and Gillis (1992) for osteology. The names given to superficial neuromast groups reflected their respective positions.

Results

Main lateral line canals

The lateral line canal system comprised 7 cephalic [supraorbital (SOC), infraorbital (IOC), otic (OTC), preopercular (PRC), mandibular (MDC), postotic (POC) and supratemporal (STC)] canals, and a single trunk (TRC) canal (Figs. 1–3).

The SOC began above the hind margin of the eye and extended anteriorly to the anterior margin of the snout (except upper jaw), being connected with the IOC and OTC posteriorly. The IOC coursed downward behind the eye and subsequently curved anteriorly just below the eye, extending below the anterior nostril. The OTC lay between the SOC-IOC junction and the POC-PRC junction. The PRC coursed downward and subsequently curved anteriorly to be connected with the MDC anteriorly. The MDC extended anteriorly close to the tip of the lower jaw. The POC was short, connecting the OTC-PRC and STC-TRC junctions. The STC coursed mid-dorsally and thence posteriorly; with growth it extended posteriorly from the nape (Fig. 1; ca. 60 mm SL) to the dorsal fin origin (at 149.1 mm SL). The TRC, undulating slightly, extended from the POC-STC junction to the caudal fin base.

All of the main lateral line canals were associated with some bony elements of the cranium and pectoral girdle (Fig. 2): the SOC was contained in the nasal and frontal, the IOC in the infraorbitals, the OTC in the frontal and pterotic, the PRC in the pterotic and preopercle, the MDC in the anguloarticular and dentary, the POC in the pterotic and extrascapula, the STC in the extrascapula, and the TRC in the extrascapula, posttemporal and supracleithrum. Cutaneous parts were also present in some main canals, including the anterior tip of the MDC, the part

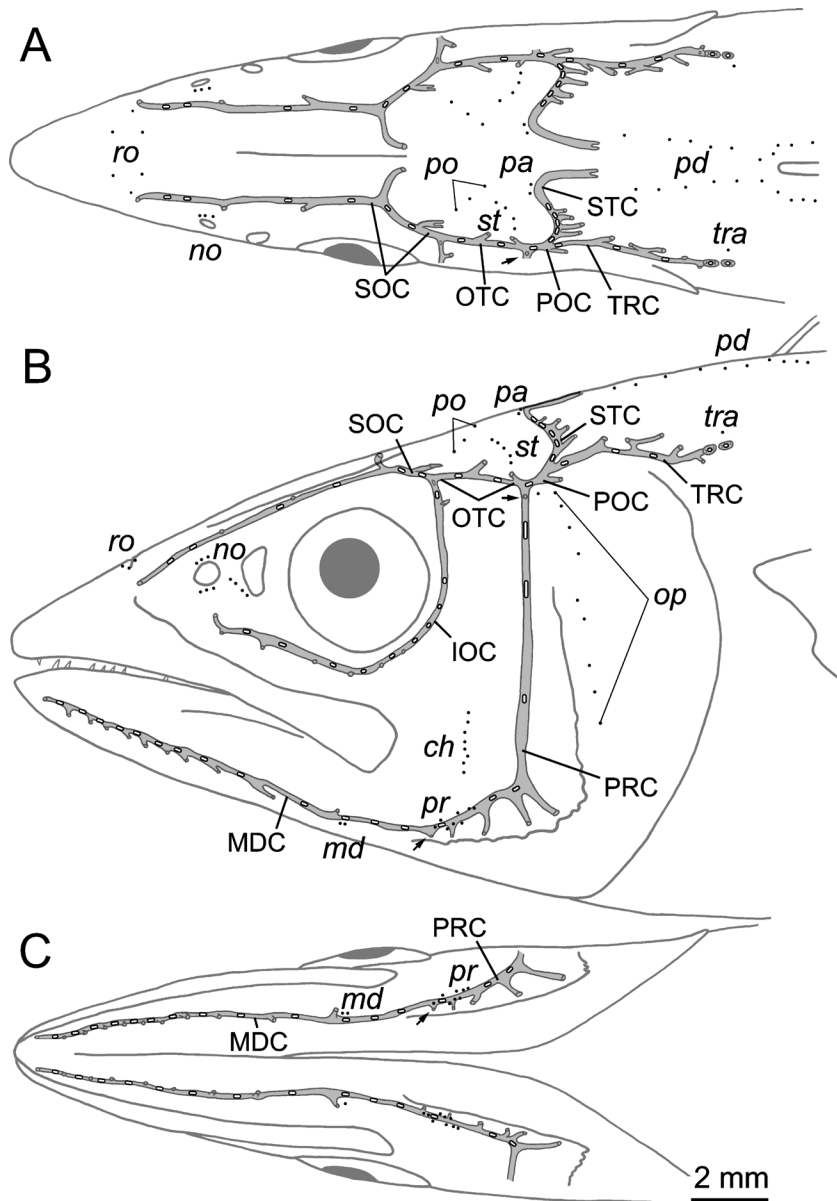


Fig. 1. Cephalic lateral line system in *Scomberomorus niphonius* (mostly based on NSMT-P 108635, 63.8 mm SL; number and distribution of neuromasts supplemented by 7 specimens, 37.4–65.0 mm SL). — A–C, dorsal, lateral and ventral views. Abbreviations: *ch*, cheek group; IOC, infraorbital canal; MDC, mandibular canal; *md*, mandibular group; *no*, nostril group; *op*, opercular group; OTC, otic canal; *pa*, parietal group; *pd*, predorsal group; *po*, postotic group; POC, postotic canal; *pr*, preopercular group; PRC, preopercular canal; *ro*, rostral group; SOC, supraorbital canal; *st*, supratemporal group; STC, supratemporal canal; *tra*, trunk accessory group; TRC, trunk canal. Arrows indicate short canals on PRC (see text).

between the PRC and MDC, and dorsal parts of the IOC, PRC and STC.

Secondary lateral line canals

Although the secondary lateral line canals (branched from main canals) were short and sim-

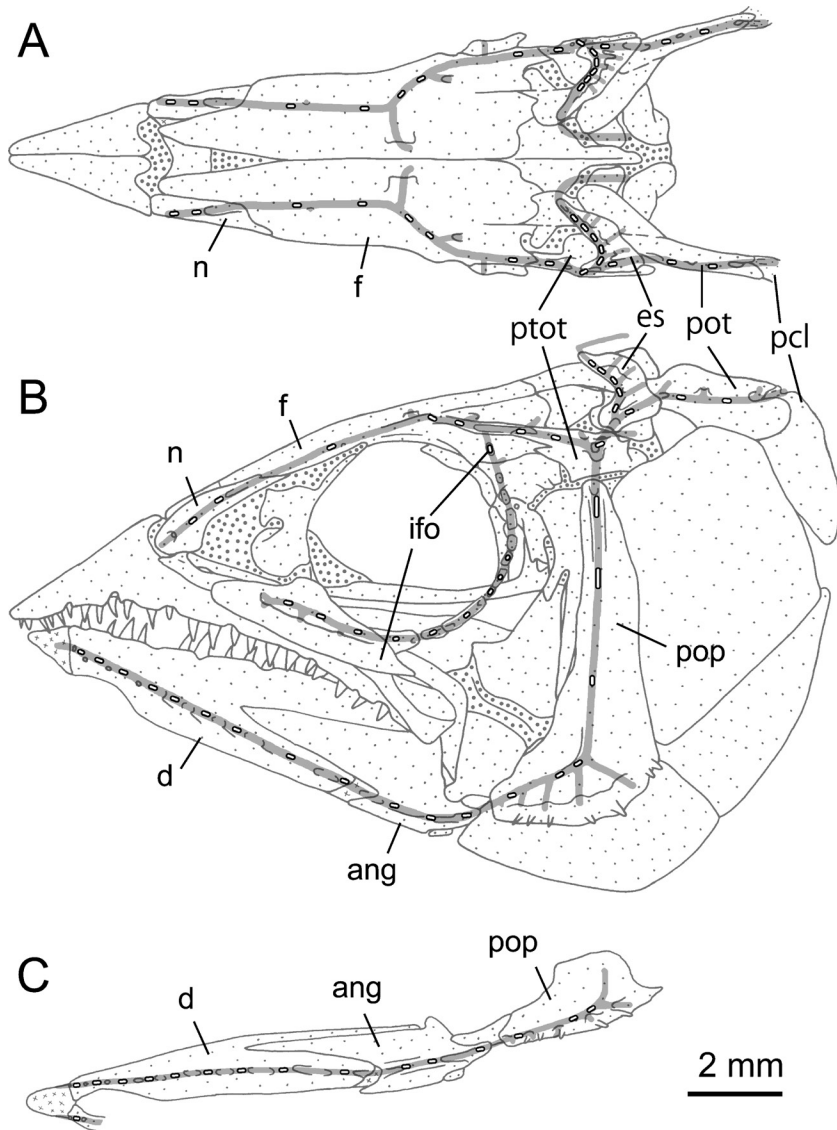


Fig. 2. Canal neuromasts of cephalic lateral line system and their associated bones in *Scomberomorus niphonius* (mostly based on NSMT-P 108643, 57.5 mm SL; number and distribution of neuromasts supplemented by 5 specimens, 47.2–63.8 mm SL). — A–C, dorsal, lateral and ventral views. Abbreviations: ang, anguloarticular; d, dentary; es, extrascapula; f, frontal; ifo, infraorbitals; n, nasal; pop, preopercle; pot, posttemporal; ptot, pterotic; scl, supracleithrum.

ple in the smaller specimens examined (34.5–65.0 mm SL; Fig. 1), they gradually developed with growth, being highly branched with many distal pores in the specimens larger than ca. 150 mm SL (Fig. 4: adult condition). The canals were cutaneous, excluding the basal parts of some which passed through bony elements (see

below). The secondary lateral line canals in the smaller specimens are briefly described first (Figs. 1–3), followed by the adult condition.

The SOC gave off 3 very short anterior and 2 rather long posterior canals. In the larger specimens, the anterior canals were highly branched, covering the surfaces lateral to the snout and

adjacent area, dorsomedial to the nostrils, and anterodorsal to the eye, respectively. The posterior canals were also extensively branched posterodorsally, forming a network of canals on the medial surface of the interorbital space (Fig. 4A, B) and anterior surface of the temporal region, respectively; many canals on the interorbital space were interconnected with their opposite number.

The IOC gave off 9 or 10 very short canals (Fig. 1B). In the larger specimens, they were highly branched below the eye (i.e., on infraorbital 1 and adjacent area) and on the surface anteroventral to the temporal region (i.e., dorso-posterior to the eye) (Fig. 4A).

The OTC gave off 2 short canals, the anterior one being cutaneous and the posterior one passing through the pterotic. In the larger specimens, both canals ramified posterodorsally to form a tubular network on the temporal region with highly branched tubes derived from the SOC, IOC, PRC, POC, STC and cephalic portion of the TRC (Fig. 4A, B).

The PRC gave off 4 or 5 short canals at the angle passing through the preopercle, in addition to a few slightly risen canals (Fig. 1: arrows) distinctly dorsal to and slightly ventral to the short canals. In the larger specimens, all of the canals were extensively branched, occupying the ventrolateral surface of the temporal region and ventral part of the preopercle (Fig. 4A, C).

The MDC gave off 9 or 10 short canals, directed posteriorly (Fig. 1B). In the larger specimens, the branches were more or less ramified, most canals being oriented posteriorly (Fig. 4C).

The POC gave off a single cutaneous canal. In the larger specimens, the canal was highly branched to form the ventrolateral portion of the cutaneous tube network on the temporal region with canals from the PRC (Fig. 4A, B; see above).

The STC gave off 4 or 5 posteriorly-oriented canals, passing through the extrascapula (Figs. 1–3). In the larger specimens, many cutaneous tubes were derived posteriorly from these canals to cover the dorsal surface of the temporal region

(Fig. 4A, B). In the dorsal mid-line, some cutaneous tubes on opposite sides shared many pores in common.

The cephalic part of the TRC gave off 3 short cutaneous canals. In the larger specimens, they were highly ramified to cover the posterodorsal surface of the temporal region, in part extending close to the dorsal fin origin (Fig. 4).

Neuromasts

Canal neuromasts in each main canal numbered as follows (Figs. 1–3): 6 in the SOC (4 in the frontal and 2 in the nasal), 9 or 10 in the IOC, 2 in the OTC (1 each in the frontal and pterotic), 5 or 6 in the PRC, 12 or 13 in the MDC (2 or 3 in the anguloarticular and 9 or 10 in the dentary), 1 in the POC (in the pterotic), 5 or 6 in the STC and 3 + 234–243 in the TRC (cephalic + trunk regions, respectively, 1 in the extrascapula, 2 on the posttemporal and 234–243 on the pored lateral line scales; one neuromast per scale).

Twelve groups of superficial neuromasts, comprising 9 cephalic and 3 trunk groups, were recognized (Figs. 1–3; ca. 60mm SL): rostral (*ro*), nostril (*no*), cheek (*ch*), opercular (*op*), preopercular (*pr*), mandibular (*md*), postocular (*po*), supratemporal (*st*) and parietal (*pa*), and predorsal (*pd*), trunk accessory (*tra*) and caudal fin (*cf*). The *ro* group, comprising 1–4 neuromasts, occurred on the snout, medial to the anterior part of the SOC. The *no* group (10–13) consisted of 3 lines, dorsal (3–5 neuromasts) and ventral (3 or 4) to the anterior nostril, and anteroventral to the posterior nostril (3–5). The *ch* (6–10) and *op* groups (7–12) were arranged vertically on the cheek and opercular regions, respectively. The *pr* and *md* groups, comprising 7–10 and 0–3 neuromasts, respectively, were scattered on the lateral surface of the anteroventral part of the preopercle and posterior surface of the lower jaw (i.e., posteroventral part of the anguloarticular), respectively. The *po* (3 or 4) and *st* groups (4–6) occurred on the temporal region, both orientated obliquely. The *pa* group, comprising 1 or 2 neuromasts, occurred immediately in front of the curved part of the STC. The *pd* group (10–13)

was arranged longitudinally from the nape to the base of the second dorsal fin spine. The *tra* group (36–43) was arranged along the dorsal rim of the TRC; neuromasts occurred continuously along the anterior part of the trunk, but became widely separated posteriorly. The *cf* group (3–7) consisted of dorsal (2–5) and ventral (1–2) lines, usually extending between the 3rd and 4th dorsal rays and 2nd and 3rd ventral rays of the caudal fin, respectively. In the larger specimens (ca. 150 mm SL), the basic distribution of the 12 groups was identical, despite the development of the secondary lateral line canals, although exact counts of the neuromasts were difficult.

Discussion

Conditions of the lateral line system

The lateral line system in *Scomberomorus niphonius* comprises 8 main canals including canal neuromasts [7 cephalic canals (SOC, IOC, OTC, PRC, MDC, POC and STC) and 1 trunk (TRC)], and 12 groups of superficial neuromasts [9 cephalic (*ro*, *no*, *ch*, *op*, *pr*, *md*, *po*, *st* and *pa*) and 3 trunk (*pd*, *tra* and *cf*) groups], the number of main canals and their topographies being typical of teleosts (Webb, 1989). However, superficial neuromasts were recognized for the first time in post larval Scombridae, having been otherwise noted only on the caudal fin in larval *Thunnus thynnus* (see Ghysen *et al.*, 2010: supplementary fig. 4B).

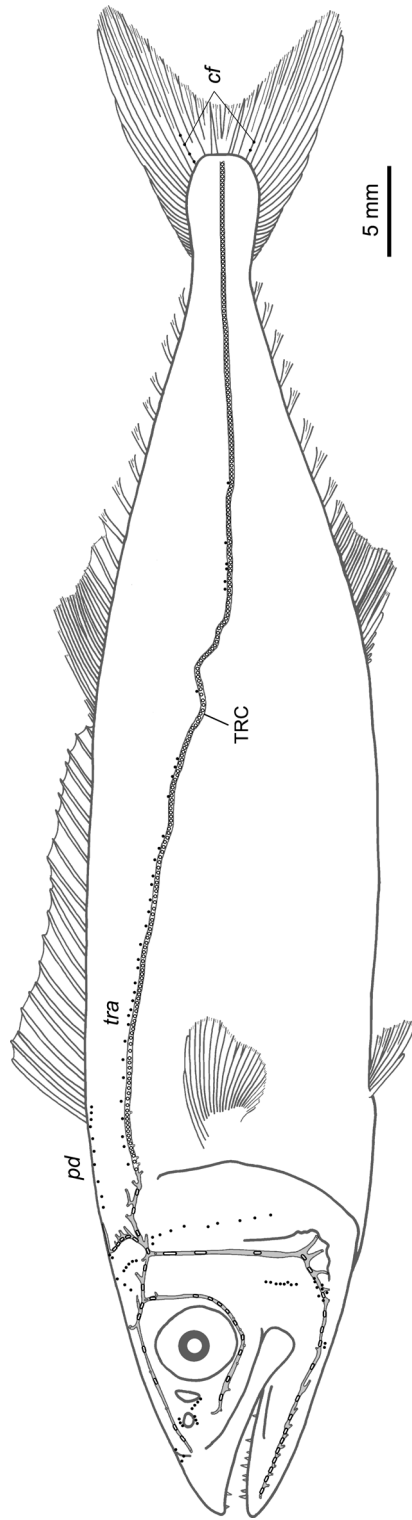
The lateral line canal system in *S. niphonius* (larger than 149.1 mm SL in this study) was characterized by narrow, highly branched cutaneous canals, similar to those reported for several other teleosts, e.g., the clupeid *Brevoortia tyrannus* (Latrobe, 1802) (Hoss and Blaxter, 1982), carangid *Parastromateus niger* (Bloch, 1795), menid *Mene maculata* (Bloch and Schneider, 1801), lactariid *Lactarius lactarius* (Bloch and Schneider, 1801) and scombroid *Scombrops boops*

(Houttuyn, 1782) (Deng and Zhan, 1986). Within Scombridae, *Thunnus orientalis* (Temminck and Schlegel, 1844) (Nakae *et al.*, unpublished preliminary survey) and *Rastrelliger kanagurta* (see Deng and Zhan, 1986) are characterized by branched lateral line canals similar to those in *Scomberomorus niphonius*, although the branches tend to be simpler and shorter than those in the latter. *Scomber scombrus* lacks a cutaneous tube network on the temporal region (Allis, 1903: figs. 1–3). Evidence to date, therefore, indicates that although highly branched cutaneous canals are not uncommon in teleosts, they are somewhat variable within scombrids.

Allis (1903: fig. 1a) observed canal neuromasts in the cephalic lateral line canals of *Scomber scombrus*, reporting their number in each canal: 7 in the SOC (vs. 6 in *Scomberomorus niphonius*), 11 (his 2nd neuromast counted as 2 in this study, judging from his illustration) in the IOC (vs. 10), 2 in the OTC (vs. 2), 5 in the PRC (vs. 5 or 6), 5 in the MDC (vs. 12 or 13), 1 in the POC (vs. 1), 2 in the STC (vs. 5 or 6) and 4 in the anterior TRC (vs. 3). The fewer neuromasts in *Scomberomorus niphonius* (in three canals) have resulted from a decrease of one neuromast each on the nasal (in SOC), 1st infraorbitalis (in IOC) and supracleithrum (in TRC). On the other hand, the markedly increased numbers on the dentary and anguloarticular (both in MDC), and extrascapula (in STC), reflect the relatively greater canal lengths in the latter species.

Scomberomorus niphonius has 9 cephalic and 3 trunk groups of superficial neuromasts, including approximately 40–60 and 60 neuromasts, respectively. As a general trend in teleosts, fast swimmers or species living in high flow environments are considered to have reduced numbers of superficial neuromasts (Dijkgraaf, 1963; Janssen, 2004; Helfman *et al.*, 2009). However, compared with some slowly-swimming or sedentary perci-

Fig. 3. Lateral view of trunk lateral line system in *Scomberomorus niphonius* (mostly based on NSMT-P 108635, 63.8 mm SL; number and distribution of neuromasts supplemented by 7 specimens, 37.4–65.0 mm SL). — *cf*, caudal fin group; *pd*, predorsal group; *tra*, trunk accessory group; TRC, trunk canal.



forms, the distribution pattern and total number of neuromasts on the head (insufficient neuromast data for trunk comparisons) of rapidly-swimming *S. niphonius* do not differ significantly from such perciforms, thereby contradicting the above trend [c.f. the percids *Gymnocephalus cernua* (Linnaeus, 1758) (9 groups and ca. 55–80 neuromasts; Jakubowski, 1963), *Sander lucioperca* (Linnaeus, 1758) (9 groups and ca. 70–100 neuromasts; Jakubowski, 1966) and *Perca fluviatilis* Linnaeus, 1758 (9 groups and ca. 40–60 neuromasts; Jakubowski, 1966), and a tripterygiid *Enneapterygius theostomus* (Jordan and Snyder, 1902) (9 groups and ca. 20 neuromasts; Nakae *et al.*, 2012b; groupings in that study slightly modified)]. Beside some perciform taxa with numerous superficial neuromasts [e.g., apogonids (Hayashi, 1991; Nakae *et al.*, 2012b) and gobioids (Shibukawa *et al.*, 2001; Asaoka *et al.*, 2011, 2012)], the presence of superficial neuromasts in *S. niphonius* suggests that a basic pattern for their distribution and number exists, being linked more with phylogeny than with habitats and habits.

Function of highly branched canals

Janssen (2004) hypothesized that branching canals functioned to filter out small-scale hydrodynamic disturbances, namely “with pressure induced by flow past one pore of a branch flow occurs mainly in the branch and there is less past the neuromast.” Janssen (2004: fig. 8) showed a Y-shaped canal derived vertically upward from the main canal in which flow was restricted to the upper V-shaped part, water entering from the left pore and exiting from the right, the direction of water movement being consistent with that of external water over the fish body. In *S. niphonius*, however, highly branched canals did not appear to function primarily as “filters.” In that species, most of the cutaneous canals are derived posteriorly from the main canals, their direction

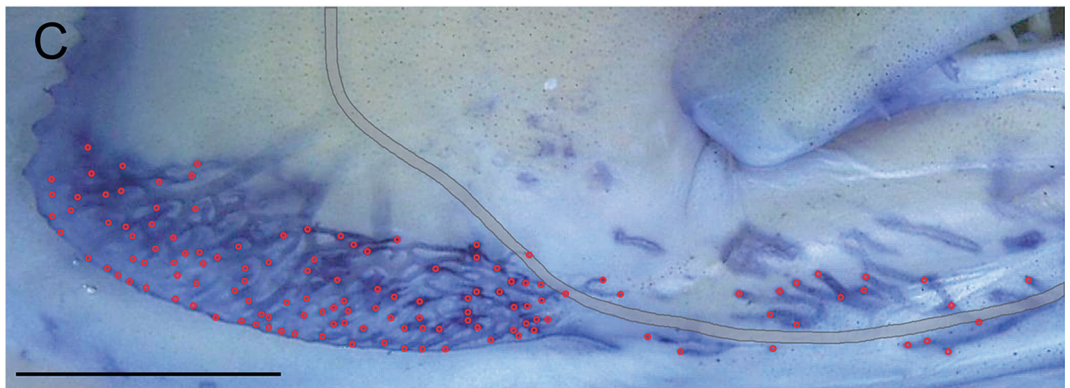
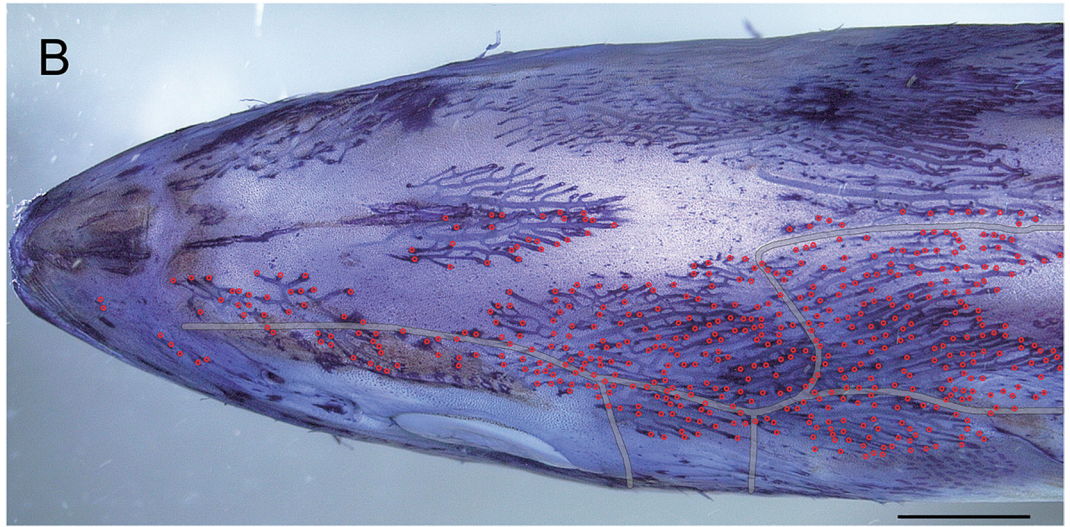
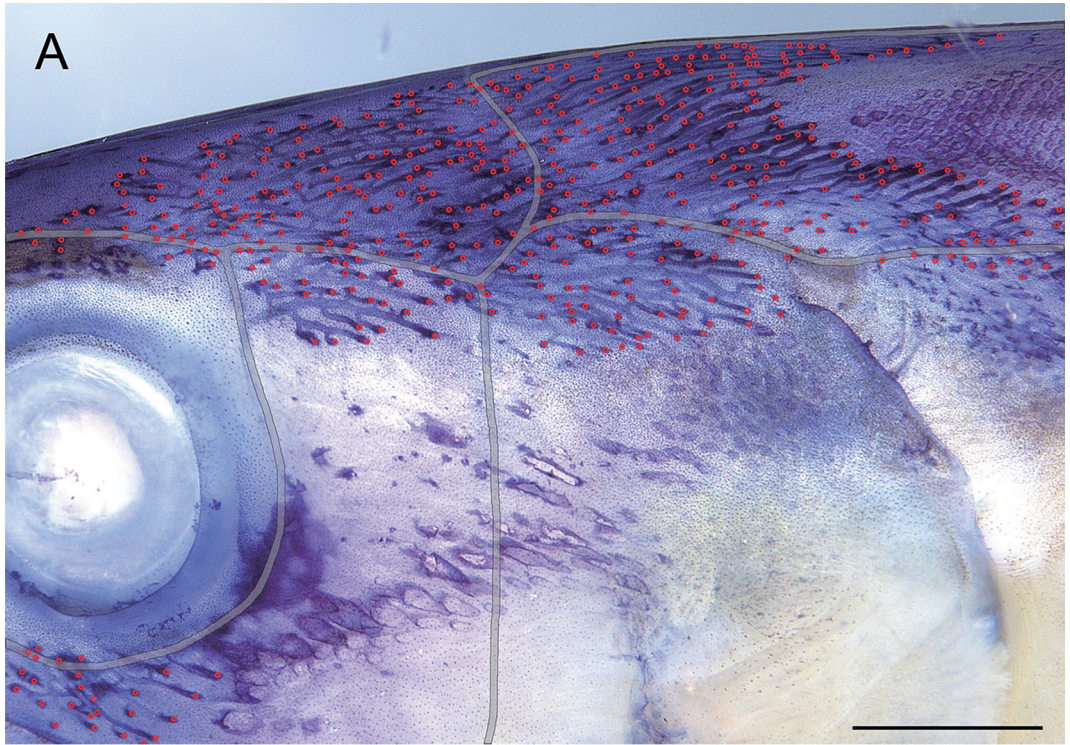
generally being identical to that of dominant water flow over the body surface when the fish is swimming forward. Accordingly, in-and-out flow within the cutaneous canals, as in the above example, is not possible because flow from the opposite direction (posterior to anterior) must be hypothesized.

Cutaneous canals and their pores in *S. niphonius* appear to function for effective water expulsion from the cephalic lateral line canals. When an individual of the species starts to swim, water within the canals begins to be sucked out from the above pores owing to the Bernoulli Effect (see experiment using artificial canals in a model fish in Abdel-Latif *et al.*, 1990). Branched canals and their pores apparently enhance such expulsion by providing additional routes and exits for water. These structures may therefore play an important role in the supply of a regulated water flow to the narrow main lateral line canals (housing neuromasts) relative to the swimming speed. Functional aspects of highly branched canals should be further studied with data on more teleostean taxa, including other scombrids.

Materials examined. Abbreviations in parentheses in the list of specimens refer to length and methods of examination: SL, standard length, CB, Cyanine Blue treated; D, dissected; DA, 2-Di-4-ASP treated; O, osmium tetroxide treated.

Scomberomorus niphonius, NSMT-P 108635 (1, 63.8 mm SL, CB, DA; lateral line canals also observed), NSMT-P 108636 (1, 59.1 mm SL, DA), NSMT-P 108637 (1, 65.0 mm SL, DA), NSMT-P 108638 (1, 60.7 mm SL, DA), NSMT-P 108639 (1, 45.0 mm SL, DA), NSMT-P 108640 (1, 59.7 mm SL, O), NSMT-P 108641 (1, 47.2 mm SL, D, O), NSMT-P 108642 (1, 51.0 mm SL, CB, D, O), NSMT-P 108643 (1, 57.5 mm SL, D; mainly osteological observations), NSMT-P 109133 (1, 51.6 mm SL, DA), NSMT-P 109134 (1, 161.7 mm SL, CB), NSMT-

Fig. 4. Highly branched lateral line canals and their pores on the head of *Scomberomorus niphonius* (NSMT-P 111568). — A, dorsolateral view of temporal portion (left side); B, dorsal view of head; C, ventrolateral view of posterior portion of lower jaw and adjacent area (right side). Specimen stained with Cyanine Blue. Open red circles and light gray lines show position of pores and main canals, respectively. Bars 5 mm.



P 109135 (3, 149.1–156.9 mm SL, CB), NSMT-P 109894 (1, 46.0 mm SL, DA), NSMT-P 109895 (1, 49.7 mm SL, DA), NSMT-P 109896 (1, 45.7 mm SL, DA), NSMT-P 109897 (1, 39.3 mm SL, DA), NSMT-P 109898 (2, 35.0–43.8 mm SL, DA), NSMT-P 109899 (2, 39.4–41.3 mm SL, DA), NSMT-P 109900 (1, 34.5 mm SL, DA), NSMT-P 109901 (1, 39.0 mm SL, DA), NSMT-P 109902 (1, 42.7 mm SL, DA), NSMT-P 109903 (1, 38.3 mm SL, DA), NSMT-P 109904 (1, 35.3 mm SL, DA), NSMT-P 109905 (1, 37.4 mm SL, DA), NSMT-P 109906 (1, 38.2 mm SL, DA), NSMT-P 111568 (1, 156.5 mm SL, CB).

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