48 Parrinello, N., and Rindone, D., Studies on the natural hemolytic system of the annelid worm *Spirographis spallanzanii viviani* (Polychaeta). Devl comp. Immun. *5* (1981) 33–42.

49 Phipps, D., Menger, M., Chadwich, J. S., and Aston, W. P., A cobra venom factor (CVF)- induced C3 convertase activity in the hemolymph of *Gallesia mellonella*. Devl comp. Immun. *11* (1987) 37–47.

50 Platts-Mill, T. A., and Ishizaka, K., Activation of the alternative pathway of human complement by rabbit cells. J. Immun. *113* (1974) 348–358.

51 Podack, E. R., and Tschopp, J., Circular polymerization of the ninth component of complement. J. biol. Chem. *257* (1982) 15204–15212.

52 Podack, E. R., Assembly of two types of tubules with putative cytolytic function by cloned natural killer cells. Nature *302* (1983) 442–445.

53 Podack, E. R., Young, J. D. E., and Cohn, Z. A., Isolation and biochemical functional characterization of perforins from cytolytic T-cell granules. Proc. natl Acad. Sci. USA *82* (1985) 8629–8638.

54 Reich, E., Rifkin, D. B., and Shaw, E., Protease and biological control. Cold Spring Harbor Laboratory, Cold Spring Harbor, New York 1975.

55 Roch, P., Protein analysis of earthworm coelomic fluid. I. Polymorphic system of the natural hemolysins of *Eisenia foetida Andrei*. Devl comp. Immun. *3* (1979) 588–608.

56 Roch, P., Valembois, P., Davant, N., and Lassegues, M., Protein analysis of earthworm coelomic fluid, II. Isolation and biochemical characterization of the *Eisenia foetida* Andrei factor (EFAF). Comp. Biochem. Physiol. *698* (1981) 829–836.

57 Roch, P., Davant, N., and Lassegues, M., Isolation of agglutinins and lysins form earthworm coelomic fluid by gel filtration followed by chromatofocusing. J. Chromat. *290* (1984) 231–235.

58 Roch, P., Canicatti, C., and Valembois, P., Interaction between the hemolytic system of the earthworm *Eisenia foetida Andrei* and the SRBC membrane. Biochim. biophys. Acta *983* (1989) 193–198.

59 Ryoyama, K., Studies on the biological properties of coelomic fluid of sea urchin. I. Naturally occurring hemolysin in sea urchin. Biochim. biophys. Acta *320* (1973) 157–165.

60 Tack, B. R., Harrison, R. A., Janatova, J., Thomas, M. L., and Prahl, J. W., Evidence for presence of an internal thioester bound in third component of human complement. Proc. natl Acad. Sci. *77* (1980) 5464–5472.

61 Tschopp, J., Circular polymerization of the membranolytic ninth component of complement. J. Biol. Chem. *259* (1984) 10569–10573.

62 Tschopp, J., Masson, D., and Stanley, K. K., Structural/function similarity between proteins involved in complement and cytotoxic T-lymphocyte-mediated cytolysis. Nature *322* (1986) 831–834.

63 Tschopp, J., Masson, D., and Schafer, S., Inhibition of the lytic activity of perforin by lipoproteins. J. Immun. *137* (1986) 1950–1953.

64 Tschopp, J., Masson, D., Schafer, S., Peitsch, M., and Preissner, K. T., The heparin binding domain of S/protein/Vitronectin binds to complement components C7, C8 and C9 and perforin from cytolytic T-cells and inhibits their lytic activities. Biochemistry *27* (1988) 4103–4109.

65 Tuan, T. L., and Yoshino, T. P., Natural hemolysin in the hemolymph of freshwater bivalve *Corbicula fluminea*. Devl comp. Immun. suppl 3 (1984) 193.

66 Tuckova, L., Rejnek, J., Sima, P., and Ondiejova, R., Lytic activities in coelomic fluid of *Eisenia foetida* and *Lumbricus terrestris*. Devl comp. Immun. *10* (1986) 181–189.

67 Valembois, P., Roch, P., Lassegues, M., and Cassand, P., Antibacterial activity of the hemolytic system from the earthworm *Eisenia foetida Andrei*. J. Invertebr. Path. *40* (1982) 21–27.

68 Valembois, P., Lassegues, M., Roch, P., and Vaillier, J., Scanning electron microscopic study of the involvement of coelomic cells in earthworm antibacterial defence. Cell Tissue Res. *240* (1985) 479–484.

69 Valembois, P., Roch, P., and Lassegues, M., Antibacterial molecules in Annelids, in: Immunity in Invertebrates, pp. 14–93. Ed. M. Brehelin. Springer Verlag, Berlin (1986).

70 Weinheimer, P. F., Evans, E. E., Stround, R. M., Acton, R. T., and Painter, B., Comparative immunology: Natural hemolytic system of the spiny lobster, *Panulirus arguus*. Proc. Soc. exp. Biol. Med. *130* (1969) 322–326.

71 Weinheimer, P. F., Acton, R. T., Cushing, J. E., and Evans, E. E., Reactions of sipunculid fluid with erythrocytes. Life Sci. *9* (1970) 145–151.

72 Yoshino, T. P., and Tuan, T. L., Soluble mediators of cytolytic activity in hemocytes of the asian clam *Corbicula fluminea*. Devl comp. Immun. *9* (1985) 515–522.

73 Young, J. D. E., Cohn, Z. A., and Podack, E. R., The ninth component of complement and the pore-forming protein (perforin 1) from cytotoxic T-cells: Structural, immunological and functional similarities. Science *233* (1986) 184–190.

74 Ziccardi, R. J., The three components of human complement (C1): Activation and control, in: Complement, pp. 167–184. Eds H. J. Müller-Eberhard and P. A. Miescher. Springer Verlag, Berlin 1985.

0014-4754/90/030239-06$1.50 + 0.20/0

Research Articles

The morphology of the lateral line system in 3 species of Pacific cottoid fishes occupying disparate habitats

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Received 30 June 1989; accepted 24 August 1989

Summary. The superficial neuromasts in *Leptocottus armatus* (Pacific staghorn sculpin) and *Oligocottus maculosus* (tidepool sculpin) are depressed below the rim of an epidermal collar, whereas the superficial neuromasts in *Psychrolutes paradoxus* (tadpole sculpin) are surrounded by a pair of hillocks. The lateral line canal system appears identical across these species, whereas the system of superficial neuromasts shows some intraspecific variation. The sand-living *Leptocottus* has a more highly developed system of superficial neuromasts than *Oligocottus*, which lives in a rocky habitat. The present results support the correlation between lateral line system morphology and habitat features previously postulated by Dijkgraaf[1].

Key words. Cottoid fishes; mechanoreceptive lateral line system; neuromasts; scanning electron microscopy.

Cottoid fishes mainly live in marine habitats of the northern hemisphere and are most diverse along the North Pacific coastline and in Lake Baikal[2]. They are only partially scaled and bear spines which may be arranged in rows or scattered irregularly on their body surface[3,4]. Cottids are benthic, inshore fishes and feed on small invertebrates[2,4,5].

The three species investigated in this study live in distinctly different habitats and are, therefore, exposed to different types of mechanical stimuli. *Leptocottus armatus* (Pacific staghorn sculpin) lives on sand, is often buried[4] and exposed to slow water currents; in contrast, *Psychrolutes paradoxus* (tadpole sculpin), which lives on hard substrates, and *Oligocottus maculosus* (tidepool sculpin), which inhabits tidepools in the intertidal zone[4], are exposed to turbulent water flows. The distinct, habitat-related current regimes lead one to expect morphological differences in the mechanosensory lateral line systems of these species.

Dijkgraaf[1] compared the ecology of fish species with the morphology of their lateral line systems. He postulated that fish that inhabit turbulent waters should possess few superficial neuromasts but a well-developed system of lateral line canals. In contrast, fish that inhabit quiet waters should possess many superficial neuromasts and only a reduced (or in several cases even absent) canal system. One way to test this hypothesis is to examine the lateral line systems of closely related species which inhabit different habitats. The pacific cottids are one such group.

The lateral line systems of *Leptocottus, Psychrolutes* and *Oligocottus* have been investigated by histology and scanning electron microscopy (SEM). The results are compared with descriptions given for other cottoid species[6-9] and actinopterygians in general[10,11].

Material and methods

Collection of fish. Specimens of *Leptocottus armatus* were collected at Westcott Bay, and *Psychrolutes paradoxus* and *Oligocottus maculosus* were collected at Dead Man Bay, San Juan Island, Washington. The fish were kept in seawater tanks until fixation, and the species were identified on the basis of descriptions by Hart[5] and Eschmeyer et al.[4]. At least four specimens were used from each species. All were adults with relatively little variation in mean standard length (*Leptocottus*: 18.0 ± 4 cm; *Psychrolutes*: 5.5 ± 1 cm; *Oligocottus*: 7.0 ± 2 cm).

Preparation for histology. Animals used for histology were anesthetized in a 0.1 % solution of MS 222 (tricaine methanesulfonate; Sigma) and then fixed by immersion in 4% paraformaldehyde in 0.1 M phosphate buffer. After at least two days of fixation, the skin was removed with Dumont watchmaker forceps and tungsten needles, dehydrated in graded ethanols, embedded in Paraplast and sectioned with a rotary microtome at 10 µm. In order to reveal the acid mucopolysaccharides of the epidermal mucous cells, sections were stained with 0.1 % toluidine blue (Sigma) and counterstained with methylene blue (0.5 %) (Sigma) or neutral red (1 %) (Sigma). Cupulae of superficial and canal neuromasts were visualized by staining whole paraformaldehyde-fixed animals with 0.1 % methylene blue. Specimens were photographed on Kodak Pan F film with a Leitz Duoplan microscope, equipped for Nomarski interference-phase-contrast (IPC) microscopy. The lateral line canals were traced by dissection of the epidermis, and the position of the canal neuromasts was visualized by staining the opened canals with 0.5 % methylene blue.

Preparation for SEM. Following anesthesia with MS 222 (Sigma) and fixation by immersion for at least two days in 4% glutaraldehyde, individuals used for scanning electron microscopy (SEM) were decapitated and cut in half longitudinally. They were subsequently dehydrated with a graded series of dimethoxypropane (Sigma), critical-point dried (CPD) and sputter-coated with a 40 Å layer of gold-platinum and examined in a JEOL JSM-35C scanning electron microscope at 15 kV or a Hitachi S 405 A scanning electron microscope at 25 kV. The mapping of the lateral line system was accomplished either by making montages of SEM photographs or by making montages of photomicrographs, taken from CPD-specimens with a Wild M 400 photomacroscope. All numbers for canal pores and superficial and canal neuromasts are given for a single side of the specimens.

Systematic terminology. Leptocottus armatus (Pacific staghorn sculpin), *Psychrolutes paradoxus* (tadpole sculpin) and *Oligocottus maculosus* (tidepool sculpin) belong to the superfamily Cottoidea (Scorpaeniformes)[12]. Several authors[4,5,13-17] place *Psychrolutes* within the family Cottidae. All other Cottidae, however, possess six branchiostegal rays, whereas *Psychrolutes* has seven[3]. Consequently a number of investigators[3,12,18-20] place *Psychrolutes* in a separate monotypic family, the Psychrolutidae. This study follows Yabe's[12] phylogenetic and osteological analysis and recognizes the families Cottidae and Psychrolutidae as two of six monophyletic groups which form the superfamily Cottoidea.

Results

The lateral line system of *Leptocottus armatus, Psychrolutes paradoxus* and *Oligocottus maculosus* includes the lateral line canals and the superficial neuromasts. The description first notes similarities and then differences of the lateral line morphology.

Lateral line canal system. Similarities. The canal system in the three species consists of supraorbital, supratemporal, infraorbital and mandibular-preopercular canals on the head, and a single canal on the trunk (fig. 1), with no

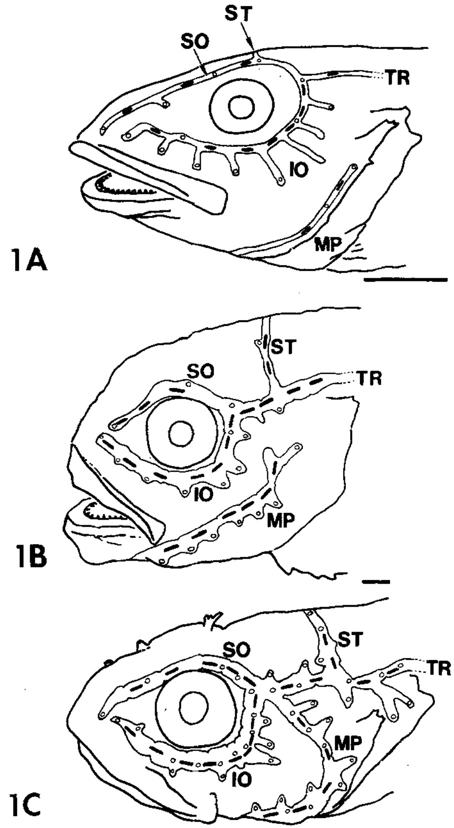

Figure 1. Distribution of the cephalic lateral line canals in *Leptocottus* (A); *Psychrolutes* (B) and *Oligocottus* (C). IO, infraorbital canal; MP, mandibular-preopercular canal; SO, supraorbital canal; ST, supratemporal canal; TR, trunk canal. Solid black lines = canal neuromasts and their orientation (length is not to scale); open circles = canal pores. The canal constrictions are not shown. Scale bars: A = 10 mm; B, C = 1 mm.

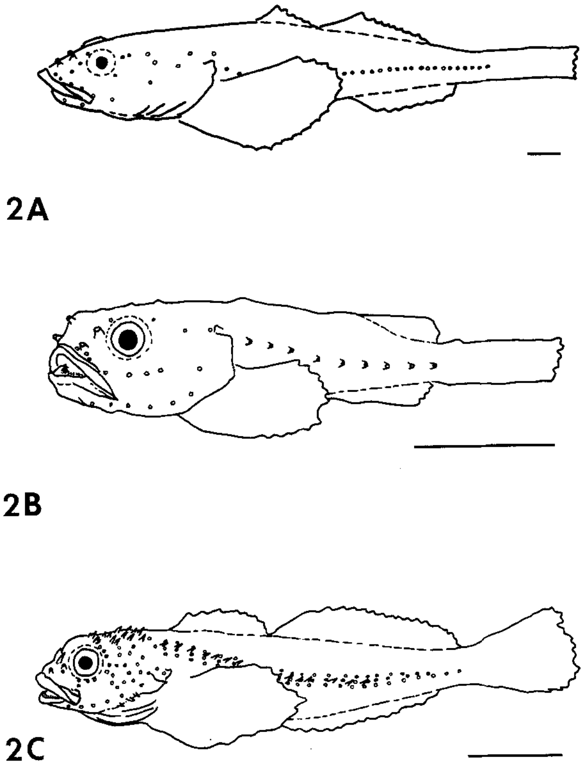

Figure 2. Distribution of the canal pores in *Leptocottus* (A); *Psychrolutes* (B) and *Oligocottus* (C). Scale bars = 10 mm.

variation among individuals of a given species. The only connection of the canal systems of the two sides of the body is established by the supratemporal commissure (fig. 1).

The cephalic canals are embedded in the nasal, frontal, parietal, suborbital, preopercular and hyomandibular bones on their medial side and covered by the epithelium which is perforated by the canal pores on their lateral side (fig. 2). In all three species, the trunk canal is slightly arched over the pectoral fin and continues to the base of the caudal fin along the horizontal septum. As scales are absent, the trunk canals of all three species are embedded in soft tissue surrounded by dermal bones.

The canal neuromasts lie at the medial base of the canal. The longitudinal axis of the sensory strip, containing the sensory hair cells and supporting cells covered by the overlaying cupula, lies parallel to the axis of the canal (fig. 1). The morphological and functional polarization of the neuromasts, as defined by Flock and Wersäll[21], is still unknown because the SEM preparations failed to reveal hair cell orientation in the canal neuromasts.

The size of the canal neuromasts is in the same range in all three species, and the cephalic neuromasts (longitudinal axis: 450–500 μm) are consistently larger than those of the trunk canal (longitudinal axis: 200–250 μm). The canal neuromasts have a significantly larger diameter than the superficial neuromasts (see below). When stained in fresh preparations with methylene blue, the cupulae of the canal neuromasts show a keel-like aspect and extend almost through the entire canal diameter (400–500 μm), perpendicular to the canal-axis.

Dissimilarities. The species differ in canal configuration and number of canal pores. Only *Oligocottus* has the mandibular-preopercular canal fused with the other canals, and its head canals show secondary and tertiary branching into caniculi with terminal pores (fig. 1 C). This species has many more constrictions in the cephalic canals than do the other two species. The supratemporal commissure of *Leptocottus* fuses with the supraorbital canal but that of *Psychrolutes* and *Oligocottus* joins the trunk canal caudal to the junction of the supraorbital and infraorbital canals (fig. 1). *Leptocottus* and *Psychrolutes* have trunk canal pores flush with the surface, whereas those of *Oligocottus* open at the tip of short protruding tubules (150–200 μm long) that are connected by caniculi to secondary trunk canal openings, located dorsal and ventral to each main trunk canal pore (fig. 3 b).

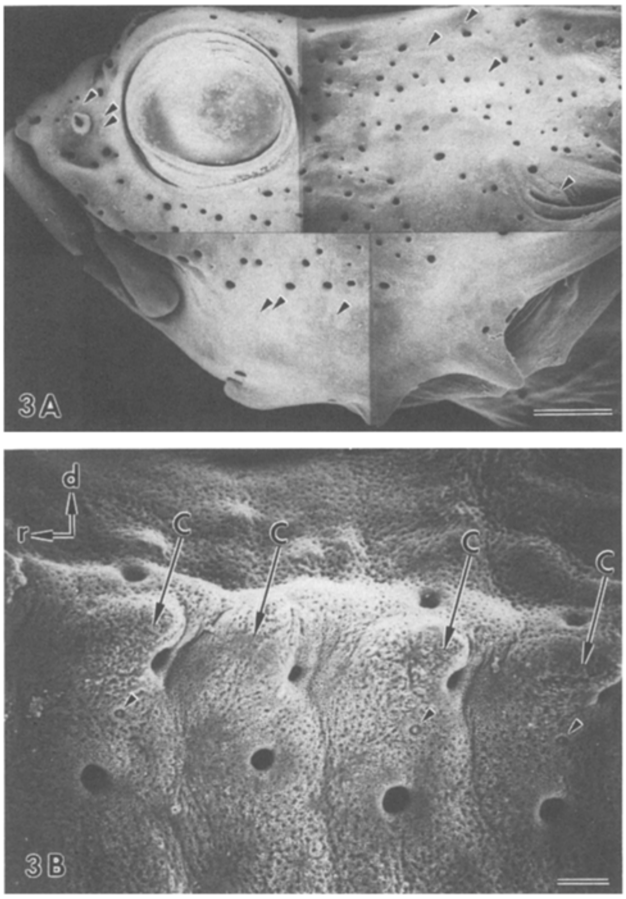

Figure 3. SEM preparations, illustrating canal pores and superficial neuromasts in *Oligocottus*. *A* Cephalic canal pores and superficial neuromasts (arrowheads). Scale bar = 1 mm. *B* Canal pores and superficial neuromasts (arrowheads) on the trunk. C, cirrus; r, rostral; d, dorsal. Scale bar = 100 µm.

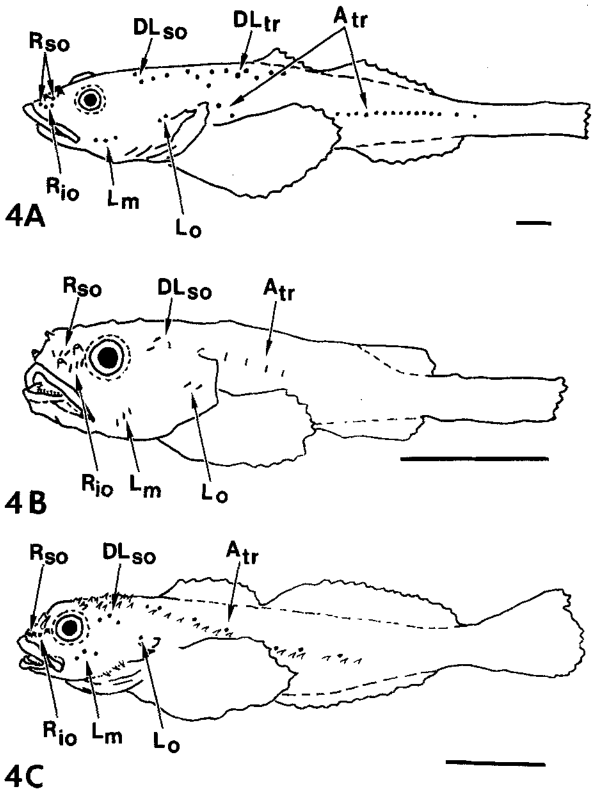

Figure 4. Distribution of superficial neuromasts (diameter is not to scale) in *Leptocottus* (A), *Psychrolutes* (B) and *Oligocottus* (C). Note the orientation of the superficial neuromasts in *Psychrolutes*. A_{tr}, accessory trunk line; DL_{so}, dorsal line of the supraorbital line; DL_{tr}, dorsal line of the trunk line; L_m, mandibular line; L_o, opercular line; R_{io}, replacement line of the infraorbital line; R_{so}, replacement line of the supraorbital line. Scale bars = 10 mm.

The number and position of the head- and trunk canal pores are constant within *Leptocottus* and *Psychrolutes*, while considerable variability was observed in the position of head and trunk canal pores and the number of trunk canal pores in *Oligocottus*. *Oligocottus* has more cephalic canal pores (53) and cephalic canal neuromasts (27) than *Psychrolutes* (23 canal pores and 23 canal neuromasts) and *Leptocottus* (17 canal pores and 16 canal neuromasts) (figs 1, 2, 3A). The number of trunk canal neuromasts has not been measured due to heavy ossification of the trunk canals. However, as *Oligocottus* has significantly more trunk canal pores (66 + 4/ − 5; n = 4) than *Leptocottus* (32) and *Psychrolutes* (9), it may also have more trunk canal neuromasts than the other two species.

Superficial neuromasts

Similarities. The nomenclature provided by Janssen et al.[9] and Coombs et al.[10] defines seven groups of superficial neuromasts in the three species (fig. 4): Supra- (R_{so}) and infraorbital (R_{io}) replacement lines, mandibular (L_m) and opercular (L_o) lines, dorsal supraorbital (DL_{so}) line and dorsal trunk replacement (DL_{tr}) line (only in *Leptocottus*), and an accessory trunk (A_{tr}) line. The number of superficial neuromasts, counted in at least three critical-point dried specimens within each species, differs considerably among the three species. The number is, however, constant among the specimens investigated within each species with the exception of the superficial neuromasts on the trunk of *Oligocottus*. The cupulae of superficial neuromasts measured 200–250 µm in all three species.

Dissimilarities. *Leptocottus* has 50 (± 2; n = 3) superficial neuromasts, whereas *Psychrolutes* and *Oligocottus* have 18 and 16, respectively (fig. 4). Approximately half of the superficial neuromasts in *Leptocottus* were located on the dorsal part of the body (dorsal lines of supraorbital and dorsal trunk lines), whereas in the two other species only about 20% of the superficial neuromasts were located dorsally.

SEM preparations reveal that the superficial neuromasts in *Leptocottus* and *Oligocottus* are sunk below the rim of an epidermal collar (figs 5, 6). The sensory strip of each

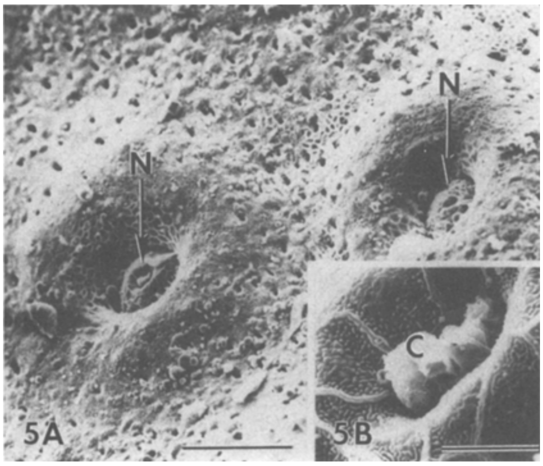

Figure 5. SEM preparation showing the morphology of superficial neuromasts in *Leptocottus*. C, cupula; N, neuromast. *B* is an enlargement of the left neuromast in *A*. Scale bars: *A* = 100 µm; *B* = 10 µm.

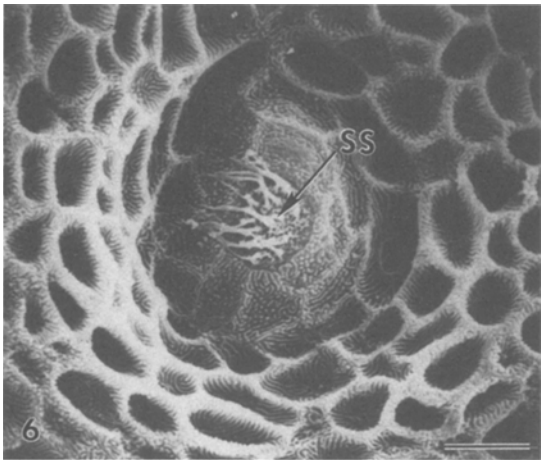

Figure 6. SEM preparation showing the morphology of a superficial neuromast in *Oligocottus*. SS, sensory strip. Scale bar = 10 µm.

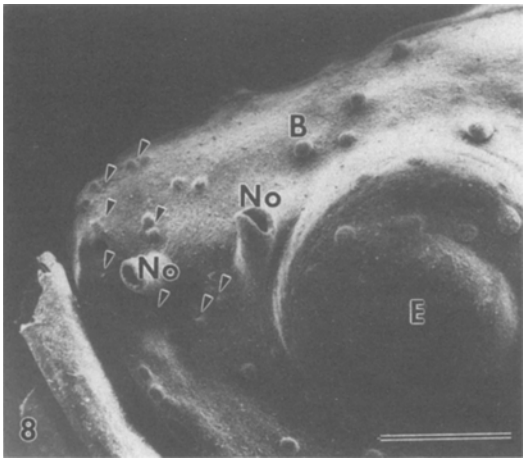

Figure 8. SEM preparation showing bumps and superficial neuromasts (arrowheads) on the head of *Psychrolutes*. Note: single bumps do not abut on superficial neuromasts. B, bump; E, eye; No, nostril. Scale bar = 1 mm.

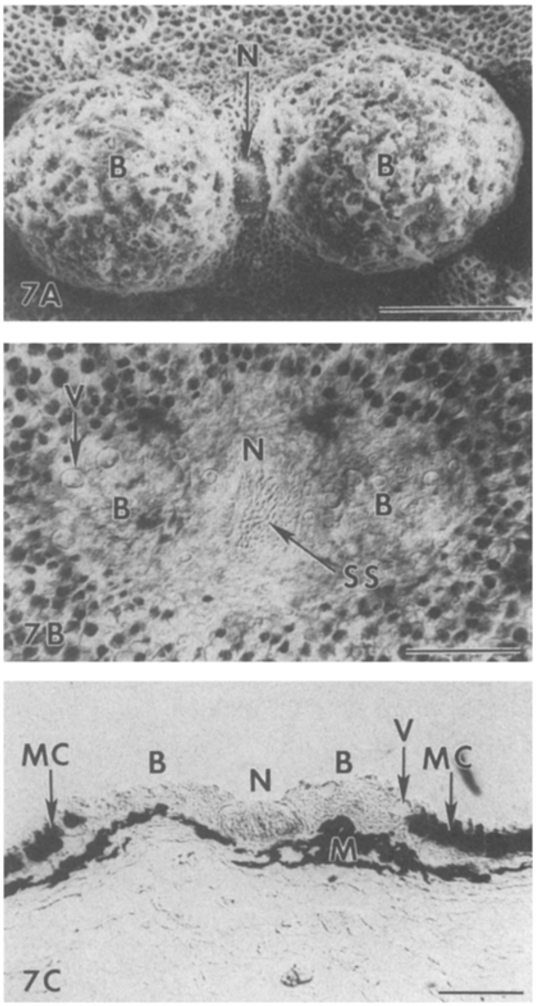

Figure 7. Superficial neuromasts of *Psychrolutes*. *A* SEM picture of two bumps which surround a neuromast. *B* Skin preparation of an epidermal area, containing a superficial neuromast, stained with toluidine blue and seen with Nomarski optics. Note the vacuole-like structures in the bumps. *C* Toluidine blue stained Paraplast section across a neuromast and adjacent bumps. B, bump; M, melanophore; MC, mucous cells; N, neuromast; SS, sensory strip; V, vacuole-like structure. Scale bars = 100 µm.

neuromast is circular with a diameter between 10 and 15 µm. In contrast, the sensory strip of the superficial neuromasts in *Psychrolutes* (fig. 7) has a distinct orientation, usually perpendicular to the nearest canal. Each of these superficial neuromasts lies between two hillock-like protrusions, or 'bumps', situated lateral to its longitudinal axis. The length of the longitudinal axis of the sensory strip is 75–100 µm, whereas the hillocks are circular, 150–200 µm in diameter and 100–150 µm high. Single hillocks occur as well, but are not associated with superficial neuromasts (fig. 8). On the other hand, no superficial neuromasts were found which were not associated with two hillocks. Histological preparations of bumps revealed that, in contrast to the surrounding epithelium, they are free of acid mucus-containing cells, and incorporate large vacuole-like spaces (fig. 7). Like other cottoids, *Leptocottus* and *Oligocottus* have small epidermal projections, or cirri, on the body surface[4]. The arrangement of these cirri is especially obvious along the trunk line of *Oligocottus* (figs 3B, 4C): A single cirrus lies next to each canal pore and can be up to 250 μm long (figs 2C, 3B). Histologically, the cirri show a typical epidermis structure with mucus cells and a layer of melanophores below the basal lamina, but no specialized sensory cells.

Discussion

Morphology. In agreement with earlier reports on other cottoid fish[6,9], the number of canal neuromasts on the head and the number of superficial neuromasts on the body are constant within each species; only *Oligocottus* shows variation in the number of its superficial trunk neuromasts. *Cottus bairdi*, however, may also show variation in the number of cephalic neuromasts (S. Coombs, pers. comm.).

Also, the pattern of the five lateral line canals in *Leptocottus, Psychrolutes* and *Oligocottus* is similar to that of other cottoid fish[6-9]; only in the Eurasian cottoid species *Cottus cognatus*, has intraspecific variation of the supratemporal commissure been reported[7].

The supratemporal commissure is the only connection between the two halves of the cephalic canal system in the three species examined. All members of the genus *Cottus*, however, have two such connections[6-9].

The three cottoid species investigated in this study show four similarities with *Cottus bairdi*[9]: 1) The longitudinal axis of the canal neuromasts is parallel to the canal-axis, whereas the axis of superficial neuromasts adjacent to canals is perpendicular to the axis of the canal neuromasts; 2) canal neuromasts are elongated, whereas superficial neuromasts are generally circular in shape; 3) superficial neuromasts are significantly smaller than canal neuromasts, which is consistent with observations by other authors in several adult actinopterygians[1,10,21]; 4) trunk canal pores are elevated to the tip of tubules (only in *Oligocottus*; also described in *Cottus gobio* in Starmach[6]) and 5) the trunk and the cephalic canals are embedded in bone and covered by soft tissue. The embedding of all cephalic canals in cranial bones has also been reported for several other cottoid species[3,6-9,12,19].

The height of the hillocks which lie adjacent to the superficial neuromasts in *Psychrolutes* (figs 7, 8) is smaller than that of the cupula, so they probably do not serve a protective function exclusively. A similar argument may be made for the cirri in *Leptocottus* and *Oligocottus*. According to Bernoulli's law the hillocks increase the flow velocity above the neuromast and may thus enhance the stimulus. Similar structures surrounding superficial neuromasts in *Solea vulgaris* are believed to channel the water current over the receptor[22].

Functional aspects. The rationale for a functional explanation of the morphology of the lateral line system in actinopterygians was provided by Dijkgraaf[1]. Based on an extensive, comparative study, he recognized that fish living on the bottom of quiet waters[1], or swimming slowly[24], have a reduced canal system with many superficial neuromasts, whereas fish living in turbulent waters[1] or swimming rapidly and/or persistently[24] have a well-developed canal system and only a few superficial neuromasts. Superficial neuromasts are directly affected by the flow of water at varying angles to the body surface. On the other hand, canal neuromasts can only be stimulated by local displacements of the canal fluid, which are maximal when the effective current is parallel to the body surface[24]. Dijkgraaf[1] states that canals protect neuromasts, which are sensitive to weak, local water displacements, not only against mechanical destruction but also against a constant overstimulation if the fish is exposed to strong water currents.

The results of this study, showing the quantitative differences of the lateral line components of the three species in reference to their different life styles, do support Dijkgraaf's hypothesis: *Leptocottus* which lives in a quiet environment has about three times as many superficial neuromasts as does *Oligocottus* (fig. 4) which inhabits a turbulent environment, whereas *Oligocottus* possesses three times as many canal pores as does *Leptocottus* (fig. 2).

A first explanation for the different degrees of the development of the two components of the lateral line system may be derived from the physical constraints associated with differences of the habitats occupied by the three species. The superficial neuromasts of *Oligocottus*, which is frequently subjected to turbulent waters of the littoral zone, are much more exposed to destruction than those of *Leptocottus*, which lives in quiet waters. The optimum strategy for protecting the lateral line receptors therefore may be to enclose them in canals and to reduce the number of superficial neuromasts to a minimum[1,25].

Several reports further document habitat-related differences of the lateral line system morphology in other taxa. Jakubowski[26] showed that several genera of the family Percidae, which live in turbulent waters, have a significantly higher canal specialization (i.e. secondary and tertiary branching of the canals) and fewer superficial neuromasts than representatives of genera living in quiet waters. Some fish living in the deep sea or in caves lack a canal system entirely[25]. Taranets[3] found a reduction of the number of canal pores in several cottoid families that show little mobility, while Janssen et al.[9] report an ontogenetic reduction of superficial neuromasts in adult *Cottus bairdi*. This is believed to be correlated with a change from exposure to more turbulent waters in juvenile stages to quiet water habitats in adults[9].

A second explanation for the differences in the lateral line morphology of the three species investigated may be derived from the different physiological properties of superficial and canal neuromasts: Canal neuromasts respond optimally to higher frequencies than do superficial neuromasts. Münz[27] reports that the superficial neuromasts of the cichlid *Sarotherodon niloticus* are most sensitive to stimuli within 10–70 Hz, whereas the canal neuromasts respond best to frequencies of 100–200 Hz. Similarly Kroese and Schellart[28] find that superficial neuromasts in the trout *Salmo gairdneri* show a maximum sensitivity to water displacement at a frequency of 36 Hz, whereas canal neuromasts respond best at 93 Hz.

The size and shape of the cupula are believed to cause different response properties of canal and superficial neuromasts[9, 27, 28]. Based on the observation that canal neuromasts respond best to higher frequencies than do the superficial neuromasts, Münz[27] agrees with earlier investigators[1, 25] who suggested that canals suppress low-frequency noise produced by water currents. If these results could be reproduced for other species living in various habitats, they would strongly support the claim that fish with a more highly developed canal system have a competitive advantage in more turbulent habitats.

In conclusion, the distribution of superficial and canal neuromasts in the lateral line system of the three cottoid species *Leptocottus armatus, Psychrolutes paradoxus* and *Oligocottus maculosus* is in accordance with Dijkgraaf's[1] observations that turbulent water conditions and fast-swimming behavior are correlated with a well-developed canal system, whereas quiet water conditions and slow-swimming behavior are correlated with a well-developed system of superficial neuromasts. In addition, the fact that most of the superficial neuromasts in *Leptocottus* are located on the dorsal surface of the body appears to be related to its benthic life-style and its habit of burying itself in the sand.

The superfamily Cottoidae, whose members inhabit a wide variety of different habitats, thus appears to present an interesting group for further examination of form-function relationship in the lateral line system. Conclusive ecomorphological statements, however, will not be possible before more physiological data on the different functions of superficial and canal neuromasts are available.

Acknowledgments. I would like to thank T. E. Finger, S. Coombs, W. Heiligenberg, J. G. New and J. F. Webb for critically reading earlier versions of the manuscript and providing helpful comments. H. J. Karten kindly allowed me to use his Leitz Duoplan microscope. K. Liem and B. Miller stimulated the project with many interesting and refreshing discussions at the Friday Harbor Laboratories.

1 Dijkgraaf, S., Biol. Rev. *38* (1962) 51.
2 Nelson, J. S., in: Fishes of the World, p. 268. Ed. J. S. Nelson. Wiley & Sons, New York 1984.
3 Taranets, A. Y., Mus. Contr. Inst. Fish., Univ. of British Columbia, Vancouver *5* (1959) 1.
4 Eschmeyer, W. N., Herald, E. S., and Hammann, H., A Field Guide to Pacific Coast Fishes of North America, p. 158. Houghton Mifflin Company, Boston 1983.
5 Hart, J. C., Fish. Res. Bd Can. *180* (1973) 472.
6 Starmach, J., Acta biol. cracov. Ser. Zool. *11* (1968) 244.
7 Sideleva, V. G., J. Ichthyol. *19* (1979) 434.
8 Sideleva, V. G., J. Ichthyol. *20* (1980) 119.
9 Janssen, J., Coombs, S., Hoekstra, D., and Platt, C., Brain Behav. Evol. *30* (1987) 210.
10 Coombs, S., Janssen, J., and Webb, J. F., in: Sensory Biology of Aquatic Animals, p. 553. Eds J. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga. Springer, New York 1988.
11 Northcutt, R. G., in: The mechanosensory Lateral Line. Neurobiology and Evolution, p. 17. Eds S. Coombs, P. Görner and H. Münz. Springer, New York 1989.
12 Yabe, M., Memoirs of the Faculty of Fisheries. Hokkaido University. *32* (1985) 1.
13 Watanabe, M., Biogeogr. Soc. Japan, Natl. Sci. Mus. Tokyo (1960) 1.
14 McAllister, D. E., Bull. Nat. Mus. Can. Contr. Zool. *223* (1968) 58.
15 Bailey, R. C. R., Bond, C. E., Brooker, J. R., Lachner, E. A., Lea, R. N., and Scott, W. B., 3rd Am. Fish. Soc. Spec. Publ. *12* (1970) 1.
16 Richardson, S. L., and Washington, B. B., NOAA Tech. Rept. NMFS Circ. *430* (1980) 1.
17 Robins, C. R. R. M., Bailey, C. E., Brooker, J. R., Lachner, E. A., Lea, R. N., and Scott, W. B., Am. Fish. Soc. Spec. Publ. *12* (1980) 1.
18 Bolin, R. L., Stanford Ichthyol. Bull. *3* (1947) 153.
19 Nelson, J. S., Can. J. Zool. *60* (1982) 1470.
20 Flock, A., and Wersäll, J., J. Cell Biol. *15* (1962) 19.
21 Münz, H., Zoomorphologie *93* (1979) 73.
22 Appelbaum, S., and Schemmel, C., Mar. Ecol. Prog. Ser. *13* (1983) 29.
23 Rauther, M., Naples: Stazione Zoologica *36* (1925) 1.
24 Sand, O., in: Hearing and Sound Communication in Fishes, p. 459. Eds W. N. Tavolga, A. N. Popper and R. R. Fay. Springer, New York 1981.
25 Marshall, N. B., in: The Life of Fishes, p. 127. Ed. N. B. Marshall. World Publishing Company, Cleveland 1966.
26 Jakubowski, M., Acta biol. cracov. Zool. *10* (1967) 69.
27 Münz, H., J. comp. Physiol. A *157* (1985) 555.
28 Kroese, A. B. A., and Schellart, N. A. M., J. Physiol. *394* (1987) 13.

0014-4754/90/030244-07$1.50 + 0.20/0