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Ultrastructure of Saccular Epithelium Sensory Cells of Four Sculpin Fish Species (Cottoidei) of Lake Baikal in Relation to Their Way of Life

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Abstract—Various structural elements of the apical region of hair cells and their location in the saccular macula of four sculpin fish species (Cottoidei) of Lake Baikal—two oilfish species (big golomyanka *Comephorus baicalensis* and small golomyanka *C. dybowski*), Severobaikalsk yellowfin *Cottocomephorus alexandrae,* and stone sculpin *Paracottus knerii*—were studied by scanning electron microscopy. In stone sculpin *Paracottus knerii*, which inhabits the coastal areas and leads a benthic lifestyle, the diversity of hair cells (in terms of the height of kinocilium and stereocilia) is big than that in the secondary pelagic species big and small golomyankas and in Severobaikalsk yellowfin, which inhabits the near-slope areas. Stereocilia of hair cells of stone sculpin and Severobaikalsk yellowfin are shorter than in the other species studied. The presence of such cells in the macula can ensure the sensitivity to more high-frequency acoustic signals and facilitate their perception by fish against the background of low-frequency noises characteristic of the coastal zone of the lake.

Keywords: sculpin fishes (Cottoidei), Lake Baikal, environment, auditory system, hair cells, ultrastructure, sacculus

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INTRODUCTION

Fish are characterized by a great diversity of structural and functional features of the auditory apparatus (Popper et al., 1993; Rowe and Peterson, 2004). However, so far, only several researchers have linked the macro- and ultrastructure of the auditory epithelium (the macula) with the functional parameters of fish hearing (Salem and Zaghloul, 2001; Xue and Peterson, 2006; Smith et al., 2011). Important characteristics of hearing are the frequency of perceived sounds, their threshold amplitude, and the ability of fish to detect the direction of the sound source (i.e., directional hearing) (Platt and Popper, 1981; Rowe and Peterson, 2006). The mechanisms underlying directional hearing are associated with the structural characteristic of the sensory epithelium—that is the presence of local groups of receptor (hair) cells with a similar morphological polarization (Platt and Popper, 1981; Ricci et al., 2002; Kasumyan, 2005; Popper et al., 2005; Sapozhnikova et al., 2007). Morphological polarization is understood as an acentric location of the kinocilium on the apical surface of the hair cell, where the polarization vector is directed from the stereocilia to the kinocilium (Fig. 1).

The saccular macula of fish usually includes several zones within which all hair cells have a single polarization vector. The hair cells with different directions of polarization usually differ in the lengths of stereocilia and kinocilium. The sensory sensitivity of hair cells directly depends on the length of stereocilia: the larger the length, the greater the sensitivity of fish to low-frequency acoustic signals (Platt and Popper, 1981; Saunders and Dear, 1983; Sugihara and Furukawa, 1989; Lombarte and Fortuño, 1992; Ricci et al., 2002; Popper and Fay, 2011; Smith et al., 2011).

Extensive research of sculpin fishes (Cottoidei) has shown that they are convenient objects for the study of different types of adaptations and speciation of fishes in Lake Baikal (Sideleva, 2003). Since sculpin fishes account for as much as 70–80% of all fishes of the lake (Baikal is a golomyanka- and sculpin-rich water body), the knowledge of their characteristics is also of practical value. These fishes are characterized by a high endemism and a considerable diversity of morphological structure and way of life, which allowed them to populate various ecological niches of the lake (Taliev, 1955; Sideleva, 1982; Sideleva and Kozlova, 2010).

Previosly, we reported the schemes of location of areas with different morphological polarization of hair

Table 1. Characterization of the material used in the study

Species	Average total length (*TL*), mm	Average length of otoliths, mm	Age (by otoliths), years	Fishing depth, m	Number of fish, ind.
Big golomyanka	149 143	1.72 ± 0.002 1.93 ± 0.003	3+ 2+–3+	150–200 150–200	25 25
Small golomyanka	114 129	1.65 ± 0.004 1.71 ± 0.002	2+–3+ 2+	150–200 150–200	23 27
Severobaikalsk yellowfin	117 113	1.46 ± 0.007 1.63 ± 0.006	2+–3+ 3+	3–15 3–15	32 18
Stone sculpin	119 112	4.38 ± 0.021 3.94 ± 0.023	2+–5+ 3+–4+	1–6 1–6	15 35

Data for females and males are shown above and below the line, respectively.

cells in the macula of sculpin fishes of Lake Baikal with different ways of life (Sapozhnikova et al., 2007). The purpose of this study was to assess the diversity of the ultrastructure of the apical areas of the sensory cells of the saccular epithelium in sculpin fishes from Lake Baikal and to determine the relationship between the morphologic characteristics of the auditory system of fish and the acoustic characteristics of their habitat.

MATERIALS AND METHODS

To study the interspecific differences in the ultrastructure of the sensory saccular epithelium of sculpin fishes, we selected four species significantly different in their way of life: stone sculpin *Paracottus knerii* (a benthic fish occurring in the coastal and slope areas of the lake, which is most abundant at depths of up to 40–50 m), Severobaikalsk yellowfin *Cottocomephorus alexandrae* (a benthopelagic fish inhabiting near-slope areas mostly at depths from 10 to 250 m), big golomyanka *Comephorus baicalensis* and small golomyanka *C. dybowski* (secondary pelagic fishes inhabiting the entire water column of open areas of the lake to the maximum depths and performing seasonal and diurnal vertical migrations) (Taliev, 1955; Koryakov, 1972; Starikov, 1977). Fishes for the study were caught with gillnets with different mesh in June–October 2008 in the southern part of Lake Baikal near the Bol'shie Koty village. The characteristics of the material are summarized in Table 1.

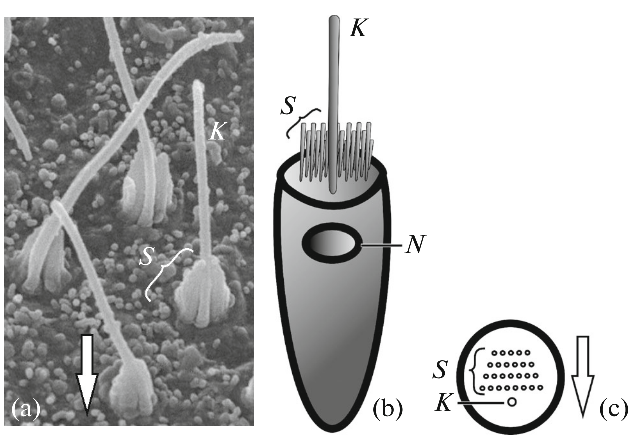

Fig. 1. Morphological polarization of hair cells: (a) fragment of the saccular macula of stone sculpin *Paracottus knerii* with hair cells with the same polarization vector (scanning electron microscopy); (b, c) scheme of location of the kinocilium and stereocilia on the apical surface of the hair cell ((b) side view and (c) top view; (↓) polarization vector (from the stereocilia to the kinocilium). Designations: *S*—stereocilia; *K*—kinocilium; *N*—cell nucleus.

Immediately after catching, the skull of the fish was opened from the ventral side, the brain was removed, the otic capsules were exposed, and the right and left labyrinths were removed with tweezers. Then, the sacculus, together with the sagitta (otolith), were isolated, fixed in 2.5% glutaraldehyde in 0.1 M phosphate buffer (pH 7.4) for 3 h, washed with the same buffer for 5 min, post-fixed in 1% osmium tetroxide for 12 h, and dehydrated in a series of increasing ethanol concentrations (30, 50, 70, and 98%) for 10 min in each. Then, the saccular sensory epithelium was separated from the otolith under a binocular, embedded in epoxy resin, and cut with an ultramicrotome (Leica Ultracut R, Austria) into 70 nm thick sections, which were examined using a LEO 906 E transmission electron microscope (Germany).

For the studies using an SEM-525M scanning electron microscope (Philips, Netherlands), the otoliths and the saccular sensory epithelium, which was fixed as described above and dehydrated in a series of increasing ethanol concentrations, were dried at a critical point using a Balzers CPD 030 instrument and sputtered with gold.

For the morphometric analysis of the sensory epithelium, 30 to 50 images in increments of 30 μm were prepared. The length, width, and area of the macula and the length of kinocilia and stereocilia were calcu-

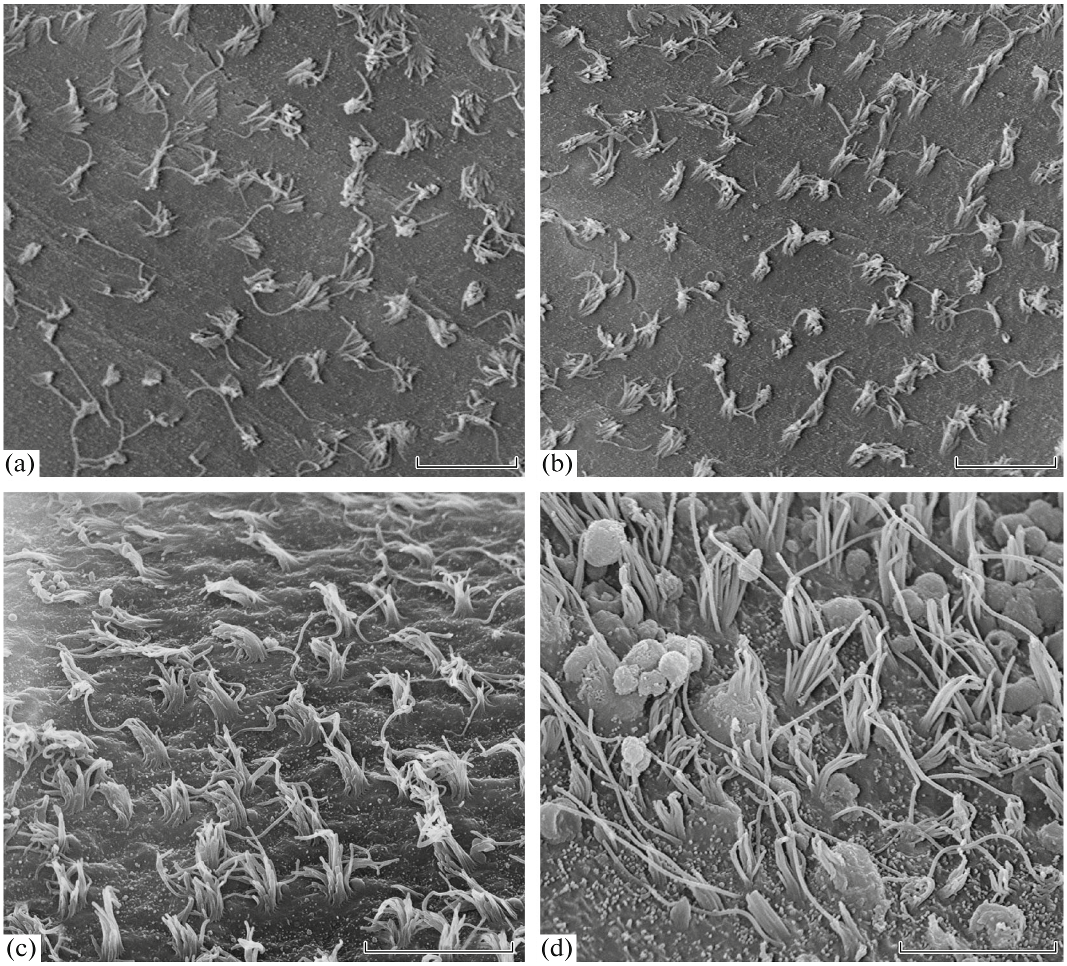

Fig. 2. Density of the hair cells in the peripheral part of the saccular macula of (a) big golomyanka *Comephorus baicalensis*, (b) small golomyanka *C. dybowski*, (c) Severobaikalsk yellowfin *Cottocomephorus alexandrae,* and (d) stone sculpin *Paracottus knerii*. Here and in Figs. 3 and 5: scanning electron microscopy, scale—10 μm.

lated using the Image-Pro Plus software. The length of each macula was measured between its rostral and caudal parts, and the width of the macula was determined for its three parts (rostral, central, and caudal). The ratios of areas of the different macula regions were calculated in relation to its total area and shown in percent.

The sensory cells were classified by cluster analysis, including *k*-means and hierarchical clustering methods, using the Statistica 8.0 software. The quantitative index of similarity of hair cells belonging to the same cluster was calculated based on the maximum and minimum lengths of stereocilia, length of the kinocilium, number of stereocilia in cell, and the thickness of stereocilia and kinocilia.

RESULTS

In the studied species, the saccular macula was located on the medial side of the otolith organ; it had an elongated shape and was oriented in the rostrocaudal direction. The length of the macula in big golomyanka was 1.295 ± 0.008 mm; in small golomyanka—1.380 ± 0.011 mm; in stone sculpin—1.670 ± 0.012 mm; and in Severobaikalsk yellowfin was 1.020 ± 0.006 mm. The maximum width of the macula in big and small golomyankas was measured in the rostral part and reached 0.230 ± 0.001 and 0.198 ± 0.001 mm, respectively. At the caudal end, the macula of these species narrowed to 0.150 ± 0.001 and 0.114 ± 0.002 mm, respectively; in the central part, the macula narrowed to 0.160 ± 0.002 and 0.138 ± 0.003 mm, respectively. The maximum width of the macula in stone sculpin (0.190 ± 0.001 mm) and Severobaikalsk yellowfin (0.120 ± 0.001 mm) was observed in the central part, and the minimum width (0.120 ± 0.001 and 0.094 ± 0.001 mm, respectively)—in the caudal part.

The saccular macula of the studied species included the hair (receptor) cells and the supporting microvillar epithelial cells. The shift of the sagitta to the macula was limited by the otolith membrane. The number of hair cells per unit of the sensory epithelium

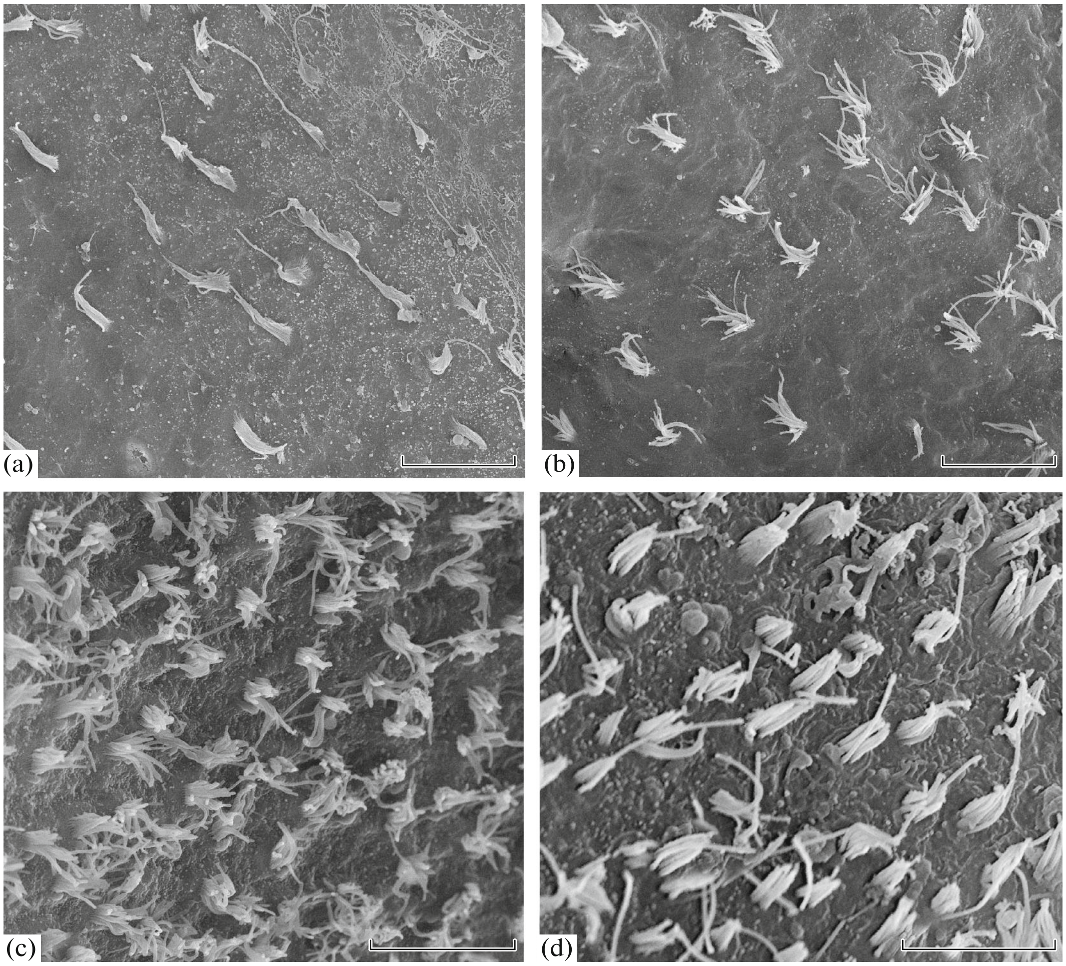

Fig. 3. Density of the hair cells in the central part of the saccular macula of (a) big golomyanka *Comephorus baicalensis*, (b) small golomyanka *C. dybowski*, (c) Severobaikalsk yellowfin *Cottocomephorus alexandrae,* and (d) stone sculpin *Paracottus knerii*.

surface is higher in the rostral and caudal parts of the macula (Fig. 2). In the central part of the macula, hair cells were considerably distant from each other, specifically in golomyankas (Fig. 3). The mean density of the hair cells was 28100 ± 1232 in big golomyanka (Figs. 2a and 3a), 27600 ± 511 in small golomyanka (Figs. 2b and 3b), 46000 ± 795 in Severobaikalsk yellowfin (Figs. 2c and 3c), and 34400 ± 358 cells/mm^2 in stone sculpin (Figs. 2d and 3d).

The apical surface of each hair cell was topped with a bundle of 10–30 stereocilia and an acentrically located kinocilium (Figs. 1, 4a and 4b). Stereocilia were arranged in four to six straight rows extending from the kinocilium. The distance between the stereocilia in the same row in the studied species was 0.43 ± 0.001 μm, which was less than that in the adjacent rows (0.85 ± 0.002 μm) (Fig. 4c). The diameter of the apical surface of the hair cells located along the periphery of the macula was 2.40 ± 0.075 μm, which was twice less than that of the hair cells in the center of the macula (3.73 ± 0.050 μm). The diameter of stereocilia gradually narrowing to the base ranged from 0.32 to 0.15 μm, and the diameter of kinocilia—from 0.44 to 0.25 microns (Figs. 4b and 4d).

Despite the general similarity of the macula ultrastructure, the studied species differed primarily in the length of stereocilia and kinocilium in the peripheral and central hair cells. Cluster analysis of the most significant and varying characteristics—the length of the kinocilium (k) and the length of the highest stereocilia (s)—distinguished six types of saccular hair cells (k13s9, k9s8, k14s4, k8s4, k9s2, and k11s1), where numbers show the length of the kinocilium and the greatest stereocilia in μm) (Fig. 5, Table 2).

Based on the images obtained, the area occupied on the macula by the fields of hair cells of different types was calculated (Fig. 6). Table 2 shows the ratios of such fields for sculpin fishes. Notably, the division of the macula into the regions with different types of hair cells in each fish species may not coincide with the division of the macula into the regions formed by the hair cells with different morphological polariza-

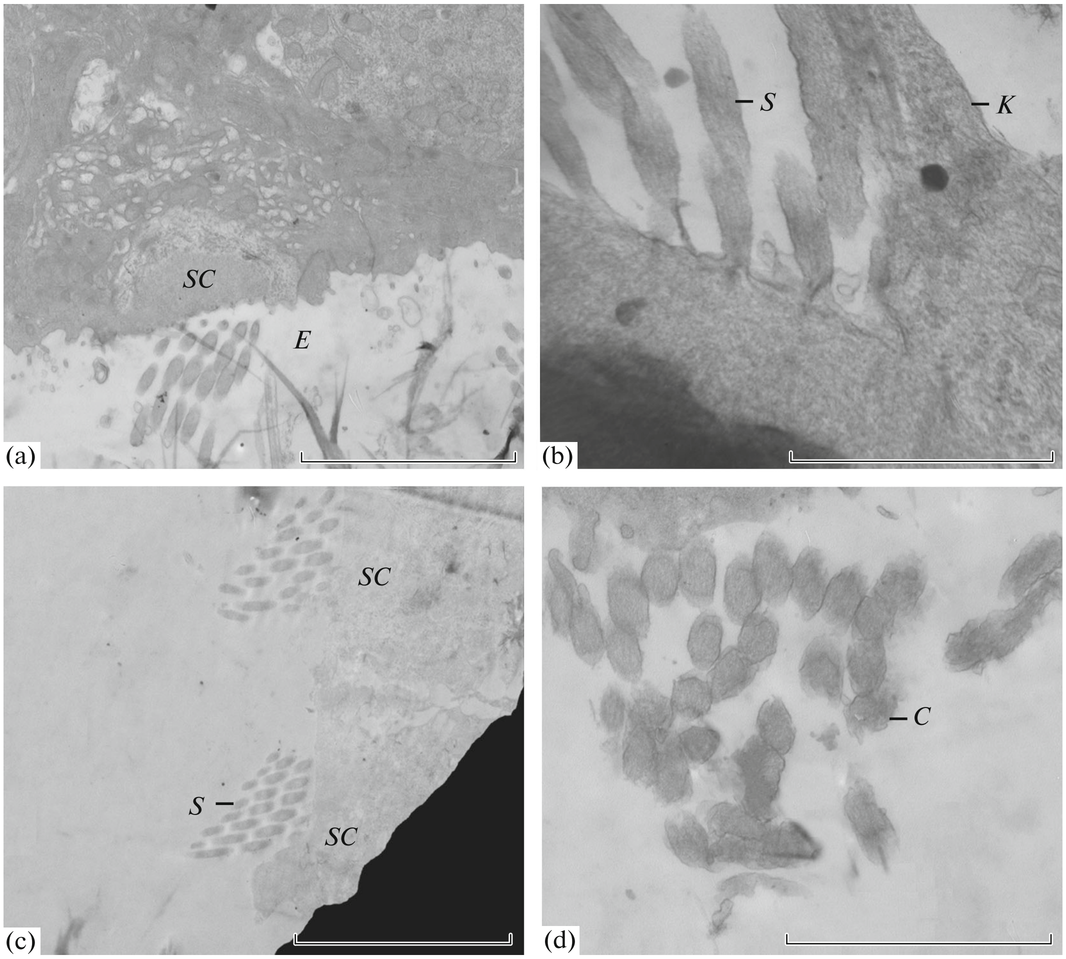

Fig. 4. Stereocilia and kinocilia on the apical surface of the hair cells in the saccular macula of stone sculpin *Paracottus knerii:* (a) longitudinal section of the macula of the apical surface of the saccular sensory epithelium, (b) the surface of the hair cell with protruding stereocilia and kinocilium; (c) the apical part of the hair cells with stereocilia, (d) cross-section of stereocilia. Designations: *SC*—sensory cell; *E*—endolymph; *S*—stereocilia; *K*—kinocilium. Transmission electron microscopy, scale: (a, c) 10 μm, (b, d) 2 μm.

tion, that were previously described for the sculpin fishes in (Sapozhnikova et al., 2007).

DISCUSSION

The results obtained by scanning and transmission electron microscopy have shown that the macrostructure and ultrastructure of saccular maculae of the Baikal sculpin fishes studied is species-specific. However, the fishes living in the same environmental conditions of the lake had some common morphological characteristics concerning the varieties of hair cells, the density of their location, and the length of stereocilia and kinocilia (Table 2).

According to the data on goldfish *Carassius auratus*, acoustic stimuli cause different electrophysiological responses in hair cells with different length of stereocilia (Sugihara and Furukawa, 1989). The Tetrapoda case study indicated that the hair cells with short stereocilia are more sensitive to high-frequency acoustic signals than the hair cells with long stereocilia (Saunders and Dear, 1983). The results of experiments with the Atlantic cod *Gadus morhua,* in which intense acoustic stimulation caused different degree of damages of hair cells in different parts of the macula (Enger, 1981) confirmed the existence of the regions with different tonal specialization in the auditory maculae of fish. In many teleost fishes the hair cells with long stereocilia are more sensitive to low frequency sounds, which corroborates the functional specialization of different parts of the auditory maculae (Lombarte and Fortuño, 1992; Ricci et al., 2002; Popper and Fay, 2011; Smith et al., 2011).

The results of this study suggest that the morphofunctional specialization of different parts of the auditory maculae varies in closely related fishes living under different environmental conditions of the lake. The presence of large (>50% of area) regions in the

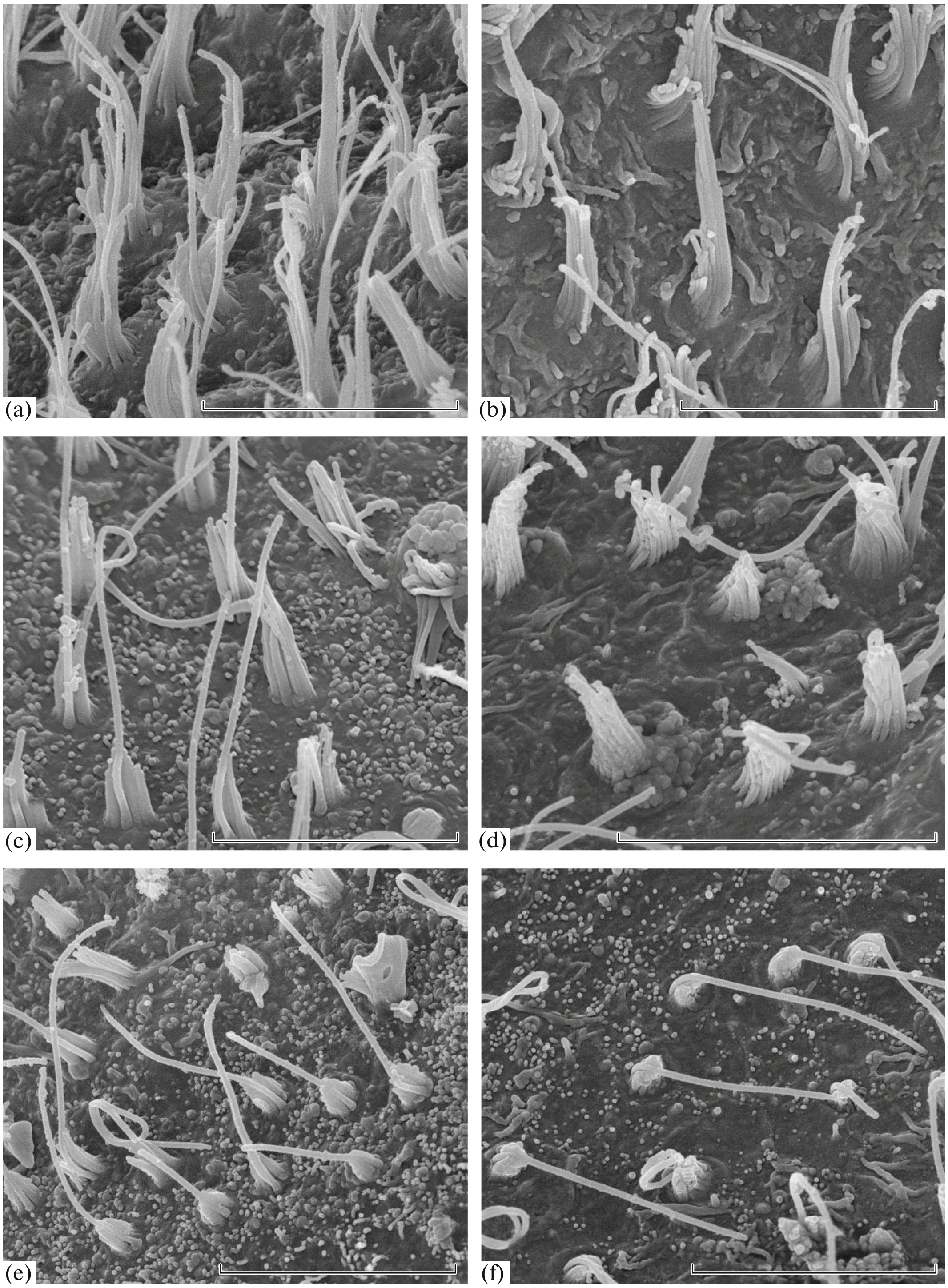

Fig. 5. Hair cells with different average length of the maximum stereocilia (s) and the average length of the kinocilium (k) in the saccular macula of stone sculpin *Paracottus knerii*, μm: (a) k13s9, (b) k9s8, (c) k14s4, (d) k8s4, (e) k9s2, and (f) k11s1.

saccular macula areas that are occupied by hair cells with elongated stereocilia (8 μm) are characteristic of the pelagic sculpin fishes (big and small golomyankas). The macula of the coastal stone sculpin and Severobaikalsk yellowfin inhabiting the near-slope zone is dominated by the areas with hair cells bearing shorter (≤4 mm) stereocilia (100 and 68%, respectively). The predominance of hair cells with long stereocilia in pelagic golomyankas is evidently associated with the acoustic conditions of the habitats of these fishes and facilitates their perception of low-frequency acoustic signals. The acoustic spectrum in the pelagic zone is in fact mostly represented by the low-frequency sounds below 300 Hz (Karlik and Marapulets, 2004). These sounds are attenuated lower than the high-frequency sounds and, therefore, are spread in the pelagic zone over large distances. The acoustic spectrum of the open pelagic area of water bodies virtually lacks the high-frequency component absent (Urik, 1978).

Unlike the pelagic zone, the coastal zone is characterized by noises with a wide range of frequencies—from 0.05 to 16 kHz (Karlik and Marapulets, 2004). Due to the presence of acoustic sources, such as wave-cut effects, relief heterogeneity, and the high density of benthic population, the acoustic spectrum of the coastal zone is saturated with high-frequency acoustic signals, which better spread in the shallow area of water bodies than the low-frequency sounds and, for many aquatic animals, have a signal character. This feature of coastal areas explains the fact that the hair cells with short stereocilia are more typical in the saccular macula of stone sculpin and Severobaikalsk yellowfin. Hair cells of this type ensure better sensitivity in these fishes to the high-frequency acoustic signals, which can be more easily identified against the background of the low-frequency noise in the coastal zone (Urik, 1978).

The low-frequency noise from the surf causes excessive noise background which can supress the communication acoustic signals (Urik, 1978). For this reason, the typical coastal habitants should be adapted for highly differentiated perception of biologically significant acoustic signals in noisy environments. In the case of stone sculpin, such adaptations include not only large areas of the macula occupied by the hair cells with short stereocilia but also a relatively large total area of the macula as well as the high morphological diversity of hair cell types and their high density (Table 2).

The presence of the so-called aberrant otoliths in the saccular apparatus of sculpin fishes can also be regarded as an example of the above-mentioned adaptations (Fig. 7). The shift of the otolith, which adjoins the saccular macula in these fishes, leads to stimulation of hair cells in the endolymph (Popper et al., 2005). The otolith is made of calcium carbonate in different modifications (aragonite, vaterite, or calcite). A characteristic feature of the coastal Baikal fishes is the

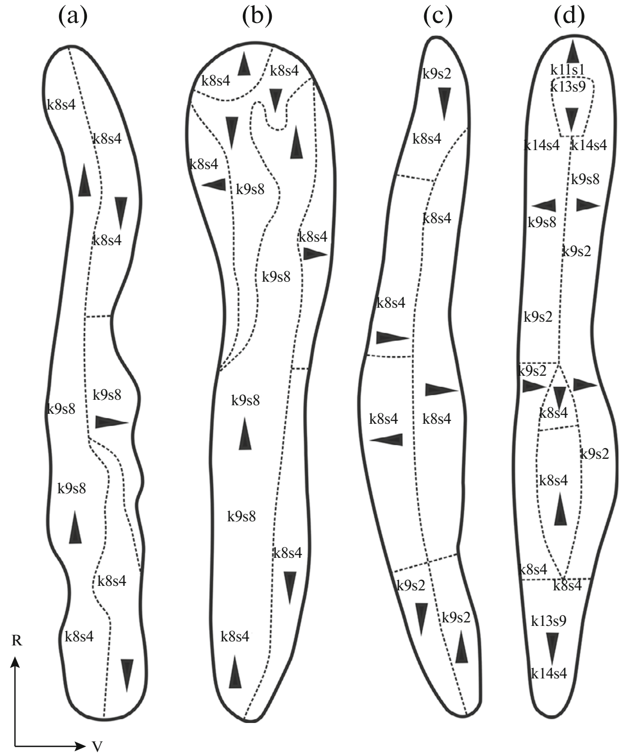

Fig. 6. Scheme of distribution of different types of hair cells in the saccular macula according to scanning electron microscopy data: (a) big golomyanka *Comephorus baicalensis,* (b) small golomyanka *C. dybowski,* (c) Severobaikalsk yellowfin *Cottocomephorus alexandrae,* and (d) stone sculpin *Paracottus knerii*. Designations: (- - -) boundaries of macula zones with different morphological polarization of the hair cells, (►) polarization vector; R, V—rostral and ventral sides of the macula. Numbers in the name of cell types are the average length of the kinocilium (k) and the highest stereocilium (s), μm.

Table 2. The morphological characteristics of the saccular macula of sculpin fishes from Lake Baikal (Cottoidei)

Species	Macula area, mm^2	Ratio of macula area to the mean length (*TL*) of specimen in sample	Density of hair cells in macula, cells/mm^2	Proportion of saccular macula occupied by different types of hair cells, %					
				k13s9	k9s8	k14s4	k8s4	k9s2	k11s1
Big golomyanka	0.27 ± 0.001	0.0018	28100 ± 1232	0	53	0	47	0	0
Small golomyanka	0.24 ± 0.001	0.0020	27600 ± 511	0	67	0	33	0	0
Severobaikalsk yellowfin	0.09 ± 0.001	0.0008	46000 ± 795	0	0	0	77	23	0
Stone sculpin	0.33 ± 0.003	0.0030	34400 ± 358	18	14	11	26	22	9

The numbers in the names of cell types (k13s9, k9s8, k14s4, k8s4, k9s2, and k11s1) are the mean length of the kinocilium (k) and the highest stereocilia (s), μm.

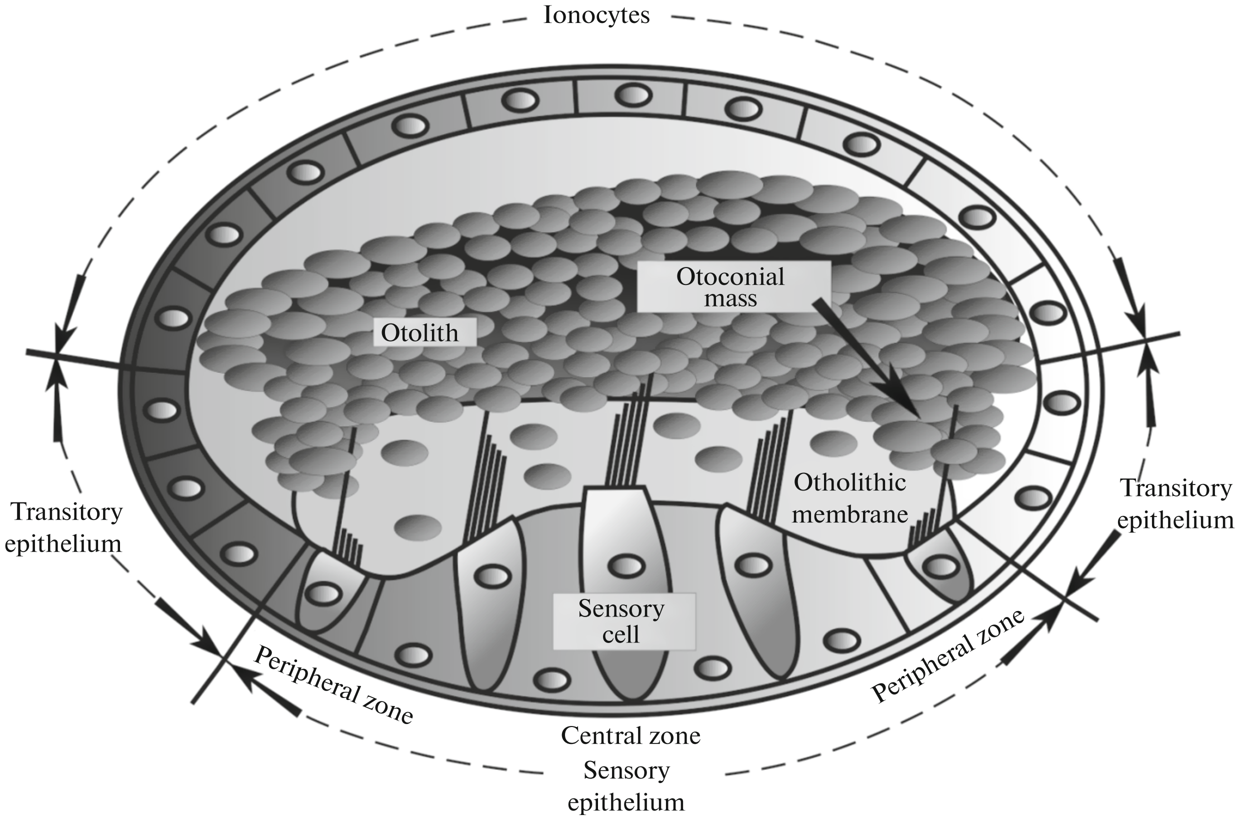

Fig. 7. Scheme of location of various types of hair cells in the saccular macula with an aberrant otolith in Baikal sculpin fishes (Cottoidei).

presence of the so-called aberrant (vaterite) otoliths, which differ from the common (aragonite) otoliths primarily by the geometry of crystals and low density (Sapozhnikova et al., 2010). The case study of juvenile chinook salmon *Oncorhynchus tshawytscha* showed that the low density of vaterite otoliths (2.65 g/cm^3) compared to aragonite otoliths (2.93 g/cm^3) results in the weakening of the connection between the otolith and the sensory epithelium and, hence, a decrease in the auditory sensitivity in fish by 2.5–6.5 dB due to increase in the hearing threshold in the low-frequency region (100–300 Hz) (Oxman et al., 2007).

Previously, we reported (Sapozhnikova et al., 2010) that aberrant otoliths grow unevenly relative to their primary anlage due to the so-called otoconial masses, which are adsorbed in the regions of additional mass growth on the periphery of the otolith (Fig. 7). The distribution patterns of different types of hair cells in the macula of sculpin fishes (Fig. 6), show that the peripheral zone of the macula contains hair cell types with short stereocilia (1–4 mm), which ensure the sensitivity of fish to higher frequencies.

The increase in the peripheral zone of the macula in the coastal fishes can broaden the sensitivity of these fishes in the high-frequency range of the spectrum and reduce the sensitivity to low frequencies in the presence of aberrant otoliths. Such mechanism may protect the sensory apparatus of fish against uninformative and biologically insignificant information under conditions of high background noise in the coastal zone.

Thus, the peripheral part of the auditory system of sculpin fishes is characterized by a high morphological specialization, which is associated with the way of life of these fish and ensures effective perception of acoustic signals by them. These results suggest that the acoustic signaling may play an important role in the regulation of behavior of sculpin fishes.

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