VISION AND SENSORY PHYSIOLOGY

The lateral line systems of three deep-sea fish

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The distribution and ultrastructure of the lateral line systems in three taxonomically dispersed deep-sea fish are described: *Poromitra capito*, *Melanonus zugmayeri* and *Phrynichthys wedli*. They are meso- to bathpelagic and are thought to feed on small crustaceans and fish. All possess highly developed lateral line systems, a feature associated with life in the deep sea. *Poromitra capito* and *M. zugmayeri* exhibit widened head canals which are connected to the outside by large pores and which contain around 60 large neuromasts. Each neuromast consists of a cupula, shield-shaped mantle and a sensory plate containing hundreds to thousands of hair cells. Direction of sensitivity is in the long axis of the canal (perpendicular to the long axis of the mantle). Depending on their position on the sensory plate, the hair cells have different morphologies. They fall into three basic classes which, from comparison with past work, may be tuned to different frequencies. Alternatively, the various hair cell morphologies could be interpreted as being members of a developmental or growth sequence. *Phrynichthys wedli* has no canal organs, these being replaced secondarily by many superficial neuromasts placed on prominent papillae in rows which cover much of the ' head ' and body. Direction of sensitivity is along the axis of the neuromast row. An extreme proliferation of superficial neuromasts are also found on the heads of *P. capito* and *M. zugmayeri* and these are of a type not described before. They consist of stitches, raised on papillae in *M. zugmayeri* and several mm long in *P. capito*, in which continuous lines of hair cells, two to three cells wide, are embedded. Direction of sensitivity is perpendicular to the long axis of the stitch. Based on the structure and direction of sensitivity, possible functional implications of all the neuromast types described are compared and discussed. © 1996 The Fisheries Society of the British Isles

Key words: lateral line; hair cell; deep sea; fish

INTRODUCTION

In the dim or lightless depths of the meso- and bathypelagic zones of the ocean, olfaction, hearing and the distance touch sense (Dijkgraaf, 1963) of the lateral line become increasingly well developed in the fish that inhabit these areas (Marshall, 1971). This paper describes the distribution, structure and ultrastructure of the lateral lines in three such fishes. All species come from different superorders but in two of the species, *Melanonus zugmayeri* Norman and *Poromitra capito* Goode & Bean, convergence has led to similar lateral line systems (*P. capito* is a stephanoberyciform fish from the super-order Acanthopterygii, *M. zugmayeri* is a gadiform from the superorder Paracanthopterygii, Nelson, 1994). Several species of these superorders have greatly widened head canals containing massive neuromasts and a proliferation of stitch-like superficial neuromasts of a type not described before. The third species, *Phrynichthys wedli* Pietchmann, a diceratiid anglerfish, has lost all canal organs on head and body secondarily, and has replaced these with many

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FIG. 1. The living specimen of *Phrynichthys wedli* with lines of papillate superficial neuromasts.

papillate superficial neuromasts typical of the ceratoid superfamily (Figs 1 and 2; Bertelsen, 1951).

Scanning electron microscopy (SEM) has been used to investigate the structure and polarity of the hair cells within each neuromast's sensory plate. In common with many sensory epithelia, the hair bundles of the lateral line consist of a single kinocilium (a true cilium, lost in the mammalian cochlea) and several shorter stereocilia (sometimes called stereovilli as they are not true cilia, e.g. Jørgensen, 1989) of varied lengths forming a staircase on one side of the kinocilium. The hair cell depolarizes most when the hair bundle is bent in the direction of the kinocilium, and hyperpolarizes when bent in the direction of the stereocilia, giving each cell a sensitivity direction or polarity (Flock, 1965). Hair cells often appear, and may develop, in pairs (Rouse & Pickles, 1991) with opposing polarity. In all lateral line sensory plates examined thus far, hair cells are arranged so as to give the whole organ an overall axis of highest sensitivity (Flock, 1965, Coombs *et al.*, 1988). In canal organs, for instance, the direction of highest sensitivity is always along the canal.

Superficial, also known as free-standing, neuromasts often occur in lines and may have their polarities arranged either along or perpendicular to the line (Marshall, 1986, Coombs *et al.*, 1988). This is determined by their phylogenetic or ontogenetic origin (Coombs *et al.*, 1992 and covered further in the discussion) but clearly must also relate to the task required of the array of organs. All three species examined here have extensive superficial neuromast systems.
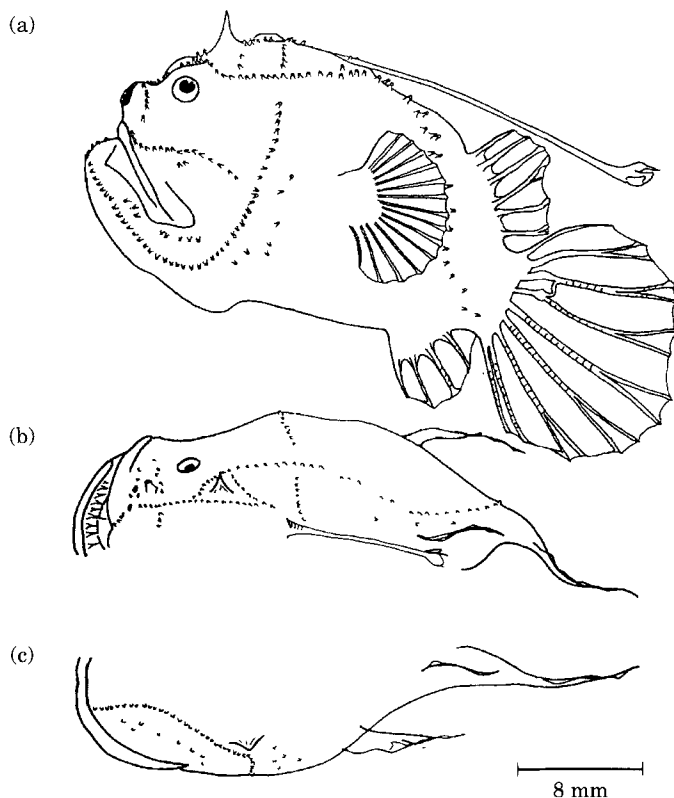
FIG. 2. Diagram of the distribution of superficial neuromasts in *Phrynichthys wedli*. Scale 8 mm. (a) Lateral aspect, (b) right dorsal aspect, (c) right ventral aspect.

Poromitra capito and *M. zugmayeri* possess many superficial neuromasts resembling stitches (Figs 3 and 4). They are only located on the head and consist of continuous lines of hair cells, two to three hair cells wide. In *P. capito*, they may be several mm long, and are raised above the head on papillae in *M. zugmayeri*. In all stitches examined, hair-cell polarity was found to be perpendicular to the stitch (the 'stitches' of *Xenopus* consist of lines of individual neuromasts, Görner & Mohr, 1989). In *M. zugmayeri*, and in a variety of other deep-sea fish, these and similar structures are presumed to be lateral line organs (Marshall & Cohen, 1973; Robins, 1989) although the presence and distribution of hair cells are not described. What is perhaps their most surprising feature is the huge number of hair cells they possess, presumably allowing great sensitivity.

MATERIALS AND METHODS

Fish were caught using two gentle capture techniques, essential for maintaining superficial lateral line organs in good condition. One specimen of *P. wedli* was caught from the submersible Johnson Sea-Link II using a suction device, or slurp gun. It was a female specimen 4 cm long, which could therefore probably be considered an adolescent (Bertelsen, 1951). Depth of capture was close to 1000 m and this individual remained alive at the surface for more than 2 days (Fig. 1). The capture was made in 1991 on Dive
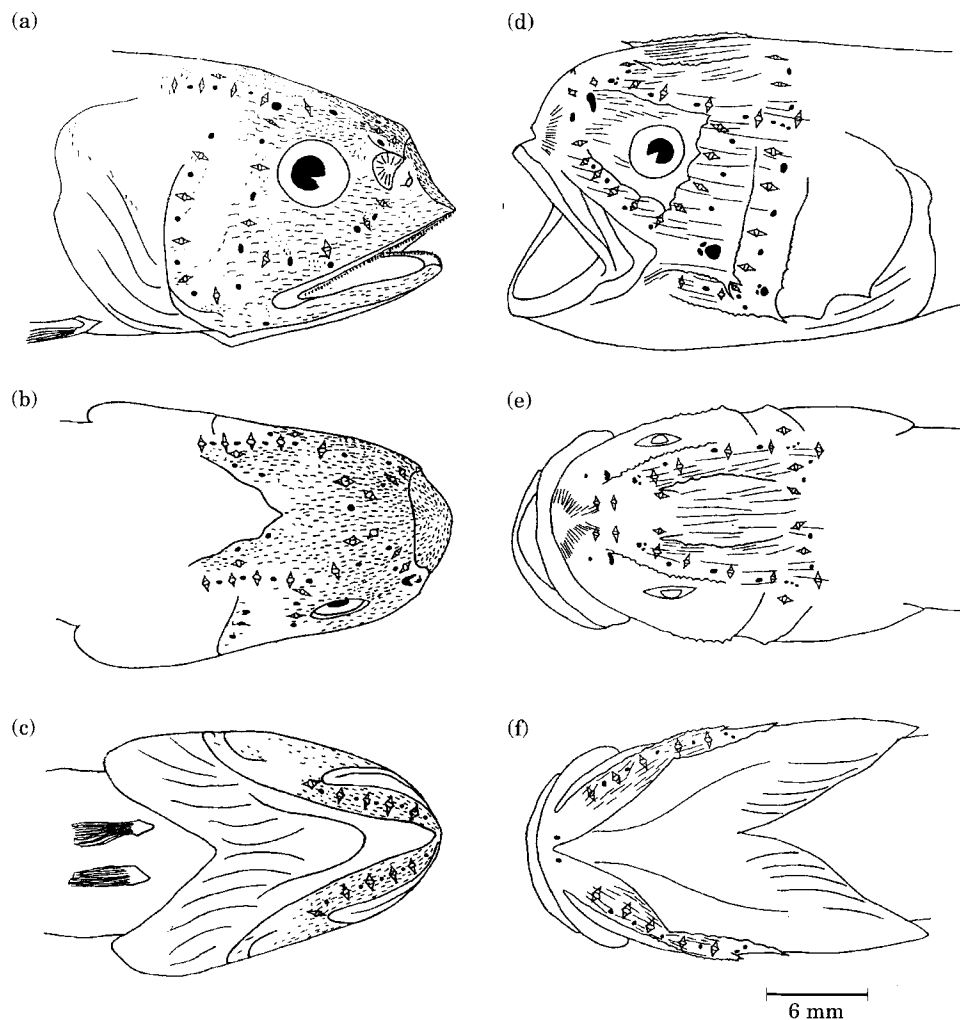
FIG. 3. Diagrams of the distribution of superficial and canal organs in *Poromitra capito* and *Melanonus zugmayeri*. Canal neuromasts are represented by diamond- or shield-shaped structures. Canal pores are represented by black circles. Superficial neuromast stitches are represented by thin lines. Scale 6 mm. (a) Lateral aspect of the head of *M. zugmayeri*, (b) dorsal aspect of the head of *M. zugmayeri*, (c) ventral aspect of the head of *m. zugmayeri*, (d) lateral aspect of the head of *P. capito*, (e) dorsal aspect of the head of *P. capito*, (f) ventral aspect of the head of *P. capito*.

Number 3169 of Johnson Sea-Link II which was deployed from the mother ship RV 'Edwin Link' at position 17°35 N 64°47 W in the Caribbean. Three individuals of *M. zugmayeri* between 7 and 10 cm were caught during the 1993 Discovery Cruise 204 at depths from 500 to 800 m close to position 19°6·6 N 19°59 W in the Atlantic. Catching gear was an RMT 8+1 net with closing cod-end (CCE), again enabling capture of live

FIG. 4. (a) Photograph of the head of *Melanonus zugmayeri* showing prominent superficial stitches and head canal pores. Scale 4 mm. (b) Photograph of the skinned head of *Poromitra crassiceps*, a close relative of *Poromitra capito* with similar placement of canal neuromasts. Note large shield-shaped mantle with centrally placed sensory plates and the widened canal structure. Scale 2·5 mm. (c) Photograph of the nasal aspect of *P. capito* with skin intact. Superficial neuromasts, in a fan-shaped array on the nose and behind the nostrils, show up as dark or light lines. Scale 1 mm.
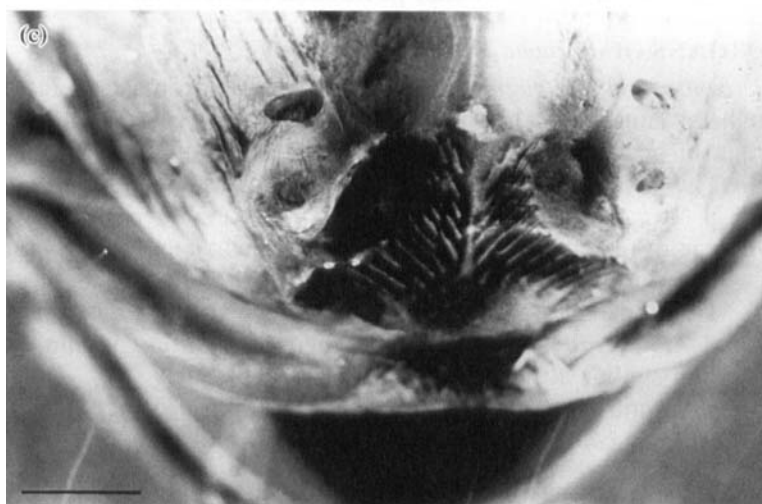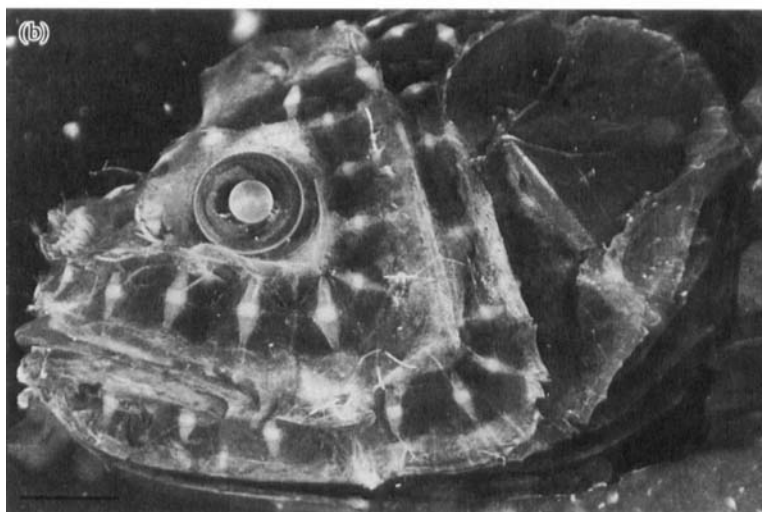
specimens in good condition. Several *P. capito* were caught on the 1995 Challenger Cruise 122 between 400 and 1000 m using an RMT 50 with CCE. However, only two specimens of *P. capito*, one 10 cm and one 8·5 cm, were used for this investigation as many had lost the head skin which is particularly delicate in the melamphaids (Ebling & Weed, 1973; Maul, 1986). Position of capture was around 31°37·97 N 16°52·8 W in the Atlantic.

Fish were photographed and videoed directly after capture using a Wild Photo-macroscope, 35-mm camera and Sony Hi8 Handycam. Lateral line organ distributions were reconstructed later from these images.

Phrynichthys wedli was fixed whole while *M. zugmayeri* and *P. capito* were decapitated and the heads fixed overnight in a modified Bouins fixative (3% glutaraldehyde, 15% saturated picric acid, 0·1 M PO_4 buffer at 7·4 and 0·1 M sucrose). Tissue was transferred into buffer for the remainder of the cruise, up to 2 weeks, thus remaining in a light fixative solution. On return to land, the head canals of *M. zugmayeri* and *P. capito* and portions of superficial neuromast lines in *P. wedli* were dissected out, and this and other tissue buffer rinsed twice more before post-fixation in 2·5% osmium tetroxide also overnight. After three further buffer rinses, tissue was dehydrated in a series of acetones, critical point dried, sputter coated in gold and examined on a Leo-Leica S420 SEM. Superficial neuromasts in *M. zugmayeri* and *P. capito* were examined on intact heads.

RESULTS

GENERAL DESCRIPTION

All three fish included in this study have extensive lateral line systems. They are of two different types, perhaps representing different biological strategies or the result of different phylogenetic constraint. The anglerfish *P. wedli* has no head canals but instead has many superficial organs raised on prominent papillae and arranged in lines on the head and body.

Although *P. capito* and *M. zugmayeri* are not closely related, they possess remarkably similar lateral line systems. They have large neuromasts housed in widened head canals, no body canal and an extensive array of superficial neuromasts consisting of long lines (stitches) of hair cells, two to three cells wide. In *M. zugmayeri*, these are raised above the skin on papillae. Stitches are found on most regions of the head although, in both species, their density thins on the opercula and there are none visible on the gill membrane. Notably, both species possess a fan-shaped array of stitches positioned between the nares.

CANAL ORGANS OF *P. capito* AND *M. zugmayeri*

Both *P. capito* and *M. zugmayeri* possess canal neuromasts (Figs 5 and 6) housed in head canals which can divided into seven types: mandibular, pre-opercular, infra-orbital, supra-orbital, otic/post-otic/temporal, supra-temporal and nasal. The head canals are wide, around 1·0–2·5 mm in *P. capito* and 1·5–4·0 mm in *M. zugmayeri* (Table I and Fig. 4), and connect to the outside via a series of large pores, usually one between each neuromast (Figs 3 and 4). In *P. capito*, single pores may be replaced by three pores packed tightly together [Fig. 3(d)]. There are a total of 60 and 57 canal neuromasts on the heads of *P. capito* and *M. zugmayeri*, respectively, their distribution within each head canal type being similar although not identical (Table I).

Cupulae, which must cover the canal organs, were lost in preparation but are said to be low in *P. capito* (Denton & Grey, 1988) and almost fill the canal in *M. zugmayeri* (Marshall, 1968). From a comparison of Figs 5 and 6, it can be
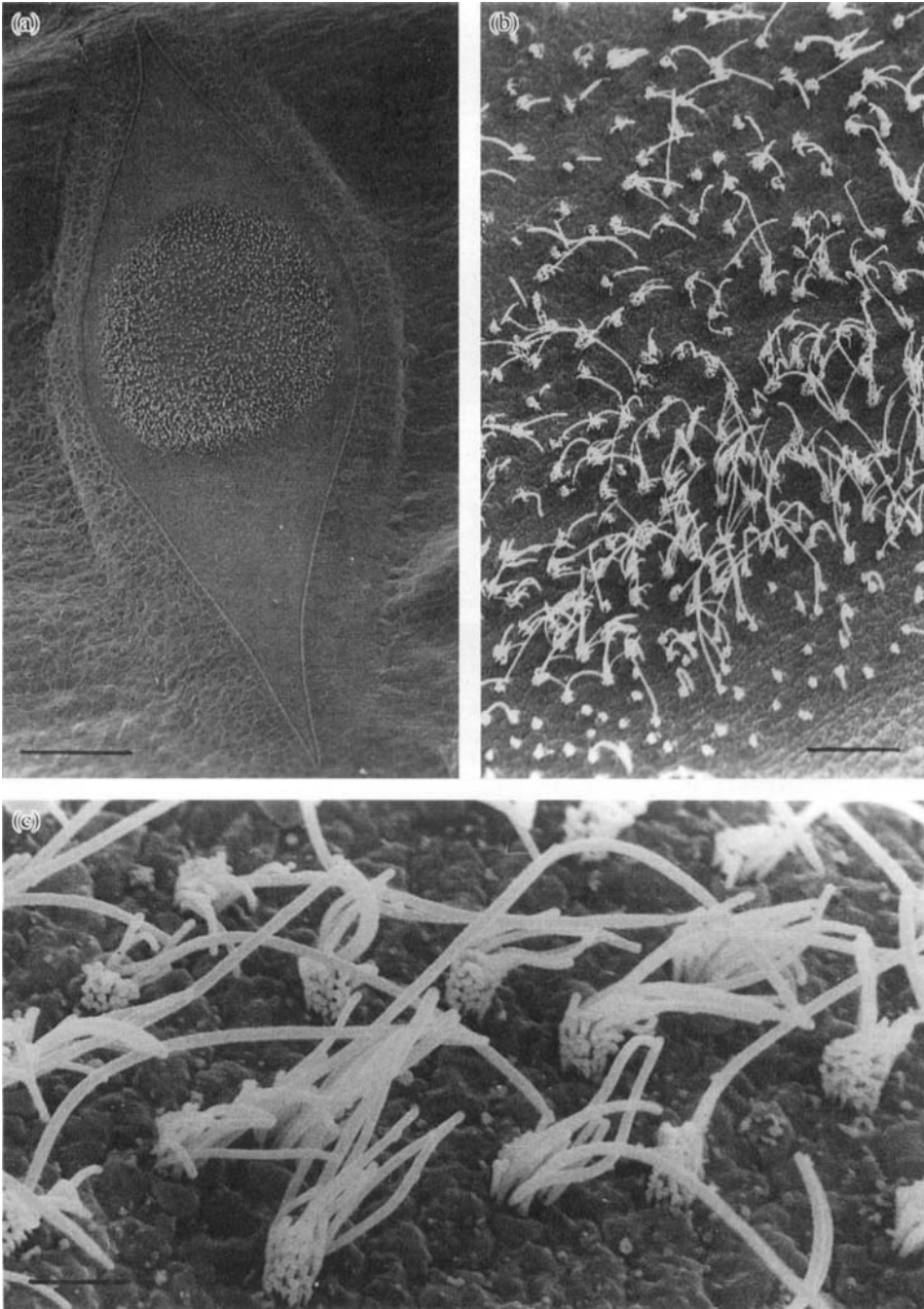
FIG. 5. Scanning electron micrographs (SEM) of the canal neuromasts of *Melanonus zugmayeri*. (a) Shield-shaped mantle with central cluster of hair cells forming the sensory plate in mandibular canal. Note slight thinning of hair cell density in the middle region. Scale 100 μm. (b) Hair bundles from the outer edge (bottom right) through the inner ring to the middle zone (top left) showing change in morphology (Table I). Scale 10 μm. (c) Hair bundles from the central ring area of sensory plate showing elongated stereocilia in first one or two rows down from kinocilium. Scale 2 μm.
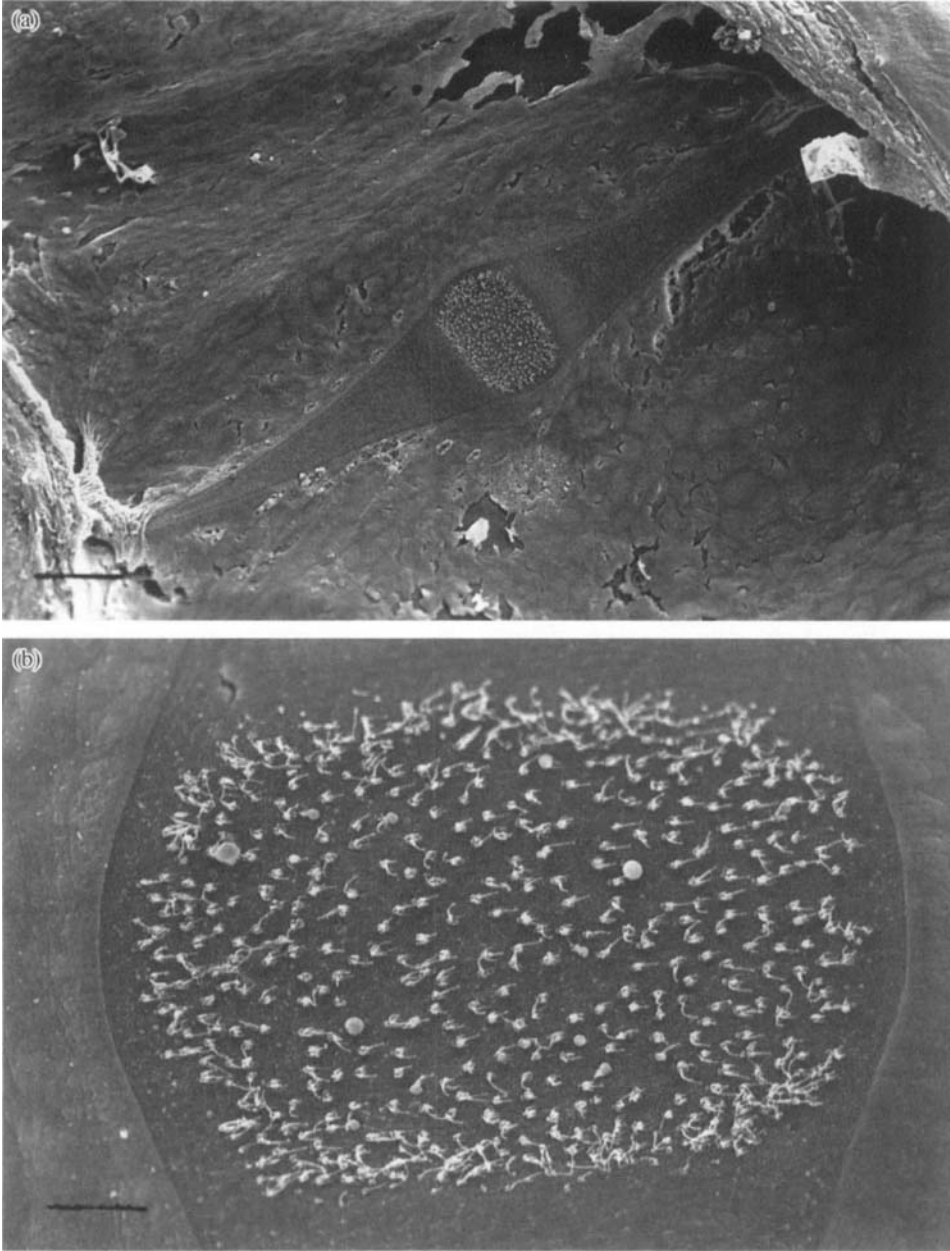
FIG. 6. Scanning electron micrographs (SEM) of the canal neuromasts of *Poromitra capito*. (a) Shield-shaped mantle with central cluster of hair cells in post-ocular part of the infra-orbital canal. Scale 100 μm. (b) Hair-cell bundles with clear ring of cells with longer cilia. Scale 20 μm.

seen that the remaining portion of the canal neuromasts in the two fish are very similar. Both possess elongate, shield-shaped mantle flanges (Coombs *et al.*, 1988) stretching almost across the canal (Table I). In the centre of the shield is a slightly rectangularized circle containing several hundred or, in very large organs, thousands of hair cells, which make up the sensory plate.

TABLE I. Anatomical dimensions of lateral line organs

		Phrynichtys wedli 40 mm	*Poromitra capito* 85 mm	*Melanonus zugmayeri* 100 mm
Canal neuromast dimensions (from one mandibular organ)	Shield flanges Length	na	1300	800
	Width	na	450	260
	Sensory plate Length	na	300	230
	Width	na	200	200
Canal neuromast hair cells (from one mandibular organ)	Hair length (K, St) Outer	na	5·5, (0·4–1·5)	6·0, (0·3–1·5)
	Middle	na	7·5, (0·5–4·4)	12·0, (0·5–5·5)
	Inner	na	6·2, (0·5–1·5)	4·3, (0·5–1·5)
	Hair-cell number	na	2300	1500
Number of neuromasts, average canal width (for *P. wedli* number of neuromasts *probably derived* from canal included)	Mandibular	22, na	3, 2·21 mm	4, 2·65 mm
	Pre-opercular	34, na	7, 2·20 mm	6, 2·78 mm
	Infra-orbital Sub-orbit	14, na	6, 1·24 mm	4, 3·89 mm
	Post-orbit	0, na	4, 2·50 mm	3, 1·67 mm
	Supra-orbital	14, na	4, 1·56 mm	2, 2·22 mm
	Otic, post-otic, temporal	10, na	2, 1·50 mm	4, 1·60 mm
	Supra-temporal	12, na	2, 1·17 mm	1, 2·08 mm
	Nasal	20, na	2, 1·50 mm	3, 2·36 mm
	Trunk	26, na	na	na
Total neuromast no. (one side) (for *P. wedli* includes 45 others situated close to 'canal' rows)		197	30	27
Superficial neuromast dimensions	Shield flanges Length	90	na	na
	Width	34	na	na
	Sensory plate/stitch Length	30	250–6000	100–700
	Width	11	6	5·5
	Papilla height	200–600	1	60–100
Superficial neuromast hair cells (mandibular)	Hair length (K, St)	11·5, (0·5–2·5)	10·0, (0·5–4·0)	10·0, (0·5–2·5)
	Hair-cell number	100	1350 mm^{-1}	1300 mm^{-1}

All measurements in μm unless stated otherwise.

On close examination, it is clear that the hair cells do not form a homogeneous population but have differing morphologies from the outside to the middle of the sensory plate (Fig. 5). They fall in to three categories: outer edge hair cells with short kinocilia and very short stereocilia, inner ring hair cells with long kinocilia and some long stereocilia in the two rows adjacent to the kinocilium [Fig. 5(b)], and middle hair cells with short kinocilia and short stereocilia (Table I).

In all cases, the direction of sensitivity of the neuromast, judged from individual hair cell polarity (Fig. 5), is perpendicular to the long axis of the shield-shaped mantle and therefore along the axis of the canal.

## SUPERFICIAL NEUROMASTS OF P. wedli

About 400 superficial neuromasts are found on the skin (200 per side), most of which are arranged in neat lines on the head. A few more randomly placed neuromasts are present, generally associated with one of the lines of organs. Each organ is raised above the skin on a fleshy papilla around 0·5 mm high, and takes the same general form, although much smaller (Table I), as the canal neuromasts of P. capito and M. zugmayeri. A shield-shaped mantle with elongated flanges is wrapped across the top of the papilla [(Fig. 7(a)]. The sensory plate, positioned in the centre of the shield, is made up of about 100 hair cells whose polarity is perpendicular to the long axis of the shield. Individual papillae are positioned within rows so their direction of highest sensitivity is along the row. This is true of both neat rows and the more randomly placed associated papillae [Fig. 2(a)]. Cupulae were lost during preparation.

SUPERFICIAL NEUROMASTS OF P. capito AND M. zugmayeri

The head of M. zugmayeri is studded with short (100–700 μm) papillate stitches around 80 μm high [Figs 3(a)–(c) and 4(a); Table I]. These are mostly arranged with their long axis running naso-caudally although a small proportion are found arranged dorso-ventrally (Fig. 3). In a flattened area between the nares, a fan-shaped array of organs is present, the centre of the fan being centred on the frontal tip of the upper jaw.

Historically, these structures have been assigned the function of lateral line organs (Marshall & Cohen, 1973) and this assumption is confirmed when examined with SEM. A line of hair cells runs along the top of each papilla (Fig. 8), two to three hair cells wide, the largest stitch containing about 1000 hair cells in total. On a 10-cm individual, there are around 200 000 hair cells within the superficial neuromasts. Two opposing hair cells can often be seen with their kinocilia usually positioned at the centre of the line of cells and the graded stair of stereocillia facing the edges [Fig. 8(c)]. Therefore, the direction of sensitivity of these organs is perpendicular to their long axis. No cupula was observed associated with these organs but, as with the canal organs, was probably lost in preparation or in the net during capture.

FIG. 7. Scanning electron micrographs (SEM) of superficial neuromasts in *Phrynichthys wedli*. (a) A single papilla with shield-shaped mantle and central sensory plate. Scale 10 μm. (b) Close up of sensory plate showing structure of hair bundles with opposing polarities along long axis of sensory plate. Scale 3 μm. (c) and (d) Photograph and drawing of portion of sensory plate, in same orientation as (a) and (b), with some hairs stripped. Note opposing polarity of hair cells and overall direction of sensitivity of neuromast across page. Scale 1 μm.
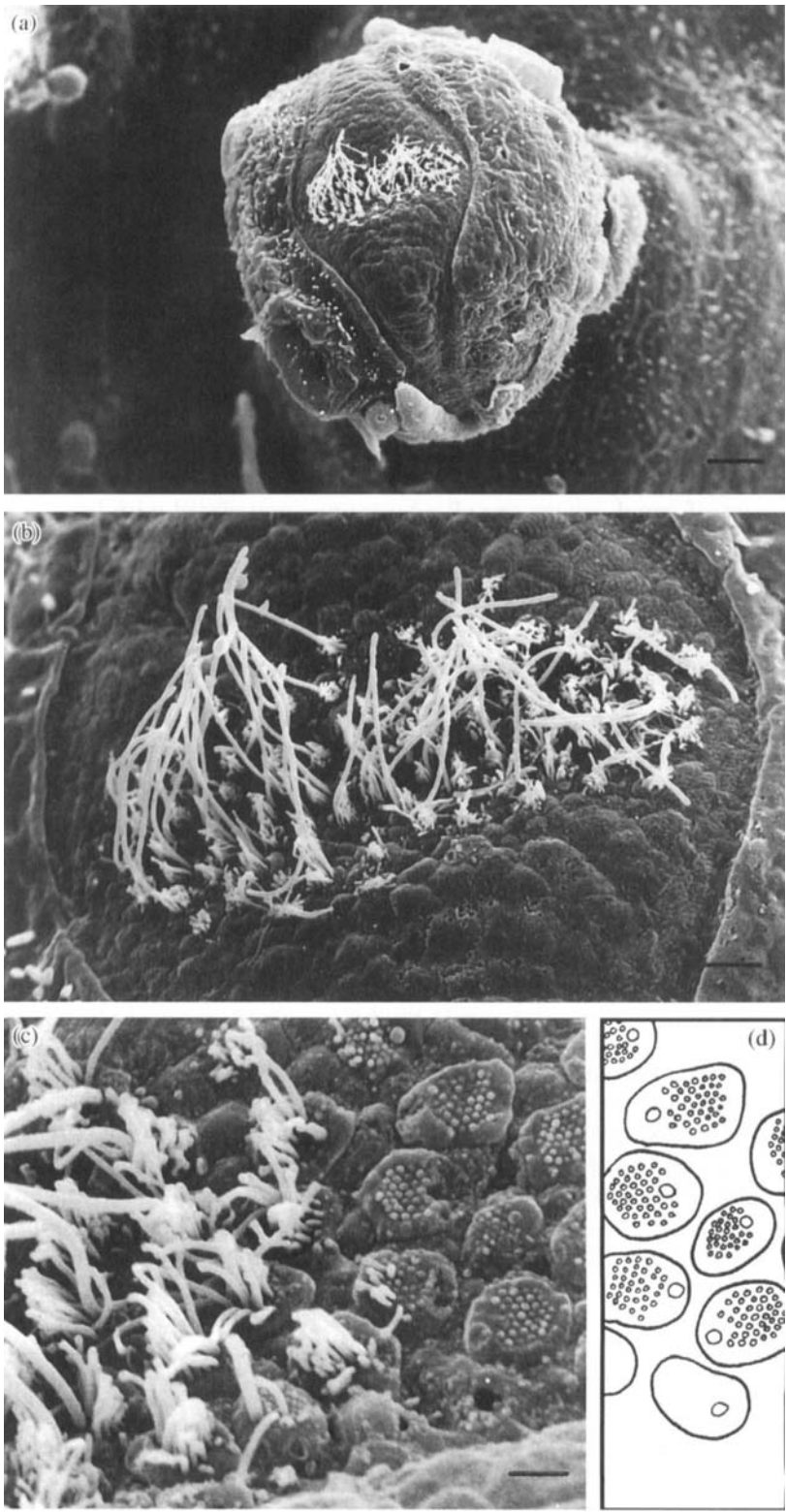
The head of *P. capito* is also covered in stitch-like structures, positioned with their long axes running naso-caudally [Figs 3(d)–(f) and 4(c)]. They are not as densely packed as those in *M. zugmayeri* [compare Fig. 3(a) and (d)] but may reach several mm in length (Table I). The elongated sensory plate is not raised on a papilla but sits slightly proud of the skin. These are also superficial lateral line organs whose sensory hair cells are arranged in a manner almost identical to *M. zugmayeri*. Lines of hair cells, two to three cells wide, are present with opposing polarity perpendicular to the long axis of the stitch. The kinocilium from each hair cell is also usually at the centre of the sensory plate (Fig. 9). In a 10-cm fish, there are about 260 000 hair cells within such receptors.

DISCUSSION

ADAPTATIONS OF LATERAL LINE SYSTEMS FOR DEEP-SEA LIFE

Proliferation of superficial neuromasts, the widening of the head canals and enlargement of canal organs are all adaptations associated with life in the deep sea or other dark, still-water habitats (Denton & Grey, 1988, 1989; Coombs *et al.*, 1988, 1992; Northcutt, 1989). As eyes become less useful for sighting prey, other sensory modalities, such as lateral lines or olfactory systems, must take over (Marshall, 1965, 1971). This is exemplified in the blind amblyopsid cave fishes and a variety of other cave dwelling genera which, like *P. wedli*, have a highly developed array of supernumary or highly proliferated free standing neuromast, often positioned on prominent papillae, and a reduced canal system (Marshall, 1971; Coombs *et al.*, 1992). *Phrynichthys wedli*, which is probably more bathypelagic than mesopelagic (Uwate, 1979), has small eyes, possibly the result of its basically lightless habitat (Fig. 1). The eyes of most deep-sea anglerfish do not develop much beyond the larval stage and, by the time the fish is adult, may be essentially functionless (Bertelsen, 1951). As a result, in common with cave fish, *P. wedli* relies principally on its lateral line system to sense the world around it and to detect prey.

Schooling behaviour, an activity also requiring lateral line input, is not known for any of these fish and is especially unlikely in the solitary anglerfish *P. wedli*. Therefore, the author has assumed that the lateral line systems described, including the canal organs where present, are principally for prey capture. There are few data on the food taken by any of the three species, although all probably feed on small crustaceans or fish (Ebeling & Weed, 1973; Uwate, 1979).

Poromitra capito and *M. zugmayeri* are found around the meso–bathypelagic boundary (Ebling & Weed, 1973) and, perhaps as a result, have larger eyes to make the best of the light reaching their habitat. The great expansion of their lateral line systems, however, suggests they may also rely on them for prey detection or other behaviour. Unlike many of the visual predatory fish living at these depths, *P. capito* and *M. zugmayeri* show no other obvious ocular

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Fig. 8. Scanning electron micrographs (SEM) of superficial neuromasts in *Melanonus zugmayeri*. (a) Low power SEM to show elongated papillae on the skin. Scale 100 μm. (b) A single papilla with line of hair cells visible along upper edge. (c) Hair cells of narrow elongate sensory plate. Note kinocilia are placed towards centre of sensory plate and different polarity opposite hair cells. Tissue is slightly damaged from abraision or poor fixation. Scale 1 μm.
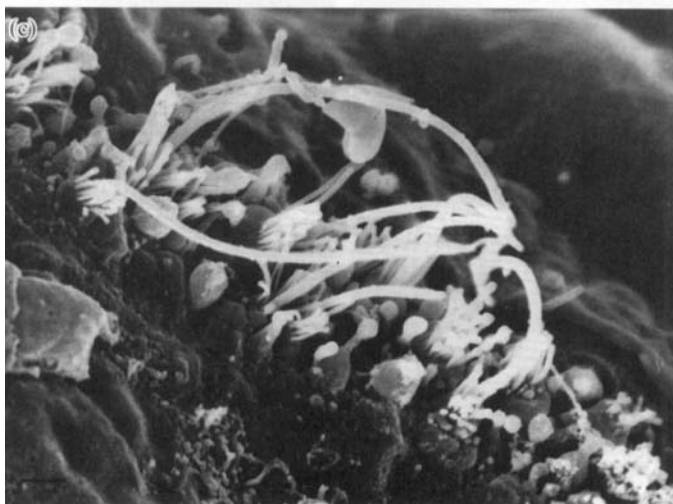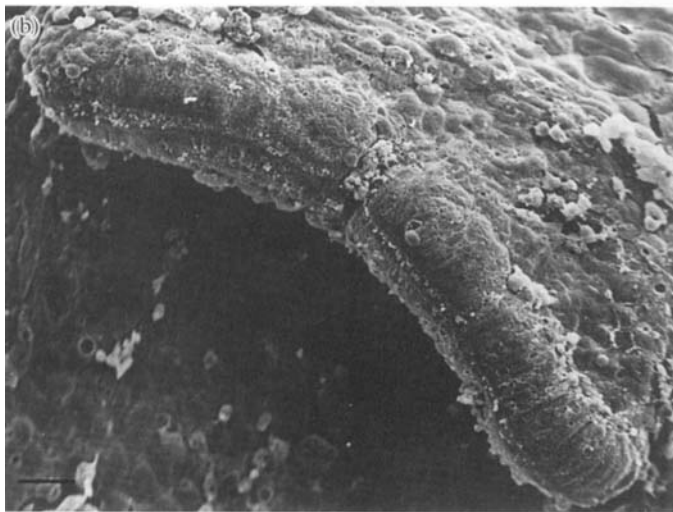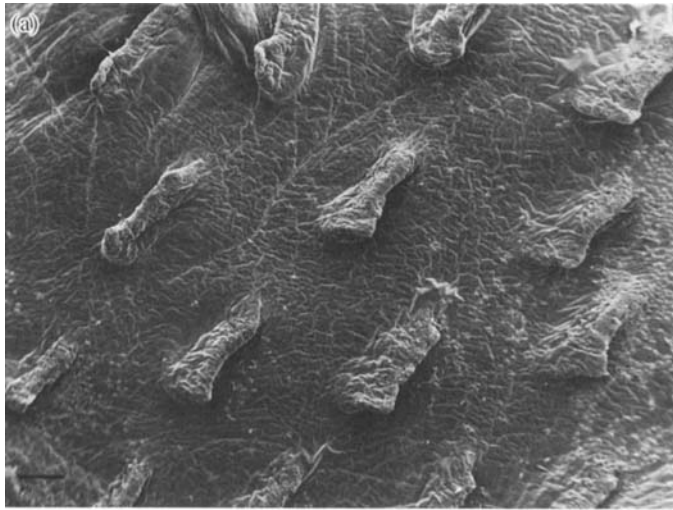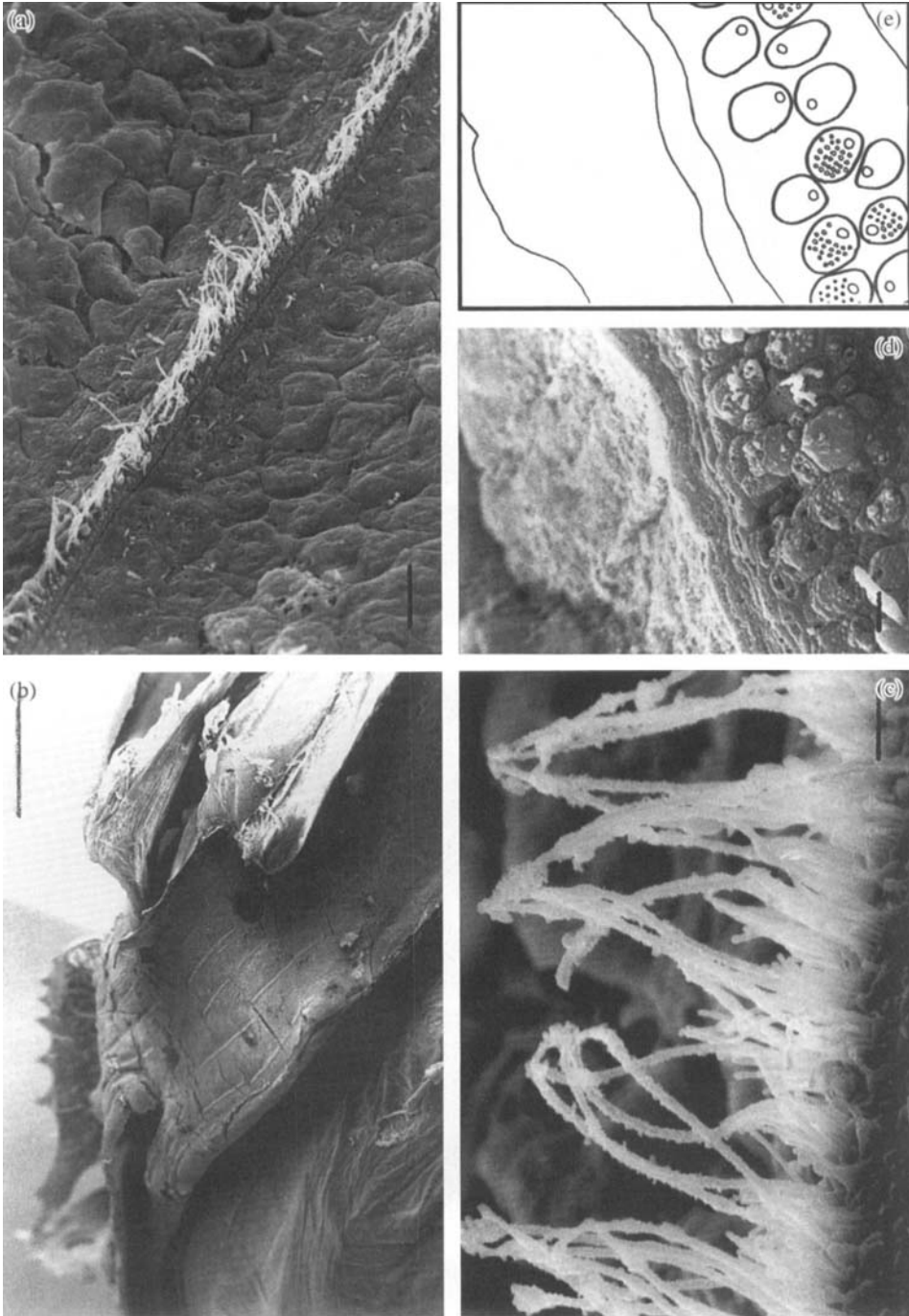
FIG. 9. Scanning electron micrographs (SEM) of superficial neuromasts in *Poromitra capito*. (a) Low-power SEM of posterior portion of right mandibular region. One canal pore is visible surrounded by long white lines which are superficial stitches. Scale 1 mm. (b) Elongate sensory plate of one stitch organ with line of hair cells two to three cells wide. Scale 10 μm. (c) Side view of hair bundles. Note placement of most kinocilia towards the mid-line of the stitch. Scale 2 μm. (d) and (e) Photograph and drawing of portion of the sensory plate surface, stripped of hairs but with insertions remaining. Note opposing polarity of adjacent hair cells and direction of best sensitivity perpendicular to stitch long axis. Scale 1 μm.

specializations, such as large aphakic gaps or increased binocularity, to help with prey capture (Locket, 1977), and may rely more on their lateral line systems. It is puzzling that *P. capito* and *M. zugmayeri* possess both extensive canal and superficial lateral line systems. In surface-dwelling fish, proliferation of superficial neuromasts usually accompanies loss of canals (More & Burris, 1956; Webb, 1989a), as it has in *P. wedli*. These supernumary neuromasts are sometimes termed replacement superficial organs for this reason (Coombs *et al.*, 1988).

CANAL ORGANS

The huge sensory plates of the canal organs in both *M. zugmayeri* and *P. capito* contain hair cells of different hair-bundle morphologies (Figs 5 and 6). This is known also from a number of other acoustico-lateralis sensory epithelia (sacculus and utriculus—Chang *et al.*, 1992; Popper *et al.*, 1993; cochlea—Hudspeth, 1983; lateral line—Dale, 1980). The different hair-cell types of the sacculus and lagena of the gourami *Trichogaster trichopterus* (Pallas) are termed F1, F2 and F3 type (Popper & Hoxter, 1981) and these are similar in hair-bundle design to the striolar, extrastriolar and juxtastriolar hair cells of other vertebrates including mammals (Popper *et al.*, 1993; Saidel *et al.*, 1995; Richardson, G., pers. comm.). In terms of the lengths of stereocilia and kinocilia, and in their arrangement on the sensory epithelium (Popper & Hoxter, 1981), these three hair cells show similar features as, respectively, the middle, inner ring and outer edge hair cells described here (Table I; Figs 5 and 6). Whether, as in the gourami and other fish (Popper & Hoxter, 1981; Popper *et al.*, 1993; Saidel *et al.*, 1995), internal cellular differences accompany different hair-bundle types is not known.

Two, not necessarily mutually exclusive, possibilities may explain this heterogeneity among the hair cells of *M. zugmayeri* and *P. capito* canal organs. Firstly, as has been suggested for other acoustico-lateralis sensory epithelia with hair cells of different ciliary lengths (e.g. Hudspeth, 1983; Dale, 1980), the three hair-cell types may respond to different frequencies. Hair cells with long ciliary bundles are generally thought to be slow and sensitive to low frequencies and those with short ciliary bundles are thought to be fast and sensitive to higher frequencies (Kroese & van Netten, 1989). Canal organs are known to respond to a range of frequencies from 50 to 200 Hz (Münz, 1989; Coombs *et al.*, 1988; see Kalmijn, 1989 for cautionary remarks), and possessing different hair cells may be an adaptation to extend the frequency range received. However, all three hair-cell types are embedded in the same large, high-inertia cupula which probably resonates at a single frequency (Denton & Grey, 1988, van Netten & Kroese, 1989), so there are some problems with this explanation. It is possible that the cilia, and their differing lengths across the sensory plate, are important for coupling to the cupula in a specific way, as this is known to affect frequency tuning in such organs (Denton & Grey, 1989; Grey & Best, 1989; van Netten and Kroese, 1989).

Denton & Grey (1988) predict, based on mechanical parameters, that the widened head canals of *P. capito*, and other fish, are most sensitive to frequencies in the range of 5–15 Hz. Therefore, widened head canals seem best adapted for sensitivity to a narrow band of low-frequency water movements. This may correlate with movements of prey items. Montgomery (1989) has shown that

swimming crustaceans, a possible source of food for both *M. zugmayeri* and *P. capito*, set up disturbances in the low-frequency 0–40 Hz range. As the deep sea is relatively still and the only disturbances are likely to come from swimming crustaceans and fish, widened head canals may have become tuned, through evolution, to this relatively narrow window of noise. Furthermore, such neuromasts, through a combination of their large number of hair cells and canal morphology, may be up to 100 times more sensitive to water movements in their frequency range than surface-dwelling fish with narrow canals (Denton & Grey, 1988; Coombs *et al.*, 1989). The faster, high-frequency canals in surface dwellers are more suited to schooling and the more phrenetic requirements of life at the surface (Coombs *et al.*, 1992).

The second possibility to explain hair-bundle differences in the canal organs of *M. zugmayeri* and *P. capito* is that the hair cells are different ages and are part of a process of growth. As the fish grows, so must its neuromasts and if one presumes that hair cells are added through life, then the cells at the centre of a neuromast are the oldest and the ones at the edge the youngest. There is good evidence for this in other fish lateral lines (Jørgensen, 1989; Rouse & Pickles, 1991) and in other sensory epithelia (Corwin, 1985). Many of the cells in the centre of the neuromast in both *M. zugmayeri* and *P. capito* do appear ragged, less well organized and are more sparsely distributed than elsewhere. Hair cells from a variety of lateral line organs are thought to age and be replaced (Jørgensen, 1989). Also, as in *M. zugmayeri* and *P. capito*, hair cells near the edge have rather short bundles of cilia, a feature of newly developed cells (Corwin, 1985). In the cardinal fish *Apogon cyanosoma* Bleeker and the bullseye *Parapriacanthus ransonetti* Steindachner, new hair cells arise in pairs with opposing polarity, usually round the edge of the sensory plate, suggesting this is an active growth zone (Rouse & Pickles, 1991). These authors also observe some newly developed cells in all areas of the neuromast. This replacement process does not appear to occur in *M. zugmayeri* and *P. capito*, which exhibit outward growth only.

It may be that the only fully functional hair cells within these large neuromasts belong to the inner ring group. The most curious feature of these hair-cell bundles is the elongation of the first one or two rows of stereocilia (counting from the kinocilium). If these do form most of the responsive cells in the epithelium, the length of cilia may tune the response of the organ to the lower frequencies as Denton & Grey (1988) suggest from gross mechanical observations.

SUPERFICIAL ORGANS

As *M. zugmayeri* and *P. capito* have such a well-developed head canal lateral line system, apparently tuned specifically to low-frequency water movements, it becomes even more puzzling that their superficial system is also so well represented. Superficial neuromasts are generally thought to be sensitive to lower frequency vibrations (10–60 Hz) than neuromasts in canals (50–200 Hz, Münz 1989; Coombs *et al.*, 1988). Canal organs tend to be more sensitive to the acceleration component of motion, while superficial neuromasts respond best to the velocity component (Denton & Grey, 1989; Kalmijn, 1989; van Netten & Kroese, 1989). This may give a sufficient difference in function to explain the

development of both systems. However, as these stitches with their elongated lines of hair cells (and presumably elongated cupulae) are not well documented, their frequency selectivity and function are unknown.

It is notable that most stitches in both fish species run naso-caudally on the fish. As their direction of sensitivity is perpendicular to the stitch, the overall sensitivity of the system is very much biased dorso-ventrally. The nasal fan-shaped array in both species [Figs 3 and 4(c)] presents a possible exception as its sensitivity direction must also be a fan-shape in front of the fish. This may, therefore, be a critical region for obstacle avoidance (based on the damming pressure wave hypothesis of Dijkgraaf, 1963). Intriguingly, *Derichthys serpentinus* Gill, a deep-sea eel with similar stitch-like papillae on its head, also possesses a fan-shaped array of these organs near its snout. The full array of superficial organs and the way they sample the environment may allow direct pinpointing of prey items in *P. capito* and *M. zugmayeri*. This has been postulated for gobies, which also possess many lines of superficial organs on their heads (Marshall, 1986), and is well known in the two dimensional world of surface feeding fish (Bleckmann *et al.*, 1988). Intriguingly again, one of these fish, the freshwater hatchetfish *Gasteropelicus*, also has a fan-shaped array of superficial neuromasts in its nasal region (Schwartz, 1970 and unpublished observation).

In the gobies (Marshall, 1986; Webb, 1989*b*), and a number of other fish with many lines of cephalic superficial neuromasts (More & Burris, 1956), many lines of neuromasts run vertically. As most of these sets of neuromasts are also arranged with best sensitivity perpendicular to the row, these give the whole system a bias for detecting water movements in the naso-caudal direction. For bottom dwellers such as gobies, this may be the direction in which most disturbances occur (Marshall, 1986). One can imagine a fish on the sea bed with possible prey items streaming horizontaly past its head. In the more three-dimensional world of the deep sea, the opposite may be so and most food items may pass the heads of *P. capito* and *M. zugmayeri* vertically, thus accounting for the sensitivity bias in these species. Many crustaceans in the mesopelagic zone, possible prey items, are known to make daily vertical migrations, so here one can imagine a fish in mid-water with food items streaming past the head vertically.

Superficial neuromasts can be divided into primary and secondary organs, depending on their phylogenetic or ontogenetic origins (Coombs *et al.*, 1988; Webb, 1989*b*). Both may appear as lines of neuromasts, although secondary neuromasts may be placed more randomly (Coombs *et al.*, 1988), and, in both, lines may follow the course of head canals. In a number of fish, the superficial organs are clearly replacements for head canals lost secondarily through evolution (Blaxter, 1987; Coombs *et al.*, 1992). Also during development from larval to adult fish, lines of free-standing organs may sink into the head and be wholly or partially covered to form canals (Blaxter, 1987; Coombs *et al.*, 1989; Northcutt, 1989). These primary neuromasts may have an embryological origin separate from the secondary organs and are generally thought to represent a plesiomorphic condition (Northcutt, 1989). Secondary superficial neuromasts never become covered over but may follow the course of canals (in covered or uncovered state), and these are described as accessory neuromasts (Coombs *et al.*, 1988). Alternatively, they may proliferate and arise *de novo* anywhere on

the fish. Functionally, primary and secondary lines of neuromasts are often distinguishable, as the direction of sensitivity is along the row in primaries (reflecting their canal origin), and is usually perpendicular to the row in secondaries (Marshall, 1986; Coombs *et al.*, 1988).

The lines of superficial neuromasts on *P. wedli* are likely to be primary organs as they follow the established lines of head canals, possess highest sensitivity along the row and seem to replace the missing head canals (Table I). They show a further feature of replacement organs in that many supernumary organs at present compared with canal systems (Coombs *et al.*, 1988 and Table I). The superficial stitch organs of *P. capito* and *M. zugmayeri*, on the other hand, are likely to have a secondary origin. They are present in conjunction with existing canals, have highest sensitivity perpendicular to their long axis and appear in many areas on the head. Unlike any other lateral line organ, either through elongation of single neuromasts or joining of adjacent organs, the stitches of *P. capito* and *M. zugmayeri* form a continuous long thin sensory plate. Due to the huge number of hair cells present in stitches (compare 200 000 and 260 000 superficial hair cells respectively for *P. capito* and *M. zugmayeri* with around 40 000 for *P. wedli*), the fish is likely to be exquisitely sensitive to water displacements using this system alone.

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