Morphology of the Brain and Sense Organs in the Snailfish *Paraliparis devriesi*: Neural Convergence and Sensory Compensation on the Antarctic Shelf

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**ABSTRACT**

The Antarctic snailfish *Paraliparis devriesi* (Liparidae) is an epibenthic species, inhabiting depths of 500–650 m in McMurdo Sound. Liparids are the most speciose fish family in the Antarctic Region. We examine the gross morphology and histology of the sense organs and brain of *P. devriesi* and provide a phyletic perspective by comparing this morphology to that of four scorpaeniforms and of sympatric perciform notothenioids. The brain has numerous derived features, including well-developed olfactory lamellae with thick epithelia, large olfactory nerves and bulbs, and large telencephalic lobes. The retina contains only rods and exhibits a high convergence ratio (82:1). Optic nerves are small and nonpleated. The tectum is small. The corpus of the cerebellum is large, whereas the valvula is vestigial. The rhombencephalon and bulbospinal junction are extended and feature expanded vagal and spinal sensory lobes as well as hypertrophied dorsal horns and funiculi in the rostral spinal cord. The lower lobes of the pectoral fins have taste buds and expanded somatosensory innervation. Although the cephalic lateral line and anterior lateral line nerve are well developed, the trunk lateral line and posterior lateral line nerve are reduced. Near-field mechanoeception by trunk neuromasts may have been compromised by the watery, gelatinous subdermal extracellular matrix employed as a buoyancy mechanism. The expanded somatosensory input to the pectoral fin may compensate for the reduction in the trunk lateral line. The brains of *P. devriesi* and sympatric notothenioids share well-developed olfactory systems, an enlarged preoptic-hypophyseal axis, and subependymal expansions. Although the functional significance is unknown, the latter two features are correlated with habitation of the deep subzero waters of the Antarctic shelf. *J. Morphol.* 237:213–236, 1998.

**KEY WORDS:** Liparidae; *Paraliparis*; Antarctic; brain; evolution

The current sample of fishes subjected to neuroanatomical analysis is biased toward laboratory-reared or easily obtainable freshwater species. For example, goldfish (*Carassius auratus*); European carp (*Cyprinus carpio*), zebrafish (*Danio rerio*), channel catfish (*Ictalurus punctatus*), and centrarchid sunfishes have been frequently used as model organisms in neuroanatomical studies (e.g., Northcutt and Davis, '83; Davis and Northcutt, '83). Brain morphology and the causes of its variation remain unexplored in numerous higher level taxa (Butler and Hodos, '96). Because of this bias, general conclusions about brain diversification and evolutionary trends within fishes must be consid-
ered provisional until sampling includes phyletically and ecologically representative species.

In our previous examination of an ecologically unique group, the perciform notothenioids from coastal Antarctic waters, we suggested that: (1) unlike other well-studied lineages (Miller and Evans, '65; Kotrschal and Janger, '88; Kotrschal and Palzenberger, '92; Huber and Rylander, '92), the overall pattern of neuronal diversification among families of the suborder is not tightly correlated with either phyletic position or ecological factors (Eastman and Lannoo, '95), and (2) both degree of subependymal expansions and the size of nuclear regions that project to the neurohypophysis are correlated with the habitation of cold water (Lannoo and Eastman, '95). We did find several examples of a phylogenetic effect on brain morphology within some lower taxonomic units. At the time of our work, however, the extent of and relationships among notothenioid families and subfamilies were not well established, and this may have obscured the recognition of higher level phylogenetic effects. More completely resolved and reliable notothenioid cladograms are now available, and familial relationships have changed (Lecointre et al., '97; Ritchie et al., '97). These developments should enhance future attempts to interpret notothenioid brain morphology in a phylogenetic context.

In the present report, we examine the sense organs and brain morphology of an Antarctic scorpiform, the liparid snailfish Paraliparis devriesi, an epibenthic species from depths of 500–650 m in McMurdo Sound (Fig. 1). Using this species as a representative of Southern Ocean liparids, we first compare its neural morphology to the known neural morphology of four scorpiform species. We then use P. devriesi to probe the generalizations we proposed concerning the causes of neuronal divergence within the sympatric but phyletically distinct notothenioids (Eastman and Lannoo, '95; Lannoo and Eastman, '95). Sensory biology has been particularly well studied in notothenioids (Macdonald and Montgomery, '91; Montgomery and Pankhurst, '97; Montgomery and Macdonald, '98).

Unlike notothenioids, which like most perciforms are coastal fishes, Antarctic liparids are a secondary deep-sea group (Andriashev, '77) inhabiting the world's largest living space—the cold, dark ocean at depths greater than 200 m (Hedrich, '96). Although liparids are the major taxonomic element of the Antarctic ichthyofauna at depths greater than 500–600 m (Andriashev and Stein, '98), their central nervous systems have not been

Fig. 1. Views (A, lateral and B, ventral) of Paraliparis devriesi (SL = 170 mm) showing overall morphology, eye size, and location of the nostril (arrow) and cephalic lateral line pores. Neuromasts of the terminal or suprabranchial pore of the temporal canal above the gill slit are innervated by the posterior lateral line nerve. Ventral most pectoral rays are separated as a lobe; pelvic fins and disk are absent. From Andriashev (80), × 0.7.
studied. The purpose of the present study is to examine the gross morphology and histology of the nervous and special sensory systems of Paraliparis devriesi. This population of P. devriesi has the most southerly distribution of any known liparid, living in water with an average temperature of $-1.9^\circ C$ and experiencing a 4-month period of winter darkness. Our work provides insight into the biology of a species typical of the scores of other morphologically similar epibenthic liparids that have successfully colonized the shelf and upper slope of the world ocean, especially in the Antarctic Region.

PHYLOGENY, DISTRIBUTION, AND ECOLOGY OF THE LIPARIDAE

The Liparidae has a worldwide distribution with >200 species living from the intertidal zone to depths of 7,000 m (Stein and Andriashev, '90; Nelson, '94; Andriashev and Stein, '98). Liparids are included in the actinopterygian order Scorpioniformes, a predominantly marine group with >1,200 species (Nelson, '94). The family is monophyletic, but phyletic relationships among genera are uncertain (Kido, '88; Balushkin, '96). There is agreement that liparids have diversified away from ancestral inshore benthic habitats to deeper water column niches. Paraliparis is a phylogenetically derived deep-water genus exemplifying this trend (Andriashev and Stein, '98). Because liparids lack a swim bladder, habituation of the water column has involved reduction and loss of bone, replacement of bone by cartilage, and loss of the pelvic fins or disk (Burke, '30; Stein, '78; Andriashev, '86; Kido, '88). An additional modification of density, conferring neutral buoyancy on P. devriesi and probably many other liparids, involves expansion of a watery, gelatinous subdermal extracellular matrix (Eastman et al., '94; Jung et al., '95).

Liparids are best represented in polar waters and probably originated and radiated in the North Pacific Region with subsequent dispersal southward along the western coast of the Americas (Andriashev, '86, '91). Liparids are one of the few fish families having both boreal and austral centers of species diversity (Stein et al., '91). In the 200–2,000 m-deep waters of the Antarctic Region, liparids underwent a radiation complementing the shallow water radiation of periform notothenioids (Andriashev and Stein, '98). The 64 known Antarctic liparids, mostly members of the genera Paraliparis and Carproctus (Andriashev and Stein, '98), represent 31% of the 208 species of benthic fishes from the continental shelf and upper slope of the Antarctic Region. With the description of these new species subsequent to the publication of recent works on Antarctic fishes (Gon and Heemstra, '90; Eastman, '93), the Liparidae has surpassed the endemic Nototheniidae as the most speciose fish family in the Antarctic Region.

MATERIALS AND METHODS

Collection of specimens

Fieldwork and fixation of specimens and tissues were conducted at the U.S. McMurdo Station (77° 51' S, 166° 40' E) on Ross Island in the southwestern Ross Sea. We captured Paraliparis devriesi (Andriashev, '80) in the Erebus Basin of McMurdo Sound during November 1978, 1991, 1992, and 1994. The collection site (77° 47’ 2134 S, 166° 09’ 5400 E-GPS coordinates) was ~22 km from McMurdo Station. Paraliparises were taken in large, conical wiremesh bottom traps fished at a depth of 635 m through holes drilled in the annual sea ice. The traps were baited with chopped fish, left on the bottom for 3–5 days, and retrieved with an oceanographic winch. The bait attracted numerous scavenging amphipods and P. devriesi. We obtained 27 specimens that we used in studying various aspects of the biology of P. devriesi (Eastman et al., '94; Jung et al., '95). We used 12 of these specimens for the present study of brain and sense organ morphology. Both males and females were included in the sample, and all were adults averaging 179 mm TL (±3 mm SEM) and 64.9 gm (±3.79 gm SEM).

Microscopy

We obtained brains for gross morphology and histology from specimens that had been fixed by immersion in 10% formalin and stored in 70% ethanol. Brains were dehydrated in alcohol, cleared in Hemo-De, and embedded in paraffin according to standard procedures. We cut 10–12 µm thick transverse and longitudinal sections that were stained with 0.1% aqueous cresyl violet acetate. Other paraffin sections were stained with Bodian’s Protargol or with hematoxylin and phloxine. We stained the entire olfactory sac with cresyl violet acetae and then destained with acid alcohol. The resulting metachromasia facilitated the camera lu-
cida illustrations of the innervation pattern of the lamellae.

For light microscopy, we prepared samples of eye, olfactory apparatus, skin of the lips, oral and branchial cavities, pectoral fin, and trunk. These were fixed in Bouin’s solution, embedded in paraffin, sectioned at 7 µm, and stained using a variety of methods (Luna, ’68; Humason, ’79). We used Mayer’s hematoxylin and phloxine for general tissue structure, periodic acid-Schiff-Alcian blue (PAS-AB) at pH 2.5 and 1.0 for nonsulfated and sulfated glycosaminoglycans, Gomori’s aldehyde fuchsin for elastic fibers and Gomori’s trichrome and Mallory’s phosphotungstic acid hematoxylin for connective tissue. Bodian’s Protargol (Clarke, ’81) was effective in staining neurons in the olfactory epithelium when slides were incubated for 24 h at 50°C.

We used an ocular reticle in a compound microscope to obtain cell counts for calculating a convergence ratio in the central retina. We counted the number of nuclei in a field 100 µm in length in each of three different Bodian-stained sections from one individual. The convergence ratio (number of visual cells:number of ganglion cells) was expressed as the average of these counts.

We viewed and photographed sections using either a Nikon SMZ-U dissecting microscope or a Jenalumar compound microscope. Cell sizes were measured using an ocular micrometer. Photographs were taken using Kodak T-Max 100 black-and-white film. Terminology for brain areas follows Nieuwenhuys (’82), Northcutt and Davis (’83), Davis and Northcutt (’83) as followed by Eastman and Lannoo (’95), and from Wullimann et al. (’96). Terminology for the spino-occipital and spinal nerves is based on Parenti and Song (’96).

**RESULTS**

Initial examination of gross brain morphology (Fig. 2) of Paraliparis devriesi revealed several distinctive features including an elongate brain, large olfactory nerves, stalked telencephalic lobes, small optic nerves and tectum, small diencephalic inferior lobes, a large pituitary and saccus vasculosus, a large corpus cerebellum, and an extended rhombencephalon with evidence of extensive sensory input. To interpret this morphology we conducted a histological examination of both the sense organs and the brain.

**Vision**

The eyes (Fig. 1A) are unremarkable in external morphology and size (four times in head length), but on dissection the optic nerve (275 µm diameter) and extrinsic eye muscles were extremely small. The pupil is spherical. Accessory vascular structures such as a choroid rete are absent. The central nervous systems **Olfactory apparatus**

The nasal cavities have a single pore-like nasal opening (Fig. 1A) and a well-developed accessory nasal sac ventrolateral to the main cavity (Fig. 3). The oval olfactory rosette is arranged as a series of 11–12 primary lamellae originating from a central raphe (Figs. 3, 4A). There are no secondary lamellae. The posterior third or four lamellae share a common stem. This pattern, type G in the classification of Yamamoto (’82), is typical of scorpaeniforms and a variety of other teleosts. There is no sexual dimorphism in the size of the olfactory apparatus and associated brain regions as in some midwater and bathypelagic fishes (Marshall, ’79).

The pseudostratified columnar olfactory epithelium is composed of 7–9 cell layers. Our sample measured 100 µm (Fig. 4C), exceptionally thick for teleosts (Yamamoto, ’82). The epithelium thins to ~25 µm near the tips of the lamellae. This epithelium consists of three cell types: basal, sustentacular, and olfactory sensory. Silver staining identified the sensory cells as bipolar neurons possessing thin (1–2 µm) apical dendrites ~30 µm long (Fig. 4C–E). Cilia are evident, but we could not determine whether these were associated with the distal end of dendrites or with nonsensory columnar epithelial cells. The nuclei of sensory neurons were difficult to distinguish from those of the numerous sustentacular cells, but were occasionally evident because of their characteristic large nucleus with a single dark nucleolus. Nonsensory and sensory areas of the epithelium could not be distinguished as the neurons are distributed along the sides of the lamellae and in the trough between adjacent lamellae. In the lamina propria beneath the basal lamina, axons of the sensory neurons form fascicles of the olfactory nerve. The pattern of branching of the fascicles of the olfactory nerve into the lamina propria of the lamellae is illustrated in Figure 3.
The retina is thin, measuring 150–175 µm. The visual cell layer consists of a single type of photoreceptor (Fig. 4F,G). Using the criteria of Nicol ('89, p. 88), we identified these as rods. They possess elongate myoids and long (63–75 µm), thin cylindrical outer segments. The visual cell layer is 50–57% of the retinal thickness, a percentage closer to that seen in deep-sea fishes than in diurnal coastal fishes (Locket, '75). There are few bipolar and ganglion cells (Fig. 4G) and the convergence ratio (number of visual cells:number of ganglion cells) is 82:1. The retinal pigment epithelium is thin and compact, suggesting limited retinomotor movement.

**Taste buds**

We conducted a histological survey of the skin of the oral cavity and trunk to document the location of taste buds. There are a few taste buds on the upper lip and in the skin over the gill arches and a moderate number of buds on the lower lip. The only taste buds not associated with the oral cavity are located on the long, separated rays of the lower lobe of the pectoral fin (Figs. 1B, 4B).

**Lateral line system**

The cephalic lateral line system of Paraliparis is well developed (Fig. 1) and docu-
Fig. 3. Olfactory sac and lamellae of Paraliparis devriesi. A: Dorsolateral view of right olfactory sac showing arrangement of typical 12 lamellae and the darkly stippled accessory nasal sac extending ventrally from the lateral aspect of the floor of the sac. Part of the roof of the sac has been removed. ×10. B: Dorsal view of the branching pattern of distal olfactory nerve into bases of olfactory lamellae. Nerves and lamellae were differentiated by gross staining with cresyl violet acetate. ×32.
mented in Burke ('30), Andriashev ('86), and Stein and Andriashev ('90). The trunk lateral line system is reduced to a single suprabranchial pore above the gill slit (Burke, '30). Balushkin ('96, p. 284) suggests that this is actually a large superficial neuromast of the trunk lateral line. This pore is supplied by the posterior lateral line nerve, which is smaller in size than the anterior lateral line nerve.

Somatosensation

In Paraliparis devriesi, free nerve endings have been observed in the gelatinous subdermal extracellular matrix (Eastman et al., '94). In general, the somatosensory system of fishes is not well known (Atema et al., '88). The thickest nerve fibers identified from the skin of fishes have a diameter of no more than 1 µm. Free nerve endings in the skin are thought to mediate touch, temperature, and proprioceptive sensations (Harder, '75; Whitear, '71, '86a,b).

Gross description of brain and cranial nerves

The following description is based on a specimen designated PDE 15 (170 mm TL; weight 52.0 g). The brain length was 11,000 µm overall (rostral olfactory bulb to the obex) and 9,800 µm from the rostral telencephalon to the obex. Measurements are given below (see Histology).

Dorsal view

The telencephalon appears “stalked” by the unique morphology of elongated preoptic peduncles and a foreshortened tectum (Fig. 2A). The telencephalic lobes (Tel) are large, extending more laterally than the tectal lobes (Tec). The preoptic peduncles (nP) have pronounced lobes on their dorsomedial surfaces. The pineal gland (P) is large. The corpus cerebellum (CCb) is large, especially wide, and is the largest structure visible on the dorsal surface. The crista cerebellae (CC) are pronounced. The fourth ventricle is wide rostrally but tapers down quickly as vagal sensory lobes (Xs) fill the floor caudally. The obex is obscured by a large dorsal decussation of the spinal sensory nucleus (Sps). More caudally and bilaterally, Sps nuclei are unusually large and form prominent bulges (Fig. 2A,B). Along the dorsal spinal cord to at least the level of the second spinal nerve, Sps nuclei are prominent and together form a pronounced dorsal midline slit.

Lateral view

In lateral view (Fig. 2B) the telencephalic lobes (Tel) form the largest structures. The pituitary (Pit) is large, as is the saccus vasculosus (SV). The optic nerves (II) cross, with the right optic nerve, destined for the left eye, located dorsally. The tectum (Tec) is relatively small, about the size of the inferior lobes (IL). The corpus cerebellum (CCb) is the most dorsal structure in this brain but forms a low, flat lobe compared to its appearance in most other fishes. The lobe of the corpus is smooth, without externally visible bends or lobules. The crista cerebellae (CC) form large prominences rostrally but not caudally. A gap forms in the dorsal profile of the medulla from the caudal cristae to the dorsal prominence of Sps.

Ventral view

The most prominent features of the ventral brain (Fig. 2C) are the pituitary (Pit) and the saccus vasculosus (SV). Both are relatively large, each about size of the visible portion of the relatively small inferior lobes (IL).

Cranial and spinal nerves

The cranial nerves exhibit several unusual features (Fig. 2). The olfactory nerve (CN I) is hypertrophied, the optic nerve (CN II) is reduced. CNs III, IV, V, VI, VII, VIII, IX, and X are normal size. The anterior lateral line nerve (LL, ant) is larger than the posterior lateral line nerve (LL, post) and is the second largest cranial nerve (diameter), after the olfactory nerve (I).

The spino-occipital nerve consists of two dorsal and three ventral roots (Fig. 2B). As verified by dissection, this nerve and the first and second spinal nerves provide sensory and motor innervation of the pectoral fin. Distal to the spino-occipital ganglion, an anterior branch of the spino-occipital nerve joins with the pectoral branch to the ramus lateralis accessorius (Freihofer, '63), which provides taste fibers to the pectoral fin. This pattern of union is identical to that in Liparis florae (Freihofer, '63, p. 183).

Histology

Parasagittal sections

The following descriptions were made using a series of parasagittal sections from a specimen designated PDE 21 (168 mm TL; weight 57.3 g). A second specimen, PDE 16, was also examined (167 mm TL; weight 38.3
Figure 4
Of the four parasagittal sections chosen from PDE 21 for detailed examination, the most lateral section was in a plane near the lateral edge of the pituitary. The second section chosen was halfway between the first section and the midline. The third section was halfway between the previous section and the midline. This off-midline section is illustrated (Figure 5). The fourth section chosen was near the midline. In these sections the total length from the tip of the telencephalon to the spinal cord is between 9,000 µm (lateral) and 10,800 µm (medial).

Olfactory Bulb (OB). The olfactory bulb is 2,000 µm long (rostrocaudally) and sessile, located at the rostrocaudal edge of the telencephalon. Histologically, this nucleus is laminated with the usual four layers present (internal cellular layer [ICL], superficial olfactory fiber layer [SOL], external cellular layer [ECL], and glomerular layer [GL]) (Fig. 5). The internal cellular layer consists of spherical cells uniformly sized (7–9 µm).

Telencephalon (Tel). The bilateral lobes of the telencephalon are relatively large (length 2,000 µm, depth 1,400 µm). The telencephalon is positioned at the end of a preoptic peduncle and is therefore located a distance (750–1,100 µm) from the tectum. The telencephalic hemispheres are shallow (1,000 µm) and ellipsoid, with rostral and caudal regions being shallower than the central region. Within the telencephalon, neuronal cell soma tend to be sparse, but neurons are dense in the transition between the dorsal and ventral divisions and in the rostral portion of the ventral division. The neurons are primarily spherical, ranging in size from 7–10 µm. There is no obvious cellular hypertrophy within the telencephalic nuclei.

Pineal (P). The pineal organ is large (~300 µm long × 300 µm high) and positioned caudal to an elaboration of the tela choroidea, which is ~300 µm long and 200
μm high. Pinealocytes are spherical, uniform in size, small (5 μm), and cluster peripherally.

Preoptic Region (nP). At the preoptic peduncle, the forebrain bundles appear as rostrocaudally directed fibers. Optic nerve fibers run from rostral ventral to caudal dorsal and form the rostral surface of this exposed diencephalic region. Laterally, the preoptic region is thick (500 μm deep) and composed of an area sparsely populated by cells. Medially, the dorsal portion of the central half of the preoptic peduncle is composed of large (30–40 μm) preoptic nucleus pars gigantocellularis (nPg) neurons. These neurons exhibit substantial preservation artifacts and were undoubtedly larger in life. This nPg cell cluster is interrupted in two areas by fiber bundles running rostrodorsally to caudodorsally. One bundle is positioned rostroventrally, the other caudodorsally. Ventrally adjacent to the nPg cell cluster is a thin layer of small (10 μm), preoptic nucleus pars parvocellularis (nPp) neurons. Ventral to this region is a thicker layer of smaller (7–9 μm) nPp neurons.

Medially, the total length (~600 μm) of the preoptic peduncle is composed of neurons (Fig. 5). The rostral portion of this region is composed of nPp neurons. The caudal portion is composed of larger (12–20 μm) nPm (preoptic nucleus pars magnocellularis) neurons. The dorsal portion of this caudal region contains a small number of nPg neurons.

Pituitary (Pit). The pituitary is large (1,100 μm long, 500 μm deep), about as large as the inferior lobes. Cells within the pituitary are small (3–6 μm), spherical, similar in size to both the adenohypophysis and neurohypophysis, and cluster along the surface of this organ. Cells (epithelial) of the adenohypophysis are most numerous.

Inferior Lobes (IL). The inferior lobes are relatively small (length ~1,300 μm) and shallow (between 500 and 900 μm). Within each lobe, three ventricular lumina are present, consisting of portions of the lateral recess and a diverticulum of the caudal recess.

Saccus Vasculosus (SV). The saccus vasculosus is relatively large (1,300 μm long, 800 μm deep) and equals in area the inferior lobes. The saccus contains coronet cells that are medium size (6–8 μm in diameter).

Tectum (Tec). The tectum is small (length ~1,500 μm long, 600 μm high). The laminae described by Northcutt ('83) and Butler ('92) for other teleosts (from central to peripheral the periventricular gray zone, deep white zone, central zone, and superficial white and gray zone) are present. Cells within the periventricular gray zone are medium size (7–10 μm), dense, and spherical. Within the remaining migrated laminae, cells are sparse, medium size, and either spherical or fusiform shaped.

Torus Semicircularis (TS). The torus semicircularis is moderately sized (length ~800 μm). The cells of this midbrain relay nucleus are spherical and medium size (7–10 μm), similar in size to tectal cells.

Cerebellum. The valvula cerebellum (VCb) is extremely small (~200 μm long and 250 μm deep). The valvula is represented by a small dorsal upturning, which consists of a continuation of the molecular layer of the corpus, and a small rostrally and ventrally positioned granular cell layer.

The corpus cerebellum (CCb) is large (2,500 μm long, 1,500 μm deep), dorsally positioned, and caudally directed. Granule cells are spherical and small (3–5 μm). Purkinje and/or eurydendroid cells are larger (14–18 μm). A transverse sulcus along the ventrocaudal surface produces a major and a minor lobe.

The eminentia granularis (EG) forms a large group of cells (~400 μm x 400 μm) located ventral to the molecular layer of the CCb. Efferent EG fibers, the crista cerebellaris (CC), are short (~1,900 μm) and end abruptly at the middle medullary level.

Medulla. The medulla is ~1,750 μm deep. Dorsally, it consists of two distinct neuropils, one rostral, the other caudal. The rostral neuropil is elongate (~1,500 μm long and 800 μm deep) and forms the vagal sensory lobe (Xs). The caudal neuropil is larger (1,500 μm long, 1,800 μm deep), globose, and more dorsally positioned. This neuropil is the spinal sensory nucleus (SpS).

In the ventral medulla, medium size (10–12 μm) motor neurons of cranial nerves V and VII are present. More caudally, vagal motor neurons are positioned ventral and caudal to Xs. More medially, medium-size (12–18 μm), spherical to fusiform shaped neurons are present. These neurons are likely efferent octavolateralis cells.
Within the caudal medulla, the fourth ventricle is \(\sim 800 \mu m\) deep. The Sps neuropil is present and continues into the spinal cord. Caudal to fourth ventricle, the Sps neuropil is \(\sim 1,000 \mu m\) deep (compared to a total brainstem depth of \(\sim 1,300 \mu m\)).

Spinal Cord. The spinal cord is \(\sim 1,000 \mu m\) deep. It contains a prominent Sps that extends through at least the rostral (S2, 3 level) cord.

Transverse sections

The following descriptions were made using 28 transverse sections from the brain of PDE 23 (160 mm TL, weight 26.8 g). Fourteen of these transverse sections are illustrated (Figs. 6–9), and were chosen for the morphological features they demonstrated, rather than according to predetermined intervals.

Olfactory Bulb (OB). The olfactory bulb is kidney shaped, concave medially, and wider dorsally than ventrally. As detailed above and delimited here, the usual four concentric layers are present (Fig. 6A).

Telencephalon (Tel). In the rostral telencephalon the medial, dorsal, lateral, and central nuclei of the dorsal telencephalon (Dm, Dd, Dl, and Dc, respectively) are present (not shown, see Fig. 6B). The Dm borders the medial and dorsal medial surfaces of the telencephalon and consists of small cells, less dense along the medial surface, and more dense dorsally; cells are denser than in the laterally adjacent Dd. The sulcus ypsilorniformes, which separates the Dm from the Dd in most teleosts, is reduced or absent in this species. The Dd comprises the dorsalmost telencephalon and consists of small cells. The Dl consists of a thick layer of small cells that forms the lateral border of the telencephalon. The Dd and the Dl are composed of cell clusters arranged in a number \(\langle 10\rangle\) of concentric rows that parallel the dorso lateral surface of the telencephalon. The Dc occupies the center of the telencephalon and consists of irregularly arranged small cells.

In addition to the dorsal nucleus of the ventral telencephalon (Vd), the ventral and lateral nuclei of the ventral telencephalon are also present (Vv and VI, respectively). The Vd is composed of a dense cluster of small cells; cells are most dense near the ventricle and scatter laterally. The Vv consists of small, densely clustered cells positioned along the ventricle, ventral to the Vd. The VI is composed of two portions, a medial portion positioned along the ventromedial surface of the telencephalon laterally adjacent to the Vv, and a lateral portion positioned along the lateral surface of the ventral telencephalon.

In the dorsal portion of the midtelencephalon (Fig. 6B), the Dm, Dd, Dc, and Dl and the posterior nucleus of the dorsal telencephalon (Dp) are present. At this transverse level, cells of the Dm are arranged in rows oriented in concentric lines parallel to the dorso medial surface of the telencephalon. The ventromedial most portion of the Dm consists of larger cells (10 \(\mu m\)) without obvious orientation. The Dc consists of two recognizable portions, a dorsolateral cluster of small, scattered cells, and a ventromedial cluster of more darkly staining cells. The Dp consists of larger, darkly staining cells arranged in concentric rows, fewer rows \(\langle 6\rangle\) than are present in the rostral DI.

In the ventral portion of the midtelencephalon (Fig. 6B), the Vd and Vv are present. The Vd is smaller than at more rostral levels. The Vv is less dense at this level than at rostral levels. The central nucleus of the ventral telencephalon (Vc; not shown) is small and present in sections between this level and the rostrally adjacent level described above. In the lateral portion of the ventral telencephalon, the endopeduncular nucleus (E) consists of a loose cluster of darkly staining cells.

In the posterior telencephalon at the level of the anterior commissure, the dorsal telencephalon is represented primarily by the Dp, with caudal portions of the Dm and Dd present dorso medially, and the caudalmost Dc present centrally. The ventral telencephalon is represented by the caudal portion of the Vv, positioned immediately dorsal to the anterior commissure (AC).

Remnants of the Dp are visible dorsolaterally at the telencephalic-diencephalon junction (Fig. 6C). At this level, the medial and lateral forebrain bundles (MFB and LFB, respectively; present on either side of the endopeduncular nucleus) are present and large.

Preoptic area. Rostrally, the parvocellular preoptic nucleus (nPp) is present along the central and ventral medial surface (Fig. 6C). More caudally, the nPp is situated ventral to the large cells of the magnocellular preoptic nucleus (nPm), which in turn is positioned ventral to the larger cells of the
Figure 6
gigantocellular preoptic nucleus (nPg; Fig. 6D). Farther caudally, the nPp and nPg are present (Fig. 6E).

Thalamus. The most rostral portion of thalamus consists of the ventral thalamus (ventromedial nucleus, VM; Fig. 6E). In the dorsal thalamus, the dorsal portion of diencephalic ventricle opens and, therefore, the cell orientation away from the ventricle is in a ventral rather than the usual lateral direction (Fig. 6E). The dorsal thalamus consists of the nucleus A rostrally and the central posterior nucleus (CP) caudally (not shown); the nucleus A forms a lobe that projects into the diencephalic ventricle. Nucleus A consists of small but variably sized cells (4–8 µm); the CP is composed of cells 6–12 µm, with the larger cells positioned laterally. In the caudal portion of the ventral thalamus, the VM contains cells 8–15 µm in diameter.

Hypothalamus. The rostral portion of the ventral hypothalamic nucleus (HV) is positioned ventral to the preoptic area (Fig. 6E). Cells of the dorsal hypothalamic nucleus (HD) spread laterally, where they surround the lateral recess (LR) of the inferior lobe (IL). The inferior lobes are small. The ventral surface of the rostral IL contains a dense cluster of small cells that we refer to as the lateral nucleus of the hypothalamus (LH); these cells are medium in size (6–8 µm) and form a lobe. Within the IL of the hypothalamus, the HD is present along the LR, the LH continues to form a lobe, and medium-size (6–8 µm) cells of the nucleus diffusus (ND) are present along the lateral margin (Fig. 7A).

Fig. 6. Transverse sections through the brain of *Paraliparis devriesi* from the olfactory bulb (A) to the diencephalon (E). x 40. Dc, dorsal central subdivision of the telencephalon; Dd, dorsal dorsal subdivision of the telencephalon; Dm, dorsal medial subdivision of the telencephalon; Dp, dorsal posterior subdivision of the telencephalon; E, entopeduncular nucleus of the telencephalon; ECL, external cellular layer of the olfactory bulb; GI, glomerular layer of the olfactory bulb; Hv, ventral division of the periventricular hypothalamic region; ICL, internal cellular layer of the olfactory bulb; nLT, lateral tuberal nucleus; nPg, gigantocellular region of the preoptic nucleus; nPm, magnocellular region of the preoptic nucleus; nPp, parvocellular region of the preoptic nucleus; nPT, posterior tuberal nucleus; Pit, pituitary gland; PG, preglomerular complex of the diencephalon; SC, suprachiasmatic nucleus; SOF, superficial olfactory fiber layer of the olfactory bulb; Vd, dorsal subdivision of the ventral telencephalon; VM, ventromedial nucleus of the thalamus; Vv, ventral subdivision of the ventral telencephalon.

Other diencephalic structures. The suprachiasmatic nucleus (SC) consists of small cells (3–7 µm) positioned lateral to the nPp (Fig. 6D). The medial and lateral forebrain bundles (MFB and LFB, respectively) are large. The MFB is prominent along the ventricular surface between the preoptic area (nP) and the ventral thalamus (Fig. 6E). The LFB forms a lobe lateral to the endopeduncular nucleus (Fig. 6C,D). The few cells of the lateral tuberal nucleus (nLT) are medium in size (8–15 µm) and located lateral to the HV along the ventral margin of the diencephalon (Fig. 6E). Neurons of the preglomerular complex (PG) are medium in size (8–10 µm) and located along the central portion of the lateral edge of the diencephalon (Fig. 6E). Smaller (4–6 µm) cells of the posterior tuberculum (TP) line the ventricle between the VM and the HD. Centrally, small-to-medium-size cells (5–7 µm) of the glomerular nucleus (G) are present (Fig. 7A).

Cerebellum. The corpus cerebellum (CCb) is large (Figs. 7B, 8A), occupying an area larger than the underlying brainstem (Fig. 7B). The CCb is lobated; the lobe is caudally directed over fourth ventricle (Fig. 8A). The granule cells of the eminentia granularis (EG) lie subpially, ventral to the molecular layer of the CCb. The crista cerebellaris (CC) forms a distinct structure, capping the medulla dorsilaterally (Fig. 8A,B).

Octavolateralis Region. Aside from the disparity in size between the anterior and posterior lateral line nerves, the octavolat-
Fig. 7. Transverse sections through the brain of Paraliparis devriesi from the rostral mesencephalon (A) to the isthmus (B). ×40. CCb, corpus division of the cerebellum; G, glomerular complex of the diencephalon; MLF, medial longitudinal fasciculus; SV, saccus vasculosus; Tec, tectum of the mesencephalon; TL, torus longitudinalis of the mesencephalon; III/IV, mesencephalic oculomotor complex.
Fig. 8. Transverse sections through the brain of Paraliparis devriesi from the medulla (A) to the bulbospinal junction (C). ×40. CC, crista cerebellaris of the rhombencephalon; CCb, corpus division of the cerebellum; MLF, medial longitudinal fasciculus; MON, medial olfactory nucleus; ON, optic nerve; RF, reticular formation; Vs, spinal sensory division of the trigeminal nerve; Xm, visceral motor division of the vagus nerve; Xs, visceral sensory division of the vagus nerve.
eralis region appears to be generalized, without either hypertrophied nuclei or nerves (Fig. 8A, B).

Other brainstem structures. The spinal trigeminal tract (Vs) forms prominent lobes in the caudal medulla (Fig. 8A–C). Internal arcuate fibers are also prominent (Fig. 8B). The brainstem motor nuclei that are visible in our transverse sections include CNs VII, IX, and X. Centrally, the cell bodies of CN VII motor neurons extend from dorsomedial to ventrolateral. The glossopharyngeal motor neurons (IXm) are large (15–18 µm) and disjunct rostrally from the similarly sized and extensive neurons in the vagal motor cluster (Xm; Figs. 8C, 9A–B).

The medial longitudinal fasciculus (MLF) is present throughout the brainstem (Figs. 7A,B, 8A–C, 9A–D). This tract is extensive in area, especially in the bulbospinal junction and the rostral spinal cord (Figs. 8C, 9A–D).

Reticular formation (RF) neurons are large (8–18 µm) and are present throughout the brainstem (Figs. 8A–C, 9A). They are replaced in the spinal cord by the motor neurons of the ventral horn (Spm; Fig. 9B–D).

Vagal Sensory Lobes (Xs). The vagal sensory lobes are large and form medial lobes that define the ventrolateral walls of IVth ventricle (Figs. 8B,C, 9A). The bulk of each vagal lobe lies rostral to the entrance of the vagal nerve. Caudally, the Xs lobes meet along the dorsal midline (Fig. 9A).

Spinal Sensory Nucleus (Sps). The spinal sensory nuclei are large (Fig. 9A–D) and associated rostrally with a dorsal commissure. Caudally, the Sps and the dorsal funiculi form a large dorsal area (Fig. 9A–D). Most caudally, the Sps forms lobes that together create a dorsal midline sulcus (Fig. 9C,D).

Interstitial Nucleus of Cajal (nC). This midline nucleus is present dorsally (Fig. 9B).

Supramedullary Neurons. A number of large (50 µm) neurons are located dorsomedial to the rostral spinal cord (Fig. 9C). These neurons resemble the supramedullary neurons (SM) of Bennett et al. (67). The function of supramedullary neurons is unknown.

**DISCUSSION**

Neural morphology is the combined result of persistent phylogenetic features—those inherited from ancestral species (plesiomorphic in cladistic terminology), and derived features (apomorphous in cladistic terminology), and those established during speciation (cladogenesis). Whereas the brain of Paraliparis devriesi is unusual, interpretations of the origins—generalized within the family or derived with speciation—and causes of this brain morphology are hindered by the absence of studies of closely related species. To provide a phylogenetic perspective regarding the origin of the brain morphology of P. devriesi, we first survey the sensory and nervous systems of four species of scorpaeniforms and then comment on the Antarctic deep-shelf habitat as it relates to the evolution of liparids and notothenioids.

**Comparative neurological studies of scorpaeniform teleosts**

Euteleostean fishes are so numerous that entire families, even orders, are without neuroanatomical description. For example, a recent compilation contains no mention of the neuroanatomy of any of the 1,200 scorpaeniforms (Butler and Hodos, ’96). Whereas the gross brain morphology of scorpaeniforms has not been previously described, several aspects of scorpaeniform neuroanatomy have been investigated (Table 1), including a description of the cranial nerves of the scorpaenid Scopraena scrofa (Allis, ’99), documentation of the pattern of the ramus lateralis accessorius in 15 scorpaeniforms (Freihofer, ’83), and studies of the innervation and chemosensory properties of the free pectoral fin rays in triglids (Finger, ’82; summaries in Whitear, ’86a and Kotrschal, ’96). Furthermore, several aspects of the brains of the scorpaenid Sebastiscus marmoratus have been studied, including the retinal ganglion cells (Ito and Murakami, ’84), thalamic fiber connections (Ito et al., ’86), ascending projections of the spinal dorsal horn (Murakami and Ito, ’85), telencephalic ascending acousticolateral system connections including the nucleus preglomerulosus (Murakami et al., ’83), connections of the telencephalon (Murakami et al., ’86), and the telencephalic area dorsalis pars lateralis (Yamane et al., ’96).

With the exception of observations on the degenerate retina of a liparid inhabiting waters at a depth of 6,000 m by Munk (’64, ’66), no work has been conducted on the sensory and nervous system biology of liparids.

In order to compare a more closely related species and to provide a basis for the discussion of the neural features in Paraliparis devriesi, we dissected the brain of the North Atlantic lumpfish, Cyclopterus lumpus (Table
Fig. 9. Transverse sections through the brain of Paraliparis devriesi from the bulbospinal junction (A) to the SN1-SN2 level of the spinal cord (D). ×40. MLF, medial longitudinal fasciculus; nC, interstitial nucleus of Cajal; RF, reticular formation; SM, supramedullary neurons; Spm, spinal motor nucleus; Sps, spinal sensory nucleus; Xm, visceral motor division of the vagus nerve; Xs, visceral sensory division of the vagus nerve.
1), a representative of the family Cyclopteridae. Until recently liparids were placed in the lumpfish family Cyclopteridae, and it is likely that cyclopterids and liparids form a monophyletic group (Nelson, '94). Cyclopterus lumpus is a sedentary inshore species with a maximum depth range of a few tens of meters (Bigelow and Schroeder, '53). Most neural features in P. devriesi depart from the generalized condition (Table 1).

Evolution of liparids and notothenioids and the Antarctic shelf

Although notothenioids dominate Antarctic shelf habitats <500 m deep, liparids prevail at mid-slope depths of 800–1,000 m (Andriashev and Stein, '98). Antarctic liparids have a North Pacific origin and have been considered to be a somewhat younger faunal element than the indigenous notothenioids (Andriashev, '65, '87; Eastman, '93). Liparids are hypothesized to have arrived in the Antarctic as deep-sea migrants during the Miocene, 25–5 mya. As the fish fauna of the Antarctic shelf and slope becomes more completely known, a more complicated chronology is likely (Andriashev and Stein, '98). For example, divergence times inferred from two different classes of molecules suggest that phyletically derived nototheniid groups may be younger than previously suspected, probably diversifying no longer than 15 mya (Bargelloni et al., '94; Chen et al., '97) and possibly much more recently. Moreover, the radiation of trematomid nototheniids is estimated to have taken place during the Pliocene, ~3.4 mya (Ritchie et al., '96). Equivalent molecular data are not available for liparids.

These faunal ages, especially the length of time in a particular habitat, are important in evaluating different degrees of adaptation to a similar environment in unrelated groups of fishes (Montgomery and Pankhurst, '97;

### Table 1. Comparison of the brain of five scorpaeniform teleosts, the generalized Scorpaena scrofa (from Allis, '09) in ventral view, the generalized Sebastiscus marmoratus (from Ito et al., '86; and Murakami et al., '86), the derived Prionotus carolinus (from Finger, '82) in dorsal view, Cyclopterus lumpus (Eastman and Lannoo, unpublished data) and the derived Antarctic Paraliparis devriesi, in ventral view

<table>
<thead>
<tr>
<th>Structure</th>
<th>Scorpaenidae</th>
<th>Triglidae</th>
<th>Cyclopteridae</th>
<th>Liparidae</th>
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(Symbols: ø = presumed actinopterygian generalized condition; ● = structure enlarged or augmented; ø = structure reduced; — = structure not examined).

1Sessile.
2DI large.
3Right nerve dorsal.
4Pleated.
5Uniformly wide.
6Narrow.
7Caudally truncated.
8Anterior larger.
9One dorsal root, two ventral roots.
10Two dorsal roots, three ventral roots.
11Derived, chemosensory.
Montgomery and Macdonald, '98). Although the sensory environment is similar, different evolutionary time scales, longer by a few tens of millions of years in the phyletically basal deep-sea fishes, may account for the more extreme sensory adaptations in primary deep-sea fishes compared to the more recently derived notothenioids (Montgomery and Macdonald, '98) or liparids, which are a secondary deep-sea group. Given the current uncertainty about the age of the Antarctic fish fauna, we will assume that liparids and notothenioids have occupied the Antarctic shelf for approximately the same length of time—10–15 my.

Interpretation of the sensory systems and brain of Paraliparis devriesi

The gross brain morphology of Paraliparis devriesi differs in almost every aspect from that of other scorpaeniforms (Table 1). It differs from notothenioids as well, and comparisons are detailed below.

Olfaction

Based on the histology of olfactory lamellae and on the size of the olfactory nerves and bulbs, olfaction appears to be an important sense in Paraliparis devriesi. The olfactory apparatus is also well developed in Cyclopterus lumpus, but not in the more generalized scorpaenid Scorpaena scrofa. In P. devriesi, olfaction is likely used for identification of mates in the deep-sea rather than for locating food (Marshall, '67). The cephalic lateral line system and possibly taste are more important in prey detection (see below).

Vision

The visual system of Paraliparis devriesi is reduced compared to more generalized shallow-water scorpaeniforms (Table 1). The visual system includes a retina consisting exclusively of rods, a high convergence ratio of photoreceptors to ganglion cells, a non-pleated optic nerve, a small tectum, and small extrinsic eye muscles. This morphology is consistent with two environmentally determined low-light conditions: life at depths of 500–650 m, and habitation of a polar region characterized by four months of darkness.

Most teleosts have both rods and cones in the visual cell layer of the retina (Nicol, '89), as do all Antarctic notothenioids examined to date (Eastman, '88). Rods, responsible for vision in dim light, are frequently the only photoreceptor present in fishes living at depths of >1,000 m (Munk, '66; Marshall, '79; Nicol, '89). A photoreceptor layer consisting exclusively of rods has also been documented in two species of Comephorus, deep-living (150–1,500 m) cottoid scorpaeniforms from Lake Baikal, an environment with a photic regime similar to the deep sea (Pankhurst et al., '94; Smirnova, '95). The liparid Liparis liparis inhabits the intertidal zone to depths of 300 m (Stein and Able, '86) and, unlike Paraliparis devriesi, has cones in its retina (Munk, '64, Plate XIII, Fig. 7).

The convergence ratio of Paraliparis devriesi is intermediate between the 58:1 of Dissostichus mawsoni (Eastman, '88), perhaps the most scotopic notothenioid, and those of some deep-sea fishes like Bathylagus in which ~150 visual cells converge on a single ganglion cell (Munk, '66, p. 53). The retina of P. devriesi shows no indication of degeneration as does the retina of the extremely deep-living (6,660 m) liparid Careproctus kermaeensis (Munk, '64, '66).

The presence of only rods and the relatively high convergence ratio (82:1) suggest enhanced visual sensitivity but with some compromise in acuity or resolution (Nicol, '89:125). The retina of Paraliparis devriesi is intermediate between shallow and deep-living liparids, but is more specialized for vision under dim light than is the retina of sympatric notothenioids, a coastal perciform group.

The functional significance of pleated optic nerves is unknown, but this condition is thought to be a basal feature of euteleosts (Northcutt and Wullimann, '88). The non-pleated optic nerve of Paraliparis devriesi represents a simplification, perhaps the result of a reduction in numbers of retinal afferents. Tectal size can also reflect the number of retinal afferents (Butler, '92) and is clearly reduced in P. devriesi.

Taste

Paraliparis devriesi has taste buds on the long, separated rays of the lower lobe of the pectoral fin. The shallow-living North Atlantic liparid Liparis inquilinus also has taste buds in this location (Able and Musick, '76). These buds in liparids are innervated by the pectoral branch of the ramus lateralis accessorius derived from the facial-vagal trunk (Freihofer, '63). The heavy innervation pattern and observation of captive specimens suggest that the liparid pectoral fin, espe-
cally the lower lobe, is an important sensory surface used in exploring the environment (Frehofer, '63; Able and Musick, '76; Gosline, '94).

Lateral line mechanoreception

In Paraliparis devriesi, the anterior lateral line nerve, the second largest cranial nerve, is larger than the posterior lateral line nerve. This morphology reflects the importance of the cephalic lateral line and the reduction in the trunk lateral line.

Brain and spinal cord

Compared to more generalized scorpaeniforms, Paraliparis devriesi possesses a relatively large telencephalon, preoptic area, pituitary, subependymal region, medulla, spino-occipital nerve, spino-sensory nucleus, and dorsal funiculus/dorsal horn (Table 1). By the same comparison, P. devriesi has a relatively small torus semicircularis, valvula cerebelli, and crista cerebellaris. Paraliparis devriesi and Cyclopterus lumpus share relatively large olfactory nerves and bulbs and a large anterior lateral line nerve. These features may be synapomorphies of the liparid-cyclopterid clade.

The stalked telencephalon is one of the most unusual features of the brain of Paraliparis devriesi. This morphology is also known from chimaeriform fishes (Northcutt, '78), where it is the result of a packing problem—the position and size of the eyes impose constraints on the neurocranium. This is not the situation in P. devriesi, where the eyes are not unusually large, dorsal, nor closely positioned.

Although Mauthner neurons are generally present in scorpaeniforms (Zottoli, '78), among liparids they are present in shallow water Liparis but absent in deep-water Paraliparis (Bone and Marshall, '83). This is testimony to the derived nature of the genus Paraliparis and reflects the general trend toward reduction or loss of these neurons in anguilliform swimmers and sedentary species.

Some of the derived sensory and neural features of Paraliparis devriesi are associated with a deep-water habitat. These include: a small optic nerve, only rods in the photoreceptor layer of the retina, a well-developed cephalic lateral line, a large olfactory nerve, a thick olfactory epithelium with the sensory cells distributed over much of the surface of the lamellae, a small tectum, and expanded sensory input to the rhombencephalon. Paraliparis devriesi does not, however, exhibit sense organ and brain specializations characteristic of primary deep-sea fishes. They do not have tubular eyes, an extremely elongated body and lateral line, sexual dimorphism in the size of the olfactory apparatus and telencephalon, hypertrophied octavolateralis system, papillate neuromasts, or photophores (Montgomery and Pankhurst, '97; Montgomery and Macdonald, '98). In this sense P. devriesi is intermediate between the phyletically derived notothenioids, a coastal perciform group with which it is sympatric in McMurdo Sound, and the primary or true deep-sea pelagic fishes that are confined to phyletically basal (and presumably older) euteleostean superorders (Nelson, '94; Haedrich, '96). This is consistent with differences in the degree of specialization of the sensory systems between notothenioids and primary deep-sea fishes (Montgomery and Pankhurst, '97; Montgomery and Macdonald, '98), as well as with the designation of deeper dwelling liparids as secondary deep-water fishes (Andriashev, '77).

There are other derived characteristics of the brain of Paraliparis devriesi that defy simple explanation: the preoptic-pituitary hypertrophy and a suite of features that may be linked to the expanded spinal sensory nucleus (Sps). The hypertrophied preoptic area (nP) of P. devriesi is reminiscent of the hypertrophied preoptic area in the most phyletically derived notothenioid species (Lannoo and Eastman, '95). The notothenioids with the greatest preoptic hypertrophy inhabit the coldest (~1.9°C) shelf waters (Lannoo and Eastman, '95). There is, however, a major difference between notothenioids and liparids. The correlation between the size of nP and nLT neurons observed in notothenioids is absent in liparids. In P. devriesi, nLT consists of a relatively few, small cells. The causal basis for this relationship between nP and the size of the pituitary remains an open question and will be difficult to pinpoint. It may be that the same factors acting to produce preoptic hypertrophy in notothenioids underlie the preoptic hypertrophy in Paraliparis. Both liparids and notothenioids have subependymal expansions, and these curious enlargements of the vascular lacunae of the ventricular lining are correlated with the habitation of subzero waters.
The second set of features, the expanded somatosensory region of the rhombencephalon and rostral spinal cord, may be indirectly related to a distinctive somatic feature of Paraliparis devriesi, the presence of a watery, gelatinous, subdermal extracellular matrix (SECM). The SECM accounts for one-third of the body weight of P. devriesi and serves as a buoyancy agent (Eastman et al., '94). The SECM in P. devriesi may affect the performance of epidermally or dermally positioned neuromast mechanoreceptors. To function properly, neuromasts require a stable substrate against which incoming water displacements can be evaluated. In contrast, the SECM is gelatinous and therefore a less stable substrate than typical hypodermal and muscle tissue. For P. devriesi, body movement or water motion may create deformation waves in the SECM and skin. Since the SECM is 97% water (Eastman et al., '94), which is nearly incompressible, the SECM may not be stabilized even at the 500–650 m depths inhabited by P. devriesi. The ability of neuromasts to detect water displacements may, therefore, be compromised. Not only do neuromasts function optimally when they are stable relative to the stimulus, but brains have evolved elaborate feedback mechanisms to reduce noise interference in octavolateralis systems (Maler and Mugnaini, '94; Montgomery and Bodznick, '94; Montgomery et al., '95; Janssen, '96).

We suggest that the extensive SECM in Paraliparis devriesi may have had consequences for the sensory and neural biology. The SECM is thickest over the trunk, and the trunk lateral line is reduced to a single suprabranchial pore innervated by a small posterior lateral line nerve. The number and extent of free neuromasts on the trunk are unknown. The caudal crista cerebellares, responsible for feedback to the first-order mechanosensitive nucleus (MON) from the cerebellar eminentia granulares is also reduced. The torus semicircularis, the second-order lateral line nucleus, forms a small, shallow lobe. Loss of trunk canal neuromasts is common; fishes that lack scales, like P. devriesi, frequently lack trunk lateral line canals (Coombs et al., '88). It is noteworthy that in P. devriesi the SpS, a first-order somatosensory nucleus mediating touch, is hypertrophied, as are the dorsal horns and funiculi of the spinal cord. As mentioned previously, somatosensory input to the pectoral fin is expanded, possibly compensating for the reduction in the trunk lateral line.

How does this information on sensory biology relate to what is known about the ephibenthic life of Paraliparis in general and Paraliparis devriesi in particular? There are no direct observations of P. devriesi swimming or feeding at depth in McMurdo Sound. They are attracted to bottom traps baited with chopped fish, but we do not know whether they are detecting an odor plume or the swarms of scavenging amphipods that are also drawn to the bait. A similar feeding behavior is seen in Paraliparis bathybius living at 4,000 m in the North Atlantic. This species has been classified as a necrophage, perhaps chemically attracted to food falls and the associated amphipods in the deep ocean (Lampitt et al., '83; Gartner et al., '97). Photographs from submersible vehicles (Wenner, '79; Lampitt et al., '83) and observations of aquarium specimens (Eastman et al., '94) suggest that neutrally buoyant Paraliparis are inefficient swimmers and that they drift passively or hover in tidal currents near the bottom (Lampitt et al., '83). The expanded sensory modalities associated with the lower lobe of the pectoral fin may be involved in the perception of and orientation to currents as well as in the exploration of the epibenthic habitat for food.

Finally, how does sense organ and brain morphology in Paraliparis devriesi compare with that of sympatric notothenioids, both groups having occupied the Antarctic shelf for approximately the same length of time? The brain of P. devriesi diverges more from other scorpaeniform brains (see above) than nototheniod brains diverge from basal perciforms (Eastman and Lannoo, '95). Furthermore, with reduced reliance on vision, the well-developed olfactory system creates additional sense organs and brain morphology in Paraliparis devriesi. In particular, the olfactory system is expanded and better developed in P. devriesi compared to sympatric notothenioids. The brain of P. devriesi more closely resembles a primary deep-sea species than any notothenioid. The olfactory system is also expanded in some notothenioids. However, this may be a phylogenetic effect in both groups since these notothenioids are basal in the suborder, and a liparid outgroup (Cyclopterus lumpus) possesses similar morphology. Other similarities between brains of P. devriesi and notothenioids include an enlarged preoptic-hypophyseal axis and subependymal expansions. Although the functional significance is unknown, these latter two features are
correlated with habitation of the relatively deep subzero waters of the Antarctic shelf (Lannoo and Eastman, '95).

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LITERATURE CITED


