Anatomy and Histology of the Brain and Sense Organs of the Antarctic Eel Cod *Muraenolepis microps* (Gadiformes; Muraenolepididae)

Joseph T. Eastman and Michael J. Lannoo

Department of Biomedical Sciences, College of Osteopathic Medicine, Ohio University, Athens, Ohio

**ABSTRACT** Brain regions, cranial nerves, and sense organs in *Muraenolepis microps*, an Antarctic gadiform fish, were examined to determine which features could be attributed to a gadiform ancestry and which to habitation of Antarctic waters. We found that the central nervous system and sense organs are well developed, showing neither substantial regression nor hypertrophy. A detailed drawing of the brain and cranial nerves is provided. The rostral position of the olfactory bulbs and telencephalic size and lobation are common for the order. The optic tectum and corpus cerebelli are smaller than in most other gadiforms. The shape of the corpus cerebelli is not distinctive among gadiforms. The lateral line region is moderately well-developed, but not hypertrophied to the extent seen in deep-sea gadiforms. As is the case in gadids possessing barbels and elongated pelvic rays, *Muraenolepis* has well-developed facial lobes, although these are smaller and more laterally positioned. The vagal lobes are deeply placed in the rhombencephalon and project into the fourth ventricle. The brain of *Muraenolepis* resembles that of a phyletically derived gadoid, especially a phycid, more than it resembles the brain of a phyletically basal macrourid. Two histological features of the diencephalon of *Muraenolepis* appear to be unique among gadiforms: a well-organized thalamic central medial nucleus and subependymal expansions. *Muraenolepis* has a pure rod retina like many deep-sea species but lacks the superimposed layers of rod outer segments. The histology of the nonvisual sense organs, especially the olfactory and external taste systems, are well-developed in *Muraenolepis* but not hypertrophied. We relate our findings to what is known about neural morphology in other gadiforms and in phyletically distant notothenioids and liparids that are sympatric with *Muraenolepis* on the Antarctic shelf. The only feature that reflects an Antarctic existence is the diencephalic subependymal expansions, which within notothenioids mirror the habitation of cold waters and have been found in every Antarctic species examined to date. Although the waters of the Antarctic shelf are cold, dark, and deep, brain and sense organ morphology in *Muraenolepis* are remarkably free of extreme specialization. J. Morphol. 250:34–50, 2001. © 2001 Wiley-Liss, Inc.

KEY WORDS: brain morphology and histology; sense organ histology; subependymal expansions

The order Gadiformes includes 12 families and 482 species of cods (Gadidae), phycid hakes (Phycidae), merlucciid hakes (Merluccidae), grenadiers (Macrouridae), morids (Moridae), and related fishes, including the Antarctic eel cods (*Muraenolepididae*; Nelson, 1994). Gadiforms have a worldwide distribution, predominantly in deep, cold water, and are among the most abundant and commercially important marine fishes. Largely because of the diversity of macrourids in the benthopelagic zone at depths of 200–2,000 m, gadiforms are likely the most speciose group of demersal deep-sea fishes (Merrett and Haedrich, 1997). They are also among the most thoroughly studied groups of marine fishes, with extensive coverage of their morphology, biology, and systematics (Svetovidov, 1948; Rosen and Patterson, 1969; Marshall and Cohen, 1973; Cohen, 1984, 1989; Fahey and Markle, 1984; Cohen et al., 1990).
Kotrschal, 1988; Kotrschal, 1991; Kortschal et al., 1993; Kotrschal and Finger, 1996; Finger, 1997; Harvey and Batty, 1998). Consequently, medullary taste centers and their higher-order connections have received more attention than other brain regions (Kotrschal and Finger, 1996; Finger, 1997). The gadid nervous system has also been the subject of ecomorphological studies, especially with respect to activity patterns, habitat preferences, and food habits (Evans, 1935; Kotrschal et al., 1998). Finally, gadiform brain patterns and sense organ morphology have been used in systematics (Marshall and Cohen, 1973), most recently in the diagnosis of the paracanthopterygian clade that includes the Gadiformes (Lauder and Liem, 1983a,b).

Eel cods of the genus Muraenolepis, composing the family Muraenolepididae (Fig. 1), differ from other gadiforms in several aspects of their biology. This single genus of four, or possibly five (Kompowski and Rojas, 1993), species is the only gadiform family endemic to the Southern Ocean (Howes, 1990, 1991). Muraenolepidids inhabit the continental shelf and slope of the Antarctic and Subantarctic Regions at depths of 10–3,040 m, with most encountered at depths of less than 1,600 m (Chiu and Markle, 1990). They have “been neglected both taxonomically and anatomically” (Howes, 1990:73). Muraenolepidids are poorly represented in collections and, with the exception of osteology (Howes, 1990), most aspects of their biology are unknown (Chiu and Markle, 1990). Near South Georgia, Muraenolepis consume a variety of benthic and nektonic organisms including amphipods, isopods, polychaetes, cumaceans, euphausiids, shrimp, and fish (Kompowski, 1993). Although a distinct lineage, their phylogenetic relationships, whether representing basal gadiforms or derived gadoids, are subject to differences of opinion (summarized by Nelson, 1994). Finally, there is uncertainty about the length of their evolutionary history in the Antarctic Region (Andriashev, 1965, 1987; DeWitt, 1971). Howes’ (1990) study of this group led him to suspect that muraenolepidids have long been associated with the Antarctic. He hypothesizes that the circum-Antarctic distribution of muraenolepidids is the result of vicariance, in this case the isolation of Antarctica, and that it reflects the former Gondwanan coastal distribution of the ancestral population in waters off South America and Antarctica.

During recent cruises in the Ross Sea, we collected 16 specimens of Muraenolepis microps Lönberg, the muraenolepidid with the widest distribution in the Southern Ocean (Chiu and Markle, 1990). We obtained these specimens in subzero high-latitude shelf waters (Eastman and Hubold, 1999) where they live sympatriquely with notothenioids, liparids, and zoarcids, the major elements of the shelf fauna (Eastman, 1993, 2000).

In this article, we provide the first description of the brain and special sense organs of Muraenolepis microps and relate our findings to what is known about these systems in other gadiforms and in phylogenetically distant Antarctic notothenioids and liparids. We provide a detailed drawing of the brain and cranial nerves and document the histology of some regions of the brain, olfactory apparatus, retina, and cutaneous taste buds. In studying M. microps, we are interested in determining which neural and sensory components can be attributed to a gadiform ancestry and which, if any, can be attributed to factors associated with the habitation of Antarctic waters.

LITERATURE

For phylectic comparisons, we used the published descriptions and drawings of whole brains for 13 gadiform species plus the phycids Enchelyopus cimbrius and Urophycis floridana. Work has focused on the brains of phylectically derived gadiforms or “gadoids,” those families above the macrourids (Nelson, 1994). Herrick (1907) provided the initial description of the brain of Gadus morhua. Evans (1935) described the brains of the gadids G. morhua, Melanogrammus aeglefinus, Merlangius merlangus, Molva molva, and the merluccius Merluccius merluccius. He also made reference to their food and habitat preferences. Okamra (1966) illustrated an additional gadid brain as well as those of a morid, a bremgmacrotid, and a macrourid. Kotrschal et al. (1998) modified Evans’ (1935) descriptions and drawings and placed the brains of gadiforms in context relative to the brain morphology of other fishes. Other gadiforms that have received attention in the
neurobiological literature include the phycids *Ciliata mustela* and *Gaidropsarus mediterraneus* (Kotrschal and Whitear, 1988; Kotrschal and Finger, 1996; Finger, 1997).

Kotrschal et al. (1998) offer the following generalizations about the brains of gadiforms. The peripheral senses and external morphology of these fishes, which in turn reflect diet, activity pattern, and habitat preferences, are reflected in brain morphology. For example, picivorous species have larger crista cerebellares (lateral line structures) and smaller facial lobes (taste structures) than species that take predominantly invertebrate prey. The eminentia granulares and crista cerebellares are generally well-developed and largest in deep-sea species (family Macrouridae; Okamura, 1966), or in species taking small epibenthic prey. Facial lobes are large in species with barbels or pelvic fin appendages. While tectal lobes are generally large, nocturnal species tend to have larger eyes and larger tectal lobes than diurnal species. When large, the corpus cerebellum (motor control in addition to several other proposed features) extends rostrally and in some species reaches the level of the telencephalon.

For ecological comparisons, we use our earlier morphological studies of the central nervous system and sense organs of notothenioids (Eastman and Lannoo, 1995; Lannoo and Eastman, 1995, 2000) and liparids (Eastman and Lannoo, 1998). In Eastman and Lannoo (1995), we show that the brains of nototheniod fishes tend to be more similar to the brains of temperate perciforms than to the unusual notothenioid fishes tend to be more similar to the brains of cave-dwelling and deep-sea fishes. Inter-specific variation in gross brain morphology is comparable to that in Old World cyprinids, and variation tends to be centered in the primary sensory nuclei (olfactory bulbs and lateral line mechanoreceptive eminentia granulares and crista cerebellares). Association and regulatory areas are also variable, and best developed in species living in subfreezing, high latitude, waters. We have also shown that the third ventricles of notothenioids exhibit a morphology, termed subependymal expansions, that are best developed in species living in high latitudes (Lannoo and Eastman, 1995). Further, a monophyletic clade in the genus *Trematomus* that has undergone a diversification into epibenthic habitats has a larger percentage of their brains devoted to lateral line mechanoreceptive and motor (cerebellar) systems than do benthic species (Lannoo and Eastman, 2000). In this study we also demonstrate that species living at depths have low cone:rod ratios in the retina and larger olfactory structures. Finally, our examination of the Antarctic scorpaeniform liparid *Paraliparis devriesi* shows that the brain of this species has several derived features, including a well-developed olfactory system, a large telencephalon, a retina that contains only rods, a small optic system, a large corpus but small valvula cerebelli, and well-developed vagal and spinal sensory lobes (Eastman and Lannoo, 1998). It can be seen, therefore, that there is a basis for both phyletic and ecological comparisons of muraenolepidids with other species living on the Antarctic shelf.

**MATERIALS AND METHODS**

**Specimens**

We collected specimens of *Muraenolepis microps* at high-latitude stations on the shelf of the southwestern Ross Sea, Antarctica. We conducted bottom trawling during cruises 96-6 (11 Dec. 1996 to 8 Jan. 1997) and 97-9 (20 Dec. 1997 to 10 Jan. 1998) of the RVIB (Research Vessel Ice Breaker) Nathaniel B. Palmer (Eastman and Hubold, 1999). We used two types of trawls, a 9.1-m long, 7.6-m effective width Marinovich Gulf Coast-style flat trawl—a type of otter trawl—and a Blake trawl with a frame measuring 1.5 m wide by 0.5 m high. We trawled at a speed of 2.0–3.0 knots for 0.5–1.0 h. Bottom temperature varied from -1.5 to -1.9°C at the stations. We obtained a total of 16 specimens of *M. microps* at three stations. The specimens ranged in size from 89–236 mm TL (total length) and in weight from 5–115 g. The sample included males and females but we could not determine the sex of all specimens because the gonads were immature. The two specimens from station 93 (75°30′ S, 174°56′ E; bottom depth 300–310 m) were deposited at the J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa, under catalog number RUSI 57870. The single specimen from station 6 (72°59′ S, 175°08′ E; bottom depth 360 m) and the 13 specimens from station 58 (74°21′ S, 176°88′ E; bottom depth 333–344 m) were deposited at the Smithsonian Institution, National Museum of Natural History under catalog numbers USNM 358815 and 358816, respectively. We also used two uncataloged specimens of *M. microps* from South Georgia for histology and dissection. In addition, we examined brains of the phycids *Enchelyopus cimbrius* and *Urophycis floridana* from our collection.

**Histology**

While most fish were preserved by immersion in 10% formalin, others, including most used for histological analyses, were fixed by transcardial perfusion of Bouin’s fixative onboard ship, according to procedures described previously (Eastman and Lannoo, 1995) and summarized briefly here. After anesthetization in a 150-mg L⁻¹ solution of 3-amino-benzoic acid ethyl ester (MS-222, Sigma, St. Louis, MO), the heart and bulbus arteriosus were exposed. Notothenioid saline solution (O’Grady et al., 1982) was prepared, adjusted with NaCl to a concentration of 600 mOsm L⁻¹, maintained at ambient sea water temperature (-1.5°C), and perfused through the heart. Saline was followed by Bouin’s fixative. Dur-
ing this perfusion the gills were periodically irrigated with subzero seawater.

Brains from two perfused specimens were removed, dehydrated in alcohol, cleared in Hemo-De, and embedded in paraffin according to standard procedures (Kiernan, 1990). Embedded brains were cut in the transverse plane on a rotary microtome to produce sections 10–12 μm thick. Sections were mounted on slides, dried, deparaffinized, stained with hematoxylin and eosin, dehydrated, and coveredslipped using Permount as the mounting medium. We viewed sections using either a Nikon SMZ-U dissecting microscope or a Zeiss Jenalumar compound microscope and took photographs using Kodak T-Max 100 black and white film.

We also cut histological sections of olfactory apparatus, eyes, cephalic lateral line, barbels, fins, and skin of four specimens. In the eyes, we took samples from the central retina adjacent to the optic nerve of the left eye. We employed the protocol outlined above except that sections were cut at 7 μm. Sections were stained with hematoxylin and eosin, periodic acid-Schiff procedure, including Harris hematoxylin with glacial acetic acid, Gomori’s one-step trichrome or Bodian’s Protargol (Clark, 1981) for 24 h at 50°C. The epidermis of much of the skin was abraded when fish tumbled inside the trawl with hard-bodied benthic invertebrates, sponge spicules, and rocks from the substrate. We were therefore unable to thoroughly examine the skin for taste buds and solitary chemo sensory cells or to quantitatively evaluate their distribution.

RESULTS
Gross Morphology of the Brain of Muraenolepis microps

The brain appears generalized, without hypertrophy of sensory or motor regions (Fig. 2). The telencephalon is small in proportion to the remainder of the brain, similar in proportion to the telencephalons of Melanogrammus aeglefinus, Merlangius merlangius, and Pollachius pollachius, illustrated by Evans (1935) and Kotrschal et al. (1998).

The tectum is moderate-to-small sized, in dorsal view it is not notably larger than the corpus of the cerebellum (CCb), which is also reduced. The CCb is oriented dorsocaudally, unlike most gadiforms, where this structure projects rostrally. In overall appearance the telencephalon, tectum, and CCb most closely resemble the brain of merluccid Merluccius merluccius.

In Muraenolepis microps, the lateral line eminentia granularis (EG) and crista cerebellaris (CC) are small. The CC is linearly oriented along the brain axis, unlike most gadiforms, which have CCs that are lobular, curved, and widest rostrally. The facial lobes (FL) form dorsolateral medullary swellings that appear to be intermediate in size when compared to other gadiforms, but are large structures in M. microps and extend far caudally, to the middle portion of the spinal sensory nucleus (Sps). The vagal lobes (VL) are small but prominent, running from the spinal sensory nucleus rostrally to the middle of the medulla. They are positioned deeply and only their rostral portions are visible along the floor of the fourth ventricle (Figs. 2B, 3H). Thus, in M. microps and some other gadiforms (Kotrschal and Finger, 1996), unlike most other teleosts, the facial lobes are located caudal to the vagal lobes (Fig. 2B).

As in many other gadiforms (Svetovidov, 1948; Marshall and Cohen, 1973), Muraenolepis microps exhibits ontogenetic variability in the position of the olfactory bulbs relative to the telencephalon and olfactory organ. The specimen illustrated in Figure 1 is our largest specimen, approximately 67% of maximum known total length for this species (Chiu and Markle, 1990). The olfactory bulbs are pedunculate, located far anteriorly near the olfactory sac. They are connected to the telencephalon by elongated medial and lateral olfactory tracts which are visible through the transparent meninges. In smaller specimens the olfactory bulbs are in a relatively more posterior location. For example, in a 135-mm TL specimen they are positioned midway between the olfactory sac and the telencephalon. In the smallest of our specimens (89 mm TL) the olfactory bulbs are closer to the telencephalon than to the olfactory sac and separated from the former by a small gap.

There is also ontogenetic variation in the distinctness of the midline sulcus between the tectal lobes. This sulcus is deep in smaller specimens but becomes reduced to a shallow furrow in larger animals.

Histology of the Brain of Muraenolepis microps

Telencephalon. The dorsal portion of the telencephalon is small, with shallow lobes and sulci (Fig. 3A). Dorsal dorsal, dorsal central, dorsal medial, dorsal lateral, and dorsal posterior lobes are present, and while not prominent they are easily distinguished. The ventral telencephalon is relatively larger, with all three nuclei (ventral dorsal, ventral ventral, and ventral posterior) consisting of large numbers of cells covering large regions (Fig. 3A). The anterior commissure is large. The telencephalon is largest posteriorly, just caudal to the beginning of the parvocellular preoptic nucleus.

Diencephalon. The diencephalic preoptic region is extensive but otherwise unremarkable (Fig. 3A). The magnocellular preoptic nucleus consists of a tight cluster of relatively small cells rostrally, becoming scattered and more distal caudally. If gianntocellular preoptic neurons are present, they are few and scattered.

Subependymal expansions (Lanno and Eastman, 1995) into the third ventricles are present (Fig. 4A). Expansions begin rostrally at the level of the habe-nula and course caudally to the cerebral aqueduct.
Expansions are extensive in the ventral diverticula of the third ventricle.

The thalamus consists of expansive ventral medial and central posterior nuclei. Caudally, the central medial nucleus consists of a broad band of perpendicularly aligned (stacked) cells (Fig. 4B).

Among other features of the diencephalon, the nucleus glomerulosus is prominent (Fig. 3B,C).
Figure 3. (Continued.)

BRAIN AND SENSE ORGANS OF ANTARCTIC EEL COD
Fig. 3. Brain histology of Muraenolepis microps from the central portion of the telencephalon (A) to the caudal medulla (I). A–E ×15; F–I ×17. CC, crista cerebellaris; CCB, corpus cerebelli; Dc, dorsocentral nucleus; Dd, dorsodorsal nucleus; Dl, dorsolateral nucleus; Dm, dorsomedial nucleus; Dp, dorsoposterior nucleus; G, nucleus glomerulosus; EG, eminentia granularis; FR, fasciculus retroflexus; H, habenula; IL, inferior lobes; LL, lateral lemniscus; MLF, medial longitudinal fasciculus; nMLF, nucleus of the medial longitudinal fasciculus; OC, optic chiasm; Pp, parvocellular preoptic nucleus; RF, reticular formation; Sps, spinal sensory nucleus; SV, saccus vasculosus; Tec, tectum; TL, torus longitudinalis; TS, torus semicircularis; VCb, valvula cerebelli; Vd, ventrodorsal nucleus of the telencephalon; Vm, ventromedial nucleus of the thalamus; Vmot, motor nucleus of the trigeminal nerve; VII, facial lobe; VIII, acoustical region; X, vagal lobe. Scale bars = 1 mm.
Fig. 4. Brain histology of *Muraenolepis microps*. **A**: Bilaterally symmetrical diencephalic subependymal expansions. ×170. **B**: The central medial nucleus of the thalamus showing a bilateral series of stacked neurons. ×95. Scale bars: **A**, 100 μm; **B**, 200 μm.
fasciculus retroflexus (habenulo-peduncular tract) is large and prominent (Fig. 3B), as is the interpeduncular nucleus. The inferior lobes are large and laterally expanded (Fig. 3B,C). The central medial nucleus of the inferior lobes is prominent. The saccus vasculosus is large (Fig. 3C).

**Mesencephalon.** The midbrain tectum is small in cross section (Fig. 3C,D). Lobes are shallow and are flattened dorsally. Laminae are well developed. The four major laminae defined by Northcutt (1983) are present and consist, from pial to ventricular surfaces, of a periventricular gray zone, deep white zone, central zone, and superficial white and gray zone divided into a deeper stratum fibrosum et griseum superficiale and submeningeal stratum opticum. The subependymal expansions of the third ventricle extend into the tectal ventricle.

The torus longitudinalis is large and has two distinguishing features (Fig. 3C,D): it is fused along the midline and it consists of large groups of concentrically arranged cells. The torus semicircularis is also large (Fig. 3C,D,E) but exhibits no unusual histological features. Both the torus longitudinalis and torus semicircularis protrude substantially into the tectal ventricle. Caudally, the torus semicircularis forms a discrete lobe that extends nearly to the isthmus (Fig. 3E).

Although the nerves are small, the cell bodies of the motor neurons of cranial nerves III and IV are relatively large and numerous (not shown).

**Rhombencephalon**

**Cerebellum.** The valvula cerebellum is two-layered, with a fully formed ventral (rostrally migrated) component and an overlying dorsal (caudally migrated) component consisting of a well-developed molecular layer and a partial granule cell layer (Fig. 3D,E). The nucleus of the lateral valvula is large and contains cells that are ventrally migrated.

At the level of the eminentia granularis the cerebellum appears unusually dorsal, a position that is exaggerated by a lateral constriction between the dorsal medulla and the ventral eminentia (Fig. 3F). The eminentia granulare is large and form distinct lobes lateral to the ventral 40% of the corpus cerebellum. As the corpus cerebellum forms a caudal lobe, it separates from the eminentia granulare (Fig. 3F). The eminentia granularis consists of the cell bodies of cerebellar granular cells that send axons to course caudally in the crista cerebellaris, forming a type of molecular layer over the octavolateralis region. Typically, the eminentia granularis is rostral and the crista is caudal. In *Muraenolepis microps*, the caudal portion of the eminentia forms a lobe that extends over the crista, forming a dorsal–ventral relationship that is unusual. Although *M. microps* has large eminentia granulare, the cristae are small, especially caudally, and positioned along the dorsal midline. For much of their caudal extent, except for their extreme caudal portions, they are adherent along the midline (Figs. 2B, 3G).

**Octavolateralis System.** The nuclei of the octavolateralis system are not remarkable in size or extent. They are positioned relatively dorsal and medial compared with other fishes (Fig. 3G).

**Facial Lobes.** The facial lobes form lateral expansions of the medulla and represent its most prominent feature (Figs. 2B, 3H,I). Facial lobes extend throughout much of the medulla, but they are not as pronounced as in siluriform teleosts, nor are they as pronounced as in other species of gadiforms. Based on histological features, we could not distinguish dorsal from ventral facial nuclei. By inference from the phylics Gaidropsarus and Ciliata (Kotrschal and Whitear, 1988), absence of a discrete dorsal division of the facial lobe suggests that the first dorsal fin in *Muraenolepis* is not a specialized chemosensory organ, but this warrants further investigation (see below).

**Vagal Lobes.** The vagal lobes extend throughout the caudal half of the medulla (Figs. 2B, 3H). They form the floor of the fourth ventricle caudal to the cristae but are positioned more ventrally, under and caudal to the facial lobes.

**Motor Nuclei.** Neurons in the trigeminal and facial motor nuclei appear to be normal in size and number. The trigeminal motor nucleus has a large rostro-caudal extent. The facial motor nucleus is ovoid medially, and in some regions consists of a single strand of aligned cells (not shown).

We could find no evidence of Mauthner neurons or their axons.

**Spinal Sensory Nucleus.** The spinal sensory nucleus is large (Figs. 2B, 3I) and at its greatest extent forms nearly 50% of the cross-sectional area at the brainstem–spinal cord junction.

In general, nuclei are highly differentiated. An unusual characteristic of the ventral telencephalic nuclei, diencephalic nuclei, torus semicircularis, and eminentia granularis is that they are typically well-defined and often contain cells that have migrated some distance away from the ventricular surface.

**Cranial Nerves**

Since the olfactory bulbs of *Muraenolepis* are pudentate, the olfactory nerves are short but well-developed (Fig. 2). The distinct fiber bundles of the medial and lateral olfactory tracts are visible within the meninges between the telencephalon and the olfactory bulbs. The moderately sized optic nerves are not pleated; the right crosses dorsal to the left. The oculomotor, trochlear, and abducens nerves are very small. The trigeminal–facial complex is large and well-developed. The glossopharyngeal nerve is small and does not join the vagus–posterior lateral line complex as in many other fishes. It pierces the wall of the otolithic cavity and branches into the dorsal pharyngeal musculature. The anterior lateral line nerve is larger than the posterior lateral line nerve.
With cell bodies located in the geniculate ganglion, the ramus lateralis accessorius (RLA) is a branch of the facial nerve that supplies taste buds on the body and fins of teleosts (Freihofer, 1963, 1970). In Muraenolepis microps the RLA (Fig. 2B,C) is well-developed and originates medial to the anterior lateral line–trigeminal–facial complex. It runs dorsally between the optic tectum and corpus of the cerebellum, turns posteriorly to exit the skull, and runs subcutaneously toward the dorsal opercular region. Shortly after emerging from the skull, the RLA gives off a small branch to the dorsal fin and this is joined by a vagal ramus. The RLA continues as the large pectoral–pelvic branch. This courses in a ventral direction from the dorsal opercular region and is located immediately posterior to the cleithrum and superficial to the pectoral musculature. It gives off a few small branches to the skin dorsal and posterior to the operculum and a small branch to the pectoral fin, but most of the pectoral–pelvic branch continues into the base of the pelvic fin. We could not locate a dissectable branch of the RLA to the anal fin. In this respect, the RLA of Muraenolepis is unique among those of gadiforms examined to date (Freihofer, 1963, 1970; Kotrschal and Whitear, 1988). It is possible, however, that the dorsal branch gives off small segmental branches that travel ventrally with spinal branches to reach the anal fin. This is the situation in the phycids Ciliata and Gadropsarus (Kotrschal and Whitear, 1988), species convergent with Muraenolepis in body shape and in the size and position of unpaired fins.

Sensory Systems

Visual system

Eyes and Extraocular Muscles. The eyes are small to moderate in size, about 20–21% of head length. The extrinsic eye muscles and innervation pattern are typical for fish; however, the muscles are thin and poorly developed and the corresponding nerves are small.

Retinal Histology. At 175–200 μm, the central retina is moderately thick and well-developed, with typical layering (Fig. 5A–D). The photoreceptor layer consists of a relatively large number of closely packed cells of a single cell type that we identified as rods (Nicol, 1989:88, 91) on the basis of long, cylindrical outer segments and elongated myoids and ellipsoids (Fig. 5B,D). Since the myoids and ellipsoids are of varying length, a greater number of rods can be accommodated in the photoreceptor layer and the junction of the inner and outer segments therefore has a staggered appearance (Fig. 5E). The outer segments are 30–40 μm long. The external nuclear layer, consisting of the nuclei of rods, is thick and the nuclei did not contact or project scleral of the external limiting membrane (Fig. 5D,E), another characteristic of rods. The photoreceptor layer is about 40% of retinal thickness. The retinal pigment epithelium has only a few short processes between the outer segments (Fig. 5A–D), also typical of deep-living species with pure rod retinas and limited retinomotor movement. Counts of cells in the internal nuclear layer and in the ganglion cell layer are moderate, as is the convergence ratio of visual cells to ganglion cells (Table 1).

Olfactory apparatus. Anterior and posterior nasal openings are large (0.5–1.2 mm); the anterior is situated at the end of a tube with an elevated flap on the posterior margin. The olfactory chamber is oval in shape and does not have an accessory nasal sac. There is no sexual dimorphism in the size of olfactory apparatus. The olfactory rosette, or the arrangement of the primary lamellae, is most similar to the type G pattern (Yamamoto, 1982), with the lamellae arranged transversely to an elongated raphe. The lamellae at the anterior and posterior margins are small and there are no secondary lamellae. In ten specimens the number of primary lamellae ranges from 24–30 with a modal number of 26. Although the type G arrangement is common in a variety of teleosts including other gadiforms, the pattern is slightly modified in Muraenolepis. The rosette is oriented in an oblique parasagittal plane rather than in a horizontal plane. Furthermore, upon removal of the skin over the olfactory chamber only the primary lamellae on the lateral face of the raphe are evident. These project ventrolaterally onto the olfactory chamber. The raphe is fused to the overlying skin and the lumen of the olfactory chamber is less capacious medial to the raphe. When this skin is removed the primary lamellae projecting from the medial surface of the raphe are evident. Injection of dye reveals that, because the dorsomedial part of the chamber is obscured, water must first pass between the lateral primary lamellae to reach the medial lamellae.

Histology of Lamellae. The sensory portions of the lamellae are covered by a ciliated stratified columnar epithelium (Fig. 5F,G). It is 50–60 μm thick, thinning to 15–20 μm in nonsensory areas distally and near the origin of the lamellae. The epithelium includes basal cells, sustentacular cells, nonsensory ciliated epithelial cells, and primary sensory cells (Fig. 5F,G). Silver staining identifies these sensory cells as thin bipolar neurons and also stains the basal bodies of the ciliated epithelial cells (Fig. 5F). Mucous cells are common in the epithelial lining of the olfactory sac and in the nonsensory epithelium of the lamellae, but are rare in the thick sensory epithelium.

Lateral line system. The cephalic lateral line pores are small in diameter (0.2–0.4 mm) and inconspicuous. The underlying canals, however, have larger lumina (0.3–0.5 mm) and histology (not shown) reveals that they contain typical canal neuromast organs. The trunk lateral line consists of only two pores; these are close together and located dorsal to the base of the pectoral fin and anterior to...
the origin of the first dorsal fin. Because of damage to the skin, the distribution of superficial neuromasts is unknown.

**Cutaneous taste buds.** Our histological survey of the location of cutaneous taste buds was hindered by damage to the epithelium while the fish were in the trawl. Nevertheless, we identified taste buds in these locations: head, upper and lower jaws (Fig. 6A), lips, skin around jaw teeth, distally on the pectoral fin near the most dorsal rays and on the two elongated, filamentous rays of the pelvic fins (Fig. 6B). The first dorsal fin consists of one developed ray and one rudimentary ray. We did not find taste buds on this fin or on the second dorsal fin, which is confluent with the caudal and anal fins (Fig. 1). The epithelium was badly damaged in our sections of the anal fin; we are therefore uncertain whether this fin has taste buds. *Muraenolepis microps* has a short mental barbel, measuring 20–25% of head length, which also has taste buds in its skin (Fig. 6C). In summary, the densest concentrations of taste buds are on the elongated pelvic rays and the mental barbel.

**DISCUSSION**

**Brain of Muraenolepis Compared With Other Gadiforms**

The brain regions, cranial nerves, and sense organs of *Muraenolepis microps* are well developed, showing neither substantial regression nor hypertrophy. There is no morphology that is unique to the unusual light, temperature, and bathymetric regimes of the Antarctic shelf. In comparison with the illustrated brains of 13 other gadiforms (Evans, 1935; Okamura, 1966; Kotrschal and Whitear, 1988; Kotrschal et al., 1998), *Muraenolepis* is typical in most aspects of gross morphology (Table 2). For example, the rostral position of the olfactory bulb and the telencephalic size and lobation are typical for the order. The optic tectum and corpus cerebelli are relatively smaller than those of most other gadiforms for which brain illustrations are available. The caudally projecting corpus cerebelli is the most common shape among gadiforms. The lateral line region is moderately well-developed, but not hypertrophied to the extent seen in the deep-sea morid *Physiculus inbarbatum*, which also has a reduced optic tectum (Okamura, 1966). As is the case in other gadids possessing barbels and elongated pelvic rays (Kotrschal et al., 1998), *Muraenolepis* has well-developed facial lobes. The facial lobes are smaller

---

**TABLE 1. Cell counts**

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat depth (m)</th>
<th>Retinal thickness (μm)</th>
<th>Cones + rods</th>
<th>Ratio cones:rods</th>
<th>Cells in internal nuclear layer</th>
<th>Convergence ratio (cones + rods: ganglion cells)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Muraenolepididae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Muraenolepis microps</em></td>
<td>Ross Sea</td>
<td>310–1,2307</td>
<td>150–200</td>
<td>228</td>
<td>26</td>
<td>7</td>
</tr>
<tr>
<td>Liparidae</td>
<td>Southern Ocean8, 9</td>
<td>10–1,600</td>
<td>0</td>
<td>228</td>
<td>—</td>
<td>7</td>
</tr>
<tr>
<td>NototTHENiidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dissoeotichus mawsoni</em></td>
<td></td>
<td>500–7004</td>
<td>150–175</td>
<td>163</td>
<td>19</td>
<td>2</td>
</tr>
<tr>
<td><em>Trematodus loennergii</em></td>
<td></td>
<td>663–1,1916</td>
<td>239</td>
<td>166</td>
<td>22</td>
<td>2</td>
</tr>
</tbody>
</table>

1Counts are mean number of nuclei for three replicates in an area of 100 μm along the various layers of one Bodian-stained histological section, viewed at ×1,000, from each of three specimens.
3Values for convergence ratios in notothenioids (Eastman, 1988): high (58:1), moderate (30–12:1) and low (10–5:1).
5Eastman (1988).
6Lannoo and Eastman (2000).
7Eastman and Hubold (1999).
8Lannoo and Eastman (2000).
9Eastman and DeVries (2000).
10Counts are mean number of nuclei for three replicates in an area of 100 μm along the various layers of one Bodian-stained histological section, viewed at ×1,000, from each of three specimens.
and more laterally positioned than in the gadids *Melanogrammus aeglefinus* and *Gadus morhua*. The vagal lobes of *Muraenolepis* are deeply placed in the rhombencephalon and project into the fourth ventricle. The spinal sensory nucleus of *Muraenolepis* is prominent.

Table 2 indicates that there is only modest variation in the gross features of the brain among families in the order Gadiformes. Most variability involves the size of the optic tectum and the shape and size of the corpus cerebelli. This variability is to be expected in a radiation of benthopelagic fishes encompassing a range of depths, diets, and activity patterns. The only obvious phyletic trend is the derived nature of the rostrally projecting corpus cerebelli in gadids. The brain of the bregmacerotid

**TABLE 2. Comparison of major features of gross brain morphology among families of gadiform fishes**

<table>
<thead>
<tr>
<th>Feature</th>
<th>Macrouridae</th>
<th>Moridae</th>
<th>Bregmacerotidae</th>
<th>Muraenolepididae</th>
<th>Phycidae</th>
<th>Merlucciidae</th>
<th>Gadidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distinct olfactory nerves</td>
<td>–</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Distinct medial and lateral</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>olfactory tracts</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Telencephalic lobation</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>+</td>
<td>±</td>
<td>± or +</td>
<td>+</td>
</tr>
<tr>
<td>Size of optic tectum relative</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>+</td>
<td>±</td>
<td>± or +</td>
<td>+</td>
</tr>
<tr>
<td>to telencephalon</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shape of corpus cerebelli</td>
<td>U</td>
<td>C</td>
<td>C</td>
<td>C</td>
<td>C</td>
<td>U</td>
<td>R or C²</td>
</tr>
<tr>
<td>Size of corpus cerebelli</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>±</td>
<td>+</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>Lateral line region (EG + CC)</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>±</td>
<td>+</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>Ramus lateralis accessorius³</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>Facial lobe</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vagal lobe</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

+ = Present or larger; ± = intermediate; − = absent or smaller.

¹Arranged phylogenetically with sequencing and family names based on Nelson (1994).
²Data from Evans (1935), Okamura (1966); Kotrschal and Whitear (1988); Eastman and Lannoo (personal observations on phycids).
³U = upright or oval; C = extends caudally; R = extends rostrally.
⁵*Theragra chalcogramma* (Okamura, 1966).
Bregmaceros japonicus is distinctive among gadiforms (Okamura, 1966), but this is an anatomically aberrant family (Marshall and Cohen, 1973:492). The brain of Muraenolepis is discernible only by the relatively small size of the optic tectum and corpus cerebelli. Among the relatively few gadiforms for which there are data on gross brain morphology, Muraenolepis is most similar to phycids as represented by Gadropsarus and Ciliata (Kotrschal and Whitear, 1988) and by Enchelyopus cimbrius and Urophycis floridana (Eastman and Lannoo, personal observations). However, the brain of Muraenolepis also bears some resemblance to that of the gadid Theragra chalcogramma (Okamura, 1966). Theragra is unusual among gadids studied to date in having a caudally rather than a rostrally projecting corpus cerebelli. In conclusion, the brain of Muraenolepis resembles those of phyletically derived gadoids, especially phycids, more than it resembles those of phylogenetically basal macrourids.

Brain Histology

Histologically, the brain of Muraenolepis microps also resembles the brains of other gadiform species. For example, brain nuclei and their laminae tend to be well-developed and migrated. This is demonstrated in the telencephalon and in the diencephalon, where a well-defined nucleus glomerulosus is present. It is also true in the tectum, cerebellar divisions, and brainstem. In the medulla, facial and vagal lobes are well-developed, as is the lateral line system. One exception here is that a dorsal facial nucleus cannot be distinguished. Two histological features of the diencephalon of Muraenolepis appear to be unique among gadiforms: a well-organized thalamic central medial nucleus and subependymal expansions. Although their function remains unknown, subependymal expansions are correlated with the habituation of cold waters both within taxa (Lannoo and Eastman, 1995) and across taxa (Eastman and Lannoo, 1995, 1998, unpublished data), and appear to be a convergent brain feature.

Inferences From Sense Organ Histology of Muraenolepis

The structure of the retina, especially the composition of the photoreceptor layer, reflects aspects of the habitat in fishes, especially depth distribution (Ali and Klyne, 1985). Most teleosts have both rods and cones in the photoreceptor layer (Walls, 1942; Nicol, 1989). Deep-sea fishes inhabit depths greater than 1,000 m (Angel, 1997) and rods, responsible for vision in dim light, are frequently the only photoreceptor present in this group (Munk, 1966a; Marshall, 1979; Nicol, 1989). Muraenolepis has a pure rod retina like many deep-sea species but lacks the superimposed layers of rod outer segments, a specialization frequently encountered in these fishes (Munk, 1966a). Although Muraenolepis has large numbers of rods, summation is less and convergence ratios are lower than in deep-sea species because of the relatively high numbers of bipolar and ganglion cells (Table 1). While this implies some sacrifice in retinal sensitivity, resolving power or acuity is less compromised. This balance may be desirable for a species living on the Antarctic continental shelf and slope at 500–1,000 m rather than at thousands of meters in the deep sea. Among other gadiforms the composition of the photoreceptor layer of the retina reflects depth distribution. For example, Gadus morhua, a gadid living at 150–200 m, has a duplex retina, whereas morids and macrourids from depths of 1,200–1,460 m have pure rod retinas (Ali and Hanyu, 1963). Bathypelagic (Macrouroides inflatus) and abyssopelagic (Echinomacrurus mollis) macrourids living at depths of 3,400–5,000 m have small eyes, a cortical cataract, and a degenerate retina with only rods and a single row of nuclei in the external nuclear layer (Munk, 1966a,b). Viewed in this context, the pure rod retina of Muraenolepis is more specialized for vision in dim light than the duplex retina of temperate shelf-dwelling gadids. However, it is less specialized than the retina of deep-sea fishes and may be taken as representative of a fish living on the upper slope to depths of about 1,500 m elsewhere in the world.

Table 1 compares characteristics of the retina among phylogenetically diverse Antarctic species inhabiting a similar depth range on the shelf of the Ross Sea. Other than being generally adapted to low light intensities, the endemic notothenioids (Meyerochow and Klyne, 1982; Eastman, 1988; Pankhurst and Montgomery, 1989; Lannoo and Eastman, 2000) have no unique retinal specializations for enhanced sensitivity in the Antarctic marine environment. None of the notothenioids studied to date have pure rod retinas, and only two of 19 species have rod-dominated retinas (Eastman, 1988; Lannoo and Eastman, 2000; Table 1). The pure rod retina and high convergence ratio of Paraliparis devriesi reflects the secondary deep-sea origin of the Antarctic liparids (Eastman and Lannoo, 1998). Muraenolepis is sympatric with deeper living notothenioids and liparids on the Antarctic shelf. Muraenolepis has a pure rod retina in common with Paraliparis and greater numbers of rods than either Paraliparis or the deep-living notothenioids (Table 1). However, the moderate convergence ratio in Muraenolepis is more similar to those of coastal notothenioids than to that of Paraliparis. Considering the morphology of other sensory systems and the brain, Paraliparis possesses more specialized and distinctive neural morphology than notothenioids or Muraenolepis—small optic tectum, well-developed olfactory system, enlarged cephalic lateral line pores, and cutaneous taste buds and hypertrophy of somatosensation on the pectoral fins (Eastman and Lannoo, 1998).
It should also be mentioned that the histology of the nonvisual sense organs, especially the olfactory and external taste systems, are well-developed in *Muraenolepis* but not hypertrophied. As represented by the condition in macrourids and morids (Marshall, 1979:409–410), moderately to well-developed olfactory and gustatory systems are phylogenetically basal characteristics for gadiforms. As indicated by the presence of buds, a large pectoral–pelvic branch of the ramus lateralis accessorius and a relatively large facial lobe, cutaneous taste is well represented in those undamaged areas of skin that we were able to sample. Buds on the mental barbel and elongated pelvic rays suggest that these organs play a role in the chemical detection of prey. Although pharyngeal buds are present, pharyngeal taste appears less well-developed, as evidenced by the relatively small size of the vagal lobes. Although benthic organisms compose a part of the diet, it is unlikely that *Muraenolepis* engages in bottom-grubbing behavior that necessitates pharyngeal sorting of food items.

**Final Remarks**

As summarized by Nelson (1994), the phyletic relationships among gadiforms and the position of *Muraenolepis* are not firmly established. While the Muraenolepididae is frequently considered phylogenetically basal, study of the cranial osteology of *Muraenolepis* led Howes (1990) to hypothesize that the family was a relatively derived higher gadoid group related to the Phycidae and Gadidae. The brain morphology of *Muraenolepis microps* is more similar to that of gadoids than to basal macrourids. However, this distinctive genus does not have distinctive brain morphology, so it remains to be seen whether neural characters will contribute to clarifying the position of *Muraenolepis* among the gadiforms.

One of our objectives has been to determine which features of the *Muraenolepis microps* brain and sense organs are attributable to a gadiform ancestry and which are associated with habituation of the sub-zero waters on the Antarctic shelf. *M. microps* exhibits an unmistakably gadiform brain. Small reductions in brain regions such as the telencephalon, tectum, and cerebellum, and increase in the size of somatosensory lobes, exemplify trends also seen in the brains of Antarctic liparids (Eastman and Lannoo, 1998) but fall within the range of variation for gadiforms. The pure rod retina reflects depth preference among marine fishes. Olfactory and external taste are well-developed, supplementing vision at depth; a similar combination is shared with liparids. The only feature we examined that mirrors an Antarctic existence is the diencephalic subependymal expansions, which within notothenioids reflect the habitation of cold waters (Lannoo and Eastman, 1995) and have been found in every Antarctic species examined to date (Eastman and Lannoo, 1995, 1998, unpublished data).

The waters of the Antarctic shelf average 500 m in depth, with troughs to 1,200 m (Anderson, 1999). The Antarctic fish fauna therefore exhibits modest convergence with true deep-sea fishes in some aspects of sensory biology (Montgomery and Pankhurst, 1997; Montgomery and Macdonald, 1998). 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, 1997; Montgomery and Macdonald, 1998). On the Antarctic shelf the endemic notothenioids are perciforms, a coastal group that radiated to fill most niches in the past 5–15 million years (Eastman, 2000). Liparids and muraenolepidids, on the other hand, are members of more basal and presumably older teleostean clades with world-wide distributions and secondary deep-sea affinities. Their divergence times and length of residence on the Antarctic shelf are unknown, but are unlikely to exceed those of notothenioids. These three groups are currently sympatric on the Antarctic shelf. Despite their different evolutionary histories, brain and sense organ morphology in all three groups are remarkably free of exceptional specialization. The human perception of the Antarctic as an “extreme” habitat is not reflected in unusual neural morphology in fishes.

**ACKNOWLEDGMENTS**

We thank Herb Baker, Art DeVries, Al Hickey, Chris Jensen, Bob Kluckhohn, and Captain Joe Borkowski and the crew of the RV *Nathaniel B. Palmer* for their assistance in collecting the specimens. Susan Johnson Lannoo sectioned and stained the brains and proofread the manuscript. We are grateful to Danette Pratt for producing Figure 2 and to Jennifer Jacobberger for photographic assistance. This research was conducted under protocol LV95-02 as approved by the Institutional Animal Care and Use Committee of Ohio University. In collecting specimens, we adhered to provisions of the Antarctic Conservation Act. For transhipping and importing specimens, we had permits from the New Zealand Ministry of Agriculture and Fisheries (Nos. A.S. 7015 and A.S. 7016) and the United States Fish and Wildlife Service (a cleared form 3-177). Supported by National Science Foundation grant OPP 94-16870 and an Ohio University Presidential Research Scholar Award (JTE) and National Institutes of Health Grant NS37600-01 (MJL).

**LITERATURE CITED**


