Divergence of Brain and Retinal Anatomy and Histology in Pelagic Antarctic Notothenioid Fishes of the Sister Taxa Dissostichus and Pleuragramma

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ABSTRACT The neutrally buoyant Antarctic fishes of the sister taxa Dissostichus (D. eleginoides and D. mawsoni) versus Pleuragramma (P. antarcticum and P. antarcticum) are distinctive in the notothenioid radiation and filled different niches in the pelagic realm of the developing Southern Ocean. To assess the influence of phylogenetic and ecological factors in shaping neural morphology in these taxa, we studied the anatomy and histology of the brains and retinae, and determined the proportional weights of brain regions. With the brain of the non-Antarctic sister taxa Eleginops maclownius as plesiomorphic, statistically significant departures in the brains of the two Antarctic taxa include reduction of the corpus cerebelli and expansion of the mesencephalon and medulla. Compared to Eleginops, both species also have a relatively smaller telencephalon, although this is significant only in Dissostichus. There are a number of apomorphic features in the brain of Pleuragramma including reduced olfactory nerves and bulbs, an extremely small corpus cerebelli and an expanded mesencephalon. Although there is not a significant difference in the relative weights of the medulla in the two taxa, the prominence of the eminentia granularis and bulging cap-like appearance of the crista cerebellaris are distinctive in Pleuragramma. Brain histology of Dissostichus and Pleuragramma reflects typical perciform patterns and the two species of Dissostichus are histologically identical. Lateral compression in Pleuragramma and notable lobation in Dissostichus also contribute to differences between the taxa. Compression in Pleuragramma is attributable to convergence on an anchovy/herring body shape and to the relatively large brain in this small fish. The less prominent pattern of lobation of the telencephalon, inferior lobes and corpus cerebelli in Pleuragramma probably reflects underlying histology, specifically a reduction in cellularity of the neuropil in the nuclei and lobes. The retinal histology of Dissostichus and Pleuragramma encompasses the extreme seen in Antarctic notothenioids. Dissostichus has a thin scotopic retina with few cones and a high degree of summation. The retina of Pleuragramma is thick and cellular with many small single cones and rods and resembles that of Eleginops. Pedomorphy has not influenced brain morphology in these species but Pleuragramma has superficial neuromasts that are pedomorphic. Although Dissostichus and Pleuragramma are sympatric in the water column, their brains and retinae are highly divergent and reflect the influences of both phylogeny and ecological partitioning of the pelagic realm. Compared to Eleginops, the relatively smaller corpus cerebelli but relatively larger medulla probably indicates, respectively, reduced activity levels of notothenioids in subzero temperatures and expansion of the mechanosensory lateral line system as a supplement to vision under conditions of reduced light. Compared to Dissostichus, Pleuragramma has reduced olfactory bulbs and corpus cerebelli and an expanded mesencephalon. The reduction of the corpus to a small round knob is consistent with physiological parameters and video observations suggesting that, although pelagic, it is relatively inactive. Because mesencephalic weights also include the valvula cerebelli, the relatively large value for Pleuragramma may be attributable to its role in integration and somatosensory coordination of information from the highly cellular retinopexy and integration of signals from the well-developed octavolateralis system. The brain of Dissostichus displays considerable persistent morphology in its overall resemblance to that of Eleginops, especially large olfactory bulbs and the relatively large caudally projecting corpus, and Dissostichus exhibits olfactory tracking ability and migratory behavior in common with Eleginops. J. Morphol. 272:419–441, 2011. © 2011 Wiley-Liss, Inc.

KEY WORDS: relative weights of brain regions; ecological diversification; photoreceptors

INTRODUCTION

With over 31,000 species (Eschmeyer and Fong, 2010), teleost fishes have become established in nearly all the world’s freshwater and marine habitats. In adapting to these myriad environments, body systems have diversified to accommodate...
various aspects of feeding, locomotion and reproduction. Nervous and sensory systems are an integral part of these adaptations and the relative contributions of phylogeny and ecology in determining brain and sense organ morphology have been a longstanding question in ecomorphology. Although the relationships between brain morphology and ecology are well established for some teleost fishes (H.M. Evans, 1931; H.E. Evans, 1952; Schnitzlein, 1964; Davis and Miller, 1967; Ito et al., 2007), the strength of this relationship has subsequently been found to vary in different taxa. For example within North American catostomids (Miller and Evans, 1965), African Great Lakes cichlids (Huber et al., 1997), and deep-sea eels and grenadiers (Wagner, 2002) the interspecific variation in sensory and association areas of brains is tightly correlated with ecology, especially habitat and feeding. However in some European cyprinids (Kotrschal and Palzenberger, 1992) and coral reef dwelling perciform angelfish and butterflyfishes (Bauchot et al., 1989) interspecific variation is not as pronounced and the link between brain morphology and ecology is less robust. In a comprehensive review of this field, Kotrschal et al. (1998) note that primary sensory areas of the brain relate more closely to feeding whereas integration centers reflect differences in microhabitat, and in phylogenetically advanced teleosts like perciforms there is a relative shift of brain mass from sensory areas to integration centers. As a means of apportioning the influence of phylogenetic and ecological factors shaping brain morphology, Kotrschal et al. (1998) call for investigations of closely related perciform species that differ in body size, habitat utilization and behavior. Having established the large-scale pattern of neural and sensory morphology for families and genera of Antarctic perciform notothenioids (Eastman and Lanno, 1995, 2003a,b, 2004, 2007, 2008; Lanno and Eastman, 2000), we are in a position to address this topic. Using the ecologically vital but neuroanatomically unstudied genera Dissostichus and Pleuragramma, we will provide such a comparison and analysis of the brains and retinae of sympatric sister species of notothenioids that, while sharing the pelagic lifestyle, have diverged in body size, diet, habitat depth, activity levels and tendency to migrate.

The Notothenioid Radiation in Antarctica

Some historical perspective facilitates understanding the emergence of notothenioids and their dominance in the modern Antarctic fish fauna, especially their remarkable functional biodiversity. The fishes living in waters around the Antarctic component of Gondwana were subject to a nearly complete faunal replacement during the Cenozoic. A late middle Eocene, approximately 41–37 million years old (Reguero et al., 2002), fossil fish fauna from the La Meseta Formation on Seymour Island, near the tip of the Antarctic Peninsula, provides a glimpse of what a high paleolatitude (≈ 60°S) shelf fauna was like at this time. Although there were probably transitional faunas, this is the only known antecedent of the modern fauna. The taxonomically diverse La Meseta fauna was cool temperate, living in waters like those found today around Tasmania, New Zealand and southern South America. As biogeographic provinciality was less evident at high latitudes in the Eocene, the fauna was cosmopolitan rather than endemic to the Antarctic component of Gondwana. The fauna consisted of at least 30 taxonomically diverse chondrichthyans and actinopterygians, possibly including a phylogenetically basal notothenioid representative (Eastman, 2000, 2005 and references therein).

Most of the La Meseta fauna was eliminated during the course of habitat changes associated with tectonic and oceanographic events that isolated Antarctica, reduced seawater temperatures, restricted available habitats and altered the trophodynamics of the surrounding waters. As recently summarized by Convey et al. (2008), Antarctica became separated from other components of Gondwana by the opening of the Tasman Gateway and Drake Passage. Deep-water circulation ensued leading to the development of the Antarctic Circumpolar Current at 35–31 million years ago and this facilitated the thermal isolation of Antarctica and surrounding waters. Seasonal sea ice was present in the late middle and late Eocene about 40 million years ago and by about 34 million years ago large ice sheets were appearing on the continent. In the early Miocene (25–22 million years ago) water temperatures were becoming sufficiently low that antifreezes, a key adaptive innovation, were required for notothenioids to live and diversify in these waters (DeVries and Cheng, 2005). Subsequent expansions of the ice sheet onto the Antarctic shelf led to destruction and disturbance of benthic habitats by ice, with repeated groundings of parts of the ice sheet at the shelf break as recently as the Last Glacial Maximum 22,000–17,000 years ago (Anderson, 1999; Anderson et al., 2002). With the local extinction of most of the Eocene components of the fish fauna, notothenioids opportunistically radiated in this developing ecosystem. They also diversified from a benthic lineage into many different ecotypes including some that live in the water column in spite of the absence of a swim bladder. As inferred from nucleotide sequence data, the Antarctic clade of notothenioids arose 24–25 million years ago (Bargelloni et al., 2000a; Near, 2004), so there is good correspondence between the vicariant events mentioned above and the radiation of the Antarctic clade.
Diversification in Buoyancy is the Ecological Hallmark of the Notothenioid Radiation

Notothenioids are consistently supported as monophyletic (Balushkin, 2000; Near et al., 2004; Near and Cheng, 2008; Near, 2009) and are classified into eight families, 44 genera and 131 species, with 104 found in the Antarctic Region (Fig. 1). In high latitude areas of the shelf, notothenioids dominate fish diversity (76.6%), abundance (91.6%), and biomass (91.2%) at levels unparalleled in the marine realm (Eastman, 2005). Although they are a benthic group and lack a swim bladder, diversification in buoyancy is the defining ecological feature of the notothenioid radiation (Eastman, 1993). The water column was a major niche space to be filled in the developing Southern Ocean and its habitation is best exemplified by the neutrally buoyant pelagic species of the family Nototheniidae (subfamily Pleuragrammatinae), commonly known as the neutrally buoyant clade (Fig. 2). Adult specimens of Pleuragramma antarcticum, Dissostichus mawsoni, and Aethotaxis mitopteryx have been found to be neutrally buoyant by determining their weight in seawater (DeVries and Eastman, 1978; Eastman and DeVries, 1981, 1982; Eastman, 1993). There is little hydrodynamic contribution to lift because activity levels are low with intermittent swimming characteristic of nototheniids living on the high latitude shelves. The evolution of neutral buoyancy has enriched the functional biodiversity of this

Neutral buoyancy is achieved through a combination of static mechanisms including reduced skeletal ossification, with much persistent cartilage, and substantial accumulation of lipids within the white axial musculature and in subcutaneous tissue (DeVries and Eastman, 1978; Eastman and DeVries, 1981, 1982; Eastman, 1993).
group by enabling notothenioids to utilize unfilled niches in the water column, especially those involving pelagic zooplanktivory and piscivory. The best examples of this trend are the two species of *Dissostichus* and *Pleuragramma antarcticum*. Both species are extremely important in the Antarctic marine food web, and although sister taxa and sympatric in the water column, they are morphologically divergent in size, mechanisms of buoyancy and in numerous other aspects of their shared pelagic life style. As these species are the basis of our neural comparison, brief summaries of their biology follow.

**Dissostichus mawsoni** and **D. eleginoides**

The Patagonian toothfish, *Dissostichus eleginoides* (Fig. 2), and the Antarctic toothfish, *D. mawsoni* (Fig. 2), are the largest notothenioids with lengths of over 2 m and weights of more than 100 kg; an average-sized *Dissostichus* is 6-fold longer and at least 600-fold heavier than a typical *Pleuragramma*. Both toothfish species are opportunistic predators consuming primarily fish, squid and crustaceans (Eastman, 1985a; Fenaughty et al., 2003; Belchier and Collins, 2008). Cannibalism has also been documented in *D. mawsoni* (Petrov and Tatarinikov, 2010). *Dissostichus eleginoides* is known to have pelagic eggs and larvae (Evseeenko et al., 1995; Collins et al., 2007) and its life cycle is well known (Belchier and Collins, 2008). The life cycle of *D. mawsoni* is not completely understood. Eggs and larvae have never been collected anywhere within its range and specimens <40 cm SL have never been caught in the large shelf area of the Ross Sea (Hanchet et al., 2008). Although it may begin life as a pelagic larva, *D. mawsoni* is not neutrally buoyant as a juvenile and subadult, attaining neutral buoyancy only with the accumulation of substantial stores of lipid at about 81 cm SL (Near et al., 2003). The adult component of the life cycle of some populations of both species involves substantial migrations, at least 600–1,000 km in the case of *D. mawsoni*, for purposes of reproduction and feeding (Yukhov, 1982; Eastman and DeVries, 2000; Hanchet et al., 2008). Based on recapture of a tagged specimen, rate of movement/migration is estimated at 6 km/day (Petrov and Tatarinikov, 2010). Tagged *D. eleginoides* have migrated at least 1,900 km in the Indian Ocean sector of the Southern Ocean (Williams et al., 2002) and a vagrant *D. eleginoides* from the Patagonian shelf undertook a transequatorial migration of 10,000 km that terminated in Arctic waters (Møller et al., 2003). Around the Falkland Islands, *D. eleginoides* undergo seasonal migration than can extend for 1,000 km between feeding and reproductive grounds, although most fish migrate only 300–500 km (Laptikhovsky et al., 2006). Some specimens of *D. mawsoni* in the Ross Sea experience a post-spawning period of starvation with loss of lipid and white muscle and, presumably, buoyancy although this has not been measured in these emaciated so-called “axe handle” specimens (Fenaughty et al., 2008).

**Pleuragramma antarcticum**

*Pleuragramma antarcticum* (Fig. 2), with a maximum size of 25 cm total length, is an opportunistic zooplanktivore on copepods and krill, especially juvenile krill (DeWitt and Hopkins, 1977; Moreno et al., 1986; Lancauf et al., 2004). It is a key species in high latitude waters where it serves as prey for fishes, including *D. mawsoni* (Eastman, 1985a,b), as well as Weddell seals, Type C killer whales, minke whales, Adélie and emperor penguins and other marine birds (La Mesa et al., 2004; Lauriano et al., 2007; Smith et al., 2007; Ainsley and Siniff, 2009). The single species abundance and biomass of *Pleuragramma* on the high shelf (DeWitt, 1970) are comparable to that of the Argentine anchovy (*Engraulis anchoita*) in subtropical upwelling areas (Hubold, 1985). Although *Pleuragramma* may approximate the water column dominance of clupeoids and exhibits convergence with engraulid body morphology (Fig. 2), it is not aerobic and does not form dense continuously swimming schools. In another anchovy, *E. encrasicolus*, 38% of the cross sectional area of the caudal myotomes is occupied by slow red fibers of the lateralis superficialis muscle; in *Pleuragramma* this figure is only 10% (Johnston et al., 1988). Data for gill morphometrics and blood parameters also suggest that *Pleuragramma* has a low activity level (Kunzmann, 1990; Tamburrini et al., 1997; Wörhmann et al., 1997). Thus neutral buoyancy allows *Pleuragramma* to float in the water column in a sit-and-wait fashion, monitoring the water visually as well as with its lateral line system for the vibrations caused by swimming zooplankton. *Pleuragramma* is therefore an ecological paradox: a pelagic water column species with an inactive energy-conserving life style.

*Pleuragramma* is the second most lipid-rich notothenioid with levels at 38–47% of dry body weight (Freidrich and Hagen, 1994; Hagen et al., 2000) and this contributes substantially to its near neutral buoyancy. Most of the lipid is stored in large 1–2 mm-diameter sacs consisting of complex of adipocytes (Eastman and DeVries, 1989) and presumably is not available for routine metabolism. Reduction in skeletal weight is in part accomplished through pedomorphy, i.e., cartilage persists with delayed ossification of bones (Voskoboinikova et al., 1994) and adult *Pleuragramma* have a large notochord that is only slightly constricted by bone development in the vertebral centra (Totton, 1914; DeVries and Eastman, 1978).
Pedomorphy and the Radiation of the Neutrally Buoyant Clade

Silvery pelagic juveniles are characteristic of the phylogenetically basal notothenioid family Bovichtidae (Hardy, 1988; Andrew et al., 1995). Thus the pelagic lifestyle is pedomorphic in the sense that the pelagic juvenile stages of bovichtids are retained in adults of the phylogenetically derived neutrally buoyant clade of nototheniids and in other families as well. Balushkin (1984, pp. 127–128) recognized the importance of pedomorphy in the evolution and diversification of notothenioids, especially the adaptive possibilities of juvenile forms as the modern Antarctic marine ecosystem was developing and new water column niches were opening. *Pleuragramma* is the prime example in the neutrally buoyant clade of both a pedomorphic life style and several pedomorphic body systems.

Given the absence of a swim bladder, a reduction in density through alteration of skeletal mass is an essential prerequisite for habitation of the water column. As for the mechanism of skeletal pedomorphy, it has recently been found that, in comparison to benthic notothenioids and non-notothenioids, the pedomorphic decrease in branchiocranial mineralization in *Pleuragramma* is determined by heterochronic shifts in the expression of skeletal genes, specifically persistence of the chondrogenic program and a delay in the onset of the osteogenic program during larval development (Albertson et al., 2010). Other persistent pedomorphic traits in *Pleuragramma* include the encircling red-fibered lateralis superficialis muscle, subcarangiform locomotion, incomplete lateral line canal formation with neuromasts exposed on the body surface, a slender and laterally compressed body shape, and silvery coloration (DeWitt and Hopkins, 1977; Johnston et al., 1988; Eastman, 1997; Montgomery, 2000; Montgomery and Clements, 2000; Vacchi et al., 2004). Furthermore, *P. antarcticum* is the only known notothenioid species in which all stages from egg to adult are found in the water column (Vacchi et al., 2004). There is, however, vertical size segregation with larger individuals living progressively deeper in the water column, adults to depths of 400–700 m (Hubold and Ekau, 1987).

The Perciform Radiation Extends to Antarctica

With over 10,000 species, a clade that includes primarily perciform fishes is considered the most significant among the six accelerations in the tempo of net diversification that produced the extant biodiversity of jawed vertebrates (Alfaro et al., 2009). The potential of perciforms to exploit tropical marine and freshwater habitats is exceptional and includes radiations of coral reef fishes in the sea and cichlids in lakes. With old and young clades, the cichlids of the African Great Lakes and crater lakes provide classic and intensively studied examples of adaptive radiation (Schluter, 2000). Although less well known, the notothenioid radiation is evidence that perciform morphology and physiology are, with slight modifications, also suitable for polar habitats. As inferred from molecular sequence data, the notothenioid radiation in the sea around Antarctica began 24–25 million years ago (Bargelloni et al., 2000a; Near, 2004) and proceeded, with periodic episodes of phylogenetic and ecological diversification, through the Neogene and into the Pleistocene, with at least one clade suspected to be less than 1 million years old (Eakin et al., 2009). In analyses employing morphological data sets, the neutrally buoyant clade of notothenioids is pedomorphically basal in the family and represents an early burst of diversification into the water column of an ecosystem sparsely populated with pelagic fishes. With open niches, the clade underwent substantial ecological and morphological diversification with the modern species occupying two different levels in the food web, zooplanktivore (*Pleuragramma*) and large predator (*Dissostichus*). Thus the neutrally buoyant clade offers a window into the role that ecological variability plays in the evolutionary divergence of nervous and sensory systems. Using the brain of *Eleginops maclovinus*, the sister group of the neutrally buoyant clade, as a reference for pedomorphically basal morphology, we will compare the brains of *Dissostichus mawsoni* and *D. eleginoides* with *Pleuragramma antarcticum*. Divergence times inferred from nucleotide sequences suggest that the sister taxa *Dissostichus* and *Pleuragramma* have been separated for 24.1 million years (Near, 2004). We will attempt to resolve the incongruity that, while they share common ancestry, neutral buoyancy and the pelagic habitat, their brains and retinae are very different and may in part reflect their disparate roles in the pelagic ecosystem. Our null hypothesis is that there is no morphological diversification in neural and retinal morphology between the two genera, with the non-Antarctic sister species *Eleginops maclovinus* used as the basis for ancestral morphology of the nervous system. Our specific objectives are to: 1) compare the relative weights of brain regions and the gross morphology and histology of the adult brains and retinae of *Dissostichus* and *Pleuragramma*; 2) determine whether or not the brain of *Pleuragramma* exhibits pedomorphic features and 3) consider whether or not the morphological and ecological diversification exhibited by these two genera is reflected in brain and retinal morphology.
MATERIALS AND METHODS
Specimens, Phylogenies and Divergence Times, and Anatomical Nomenclature

We caught adult Dissostichus mawsoni in 1978, 1979 and 1991 by fishing with a seine through holes drilled in the sea ice over water 500 m deep near the U.S. McMurdo Station on Ross Island in the southwestern Ross Sea (77°51'S, 166°40'E). Eastman and DeVries (1981, 2000) provide additional details concerning the method of capture. We obtained D. eleginoides during the ICEFISH cruise NBP 04-04 (17 May to 17 July 2004) of the RV “Na- thaniel B. Palmer.” We deployed 0.8-m-diameter by 2-m-long traps baited with fish at depths of 200 m on the Burdwood Bank (east of Staten Island, Tierra del Fuego) and on the shelf of the Falkland Islands. We left traps in place on the bottom for 24–36 h. During the ICEFISH cruise we also stopped at Stanley (51°42'S; 57°51'W) in East Falkland Island where we captured adult Eleginops maclovinus with a 30-m-long beach seine in Fish Creek, Port Louis on 29 May 2004. We collected adult Pleuragramma antarctica in the southwestern Ross Sea during bottom trawling on cruises 96-6 (11 December 1996 to 8 January 1997) and 97-8 (20 December 1997 to 10 January 1998) of the RV Nathanial B. Palmer. We used a 9.1-m-long, 7.6-m-effective width Marinovich Gulf Coast style flat trawl, a type of otter trawl. We trawled at a speed of 2.0–3.0 knots for 0.5–1.0 h. During these cruises we also collected small samples of postlarval and juvenile Pleuragramma. These specimens were 10–15 mm SL (age class 0, early) and 60–85 mm SL (age classes 2–3), with ages based on information in Kellermann (1986) and Hubold and Tomo (1988). These small specimens were not sufficiently well preserved to be used for histology. In accordance with protocol L01-14 approved by the Institutional Animal Care and Use Committee at Ohio University, all captured fishes were euthanized either by severing the spinal cord or by immersing in a 200-μg l⁻¹ solution of 3-aminobenzoic acid ethyl ester (MS-222, Sigma, St. Louis).

As summarized in the Introduction, there are numerous phylogenetic hypotheses for the Notothenioidei and the monophyly of the group is well supported by both morphological and molecular data. The neutrally buoyant clade within the family Nototheniidae is supported by the majority of available data sets (Balushkin, 2000; Near et al., 2004; Sanchez et al., 2007; Near and Cheng, 2008) and frequency of its recovery is sufficient that it likely reflects the sister relationship of Dissostichus and Pleuragramma (Fig. 2). Near (2004) and Hedges et al. (2006) used molecular sequence data to infer divergence times for major clade- genic events within the suborder. Among those useful in our study are 1) the most recent common ancestor of the non-Antarctic Eleginopidae and the Antarctic notothenioids and 2) the most recent common ancestor of the antifreeze-bearing clade containing the basal neutrally buoyant clade (i.e., the separation of Dis- sostichus and Pleuragramma). The dates are maximum times for these events and are, respectively, 40.0 million years (a fossil calibration), 24.1 ± 0.5 million years. In addition Near’s (2004) and Hedges et al., (2006) calculations date the separation of D. mawsoni and D. eleginoides at 14.5 ± 0.5 million years. We used these divergence times in Figure 2 in conjunction with a cladogram for the Nototheniidae from Sanchez et al. (2007).

In describing brain nuclei, we follow the nomenclature of authors included in Northcutt and Davis (1983) and Davis and Northcutt (1983). What have been traditionally termed the anterior and posterior lateral line nerves of fishes are actually “complexes” consisting of several distinct cranial nerves (North- cutt, 1989; Northcutt and Bemis, 1993). We follow Northcutt (1989) in distinguishing the anterodorsal and anteroventral lateral line nerves.

Histology

Because specimens of Dissostichus mawsoni and D. eleginoides were too large to fix by perfusion in any practical way, we removed their brains and fixed them by immersion in 10% formalin. Pleuragramma antarcticum are lipid-rich and possess little bone, consequently they were damaged in the trawls and therefore it was necessary to fix the brains by immersion rather than perfu- sion. We did, however, obtain one intact specimen (TL = 189 mm; SL 170 mm) that we perfused onboard ship with Bouin’s fixative. After anesthetization, the heart and air was removed and the brain was exposed. Notothenioid saline solution was prepared, adjusted with NaCl to a concentration of 600 mosm l⁻¹, maintained at ambient seawater temperature (–1.5°C), and perfused through the heart. Saline was followed by Bouin’s fixative. During this perfusion the gills were periodically irrigated with cold seawater.

We subjected both perfusion and immersion fixed brains to the same protocol: dehydration in alcohol, clearing in Hemo-De (Fisher Scientific) and embedding in paraffin according to standard proce- dures (Kierman, 1990). We cut embedded brains in transverse planes on a rotary microtome to produce serial sections 10–12 μm thick. Sections were mounted on slides, dried, deparaffinized, stained with either hematoxylin and eosin or Bodian’s Protargol for 24 h at 50°C (Clark, 1981), dehydrated and coverslipped using Cyto- seal 60 as the mounting medium. The histological component of our study includes brains of three species Pleuragramma antarcticum, D. eleginoides, and D. mawsoni although, given the large size of Pleuragramma, the brain of the latter species was examined regionally rather than serially sectioned. The primary description is based on a serially sectioned brain of D. eleginoides and the histology of D. mawsoni is identical. With the exception of the weights, information for the brain morphology of Eleginops maclovinus (Fig. 3), the sister group to D. mawsoni and D. eleginoides, is from Eastman and Lannoo (2008).

We cut histological sections of central retina from dorsoventral strips located immediately temporal (lateral) to the optic disk. We sampled four to six specimens from each of Pleuragramma antarcticum, D. eleginoides and D. mawsoni and employed the histologi- cal protocol and staining procedures outlined above except that sections were cut at 7 μm. We stained sections with either Gomori’s trichrome (Humason, 1979) or Bodian’s Protargol.

Determining Weights of Brain Regions

Our sample consisted of 13 brains, four each from Eleginops and D. mawsoni and five from Pleuragramma. We did not have a sufficient number of specimens to utilize D. eleginoides in this aspect of our study. All fish were adults and the specimens were of typical size for each species: Eleginops were 345–430 mm SL, 700–1,212 g; Pleuragramma were 148–225 mm SL, 35–60 g, and D. mawsoni were 900–1400 mm SL, 20,000–40,000 g (exact SL and weight of all but one specimen were unknown). Brain lengths (rostral margin of olfactory bulb to caudal margin of open oeil) were: Eleginops 17.8–19.9 mm, Pleuragramma 11.8–15.5 mm and D. mawsoni 21.9–28.2 mm. Specimens were fixed by immersion of the head in 10% formalin with subse- quent storage in 70% ethanol. Shrinkage due to fixation does not substantially affect relative weights. After removal from the skull, we trimmed the cranial nerves flush with the brain and removed the meninges, blood vessels, pituitary and saccus vasculosus. Under magnification we employed either a No. 11 scalp knife (22 mm blade angled at 10°) or a Moria microcouteaux (6 mm blade angled at 15°) to divide the brain into six regions: 1) olfactory bulbs, 2) telencephalon, 3) diencephalon, 4) mesencephalon, 5) corpus division of the cerebellum and 6) medulla. Figure 4 shows the cuts we made and structures included in each of the regions. There were two cuts that did not include entire regions or distinct separations between regions. The diencephalon was separated from the mesencephalon by a horizontal cut at the dorsal margin of the inferior lobes and consisted primarily of these lobes and the neuropil between them. The mesencephalon also included part of the thalamus of the diencephalon and the ventral horn of the spinal cord arising from the tegmental ventricle from caudal attachments in the rostral medulla. The corpus of the cerebellum was removed by a horizontal cut at the dorsal margin of the eminentia granularis. The rostral cut for the medulla fell caudal to the tectum and inferior lobes and rostral to the eminentia granularis. The medulla consisted of the eminentia granularis, crista cerebell-
Fig. 3. (A) Lateral and (B) dorsal views of the brain of *Eleginops maclovinus* (SL = 34.5 cm). From Eastman and Lannoo (2008). To illustrate features of the rhombencephalon in dorsal view, the drawing was made from a slightly oblique dorsocaudal angle. Therefore structures such as the corpus of the cerebellum are not perfectly aligned in the two views of the brain. ADLL, anterodorsal lateral line nerve complex; AVLL, anteroventral lateral line nerve complex; CC, crista cerebellaris of the rhombencephalon; CCB, corpus division of the cerebellum; DI, dorsal lateral subdivision of the telencephalon; DM, dorsal medial subdivision of the telencephalon; EG, eminentia granularis division of the cerebellum; IL, inferior lobe of the diencephalon; OB, olfactory bulb; PIt, pituitary gland; PLL, posterior lateral line nerve complex; PreO, preoptic area; SN1, first spinal nerve; SN2, second spinal nerve; SN3, third spinal nerve; SV, saccus vasculosus; Tec, tectum of the mesencephalon; Tel, telencephalon; I, olfactory nerve; II, optic nerve; III, oculomotor nerve; IV, trochlear nerve; V, trigeminal nerve; VI, abducens nerve; VII, facial nerve; VIII, auditory/vestibular nerve; IX, glossopharyngeal nerve; X, vagus nerve.

Fig. 4. Parasagittal histological section of the brain of *Dissostichus mawsoni* (SL = 89 cm) showing cuts made (red) to divide the brain into six regions for the calculation of relative weights. Other major features of the brain are also indicated. Bodian's Protargol. Magnification x5. 1, olfactory bulb; 2, telencephalon; 3, diencephalon; 4, mesencephalon; 5, corpus division of the cerebellum; 6, medulla; CC, crista cerebellaris of the rhombencephalon; CCB, corpus division of the cerebellum; IL, inferior lobe of the diencephalon; Med, medulla of the rhombencephalon; OB, olfactory bulb; ND, nucleus diffusus of the inferior lobe; NG, nucleus glomerulosus of the diencephalon; SV, saccus vasculosus; Tec, tectum of the mesencephalon; Tel, telencephalon; Thal, thalamus of the diencephalon; VCB, valvula division of the cerebellum; I, olfactory nerve (proximal expansion); II, optic nerve.
ris and all other neuropil extending caudally to the origins of the dorsal roots of the first spinal nerve. We blotted the pieces to remove excess ethanol and then weighed them to an accuracy of 0.0001 g on a Mettler-Toledo AB104 electronic balance. We used the program SPSS 16.0 for statistical analysis. Because the relative brain weights were ratios, we performed an arcsine transformation to normalize the data (Sokal and Rohlf, 1981). Levene’s test indicated that the assumption of homogeneity of variances was met. Employing Shapiro-Wilk tests for normality, we found that of the six brain regions in the three species examined, only the values for the relative weight of the telencephalon in D. mawsoni were not normally distributed. Given this single exception, we concluded it was appropriate to use parametric statistics although, as a control on our assumption, we also employed a nonparametric Kruskal-Wallis $H$ test that gave the same results at significance levels of the same order of magnitude. Our null hypothesis was that there were no differences in relative weights of brain regions across the three species. We used a one-way ANOVA to test for differences among means with a Bonferroni test to adjust for multiple comparisons. Our accepted level of significance was $P = 0.04$. Data values in the tables and text are untransformed but reported levels of significance are for arcsine-transformed data.

### RESULTS

Table 1 and the bar graph in Figure 5 summarize the differences in the relative weights of six brain regions and all other neuropil extending caudally to the origins of the dorsal roots of the first spinal nerve. We blotted the pieces to remove excess ethanol and then weighed them to an accuracy of 0.0001 g on a Mettler-Toledo AB104 electronic balance. We used the program SPSS 16.0 for statistical analysis. Because the relative brain weights were ratios, we performed an arcsine transformation to normalize the data (Sokal and Rohlf, 1981). We used the program SPSS 16.0 for statistical analysis. Because the relative brain weights were ratios, we performed an arcsine transformation to normalize the data (Sokal and Rohlf, 1981). Levene’s test indicated that the assumption of homogeneity of variances was met. Employing Shapiro-Wilk tests for normality, we found that of the six brain regions in the three species examined, only the values for the relative weight of the telencephalon in D. mawsoni were not normally distributed. Given this single exception, we concluded it was appropriate to use parametric statistics although, as a control on our assumption, we also employed a nonparametric Kruskal-Wallis $H$ test that gave the same results at significance levels of the same order of magnitude. Our null hypothesis was that there were no differences in relative weights of brain regions across the three species. We used a one-way ANOVA to test for differences among means with a Bonferroni test to adjust for multiple comparisons. Our accepted level of significance was $P = 0.04$. Data values in the tables and text are untransformed but reported levels of significance are for arcsine-transformed data.

### Table 1. Relative masses (as % of total brain mass) of brain regions for formalin-preserved ethanol-stored brains of non-Antarctic Eleginops maclovinus and two closely related Antarctic nototheniids

<table>
<thead>
<tr>
<th>Species</th>
<th>$n$</th>
<th>Total brain mass Mean (range) (g)</th>
<th>Offactory bulbs Mean ± SD (%)</th>
<th>Telencephalon Mean ± SD (%)</th>
<th>Diencephalon Mean ± SD (%)</th>
<th>Mesencephalon Mean ± SD (%)</th>
<th>Corpus cerebelli Mean ± SD (%)</th>
<th>Medulla Mean ± SD (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eleginops maclovinus</td>
<td>4</td>
<td>0.3154 (0.2063–0.3852)</td>
<td>3.68 ± 0.62</td>
<td>10.35 ± 1.20</td>
<td>13.87 ± 1.80</td>
<td>30.00 ± 2.56</td>
<td>11.90 ± 1.07</td>
<td>30.20 ± 1.23</td>
</tr>
<tr>
<td>Dissostichus mawsoni</td>
<td>4</td>
<td>0.8095 (0.4465–0.9707)</td>
<td>3.90 ± 1.10</td>
<td>7.91 ± 0.83</td>
<td>11.87 ± 0.78</td>
<td>34.32 ± 1.49</td>
<td>6.88 ± 0.32</td>
<td>35.11 ± 2.18</td>
</tr>
<tr>
<td>Pleuragramma antarcticum</td>
<td>5</td>
<td>0.0745 (0.0505–0.0989)</td>
<td>2.40 ± 0.43</td>
<td>5.66 ± 0.19</td>
<td>2.31 ± 0.14</td>
<td>29.49 ± 0.001</td>
<td>195.018</td>
<td>8.358</td>
</tr>
</tbody>
</table>

$F_{2,10}$ P

<table>
<thead>
<tr>
<th>D vs. P*</th>
<th>E vs. D*</th>
<th>E vs. P**</th>
<th>D vs. P***</th>
</tr>
</thead>
<tbody>
<tr>
<td>6.230</td>
<td>5.668</td>
<td>2.315</td>
<td>29.49</td>
</tr>
<tr>
<td>0.001</td>
<td>0.023</td>
<td>0.149</td>
<td>0.0001</td>
</tr>
<tr>
<td>E vs. D*</td>
<td>E vs. D**</td>
<td>E vs. D***</td>
<td>E vs. P*</td>
</tr>
<tr>
<td>1.07</td>
<td>30.20</td>
<td>34.04</td>
<td>1.23</td>
</tr>
</tbody>
</table>

Results of a one-way ANOVA are in rows four and five and in the columns beneath are pairs of species (denoted by the first letter of the genus) that differ significantly, with $P$-values derived from Bonferroni post hoc tests (**$P < 0.0001$, *$P < 0.009$, *$P < 0.04$).
brain regions in adult *Eleginops, D. mawsoni* and *Pleuragramma*. Table 1 also provides the results of a one-way ANOVA indicating that, among the three species, there were significant differences (*P* = 0.02) in the mean relative weights of all brain regions except the diencephalon. In addition, Table

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identifies pairs of species with means that are significantly different. *Eleginops* differs from *D. mawsoni* and *Pleuragramma* in four and three regional comparisons, respectively, while there are three regional differences between the two Antarctic species. With the ancestral brain morphology of the non-Antarctic *Eleginops* as a baseline, the most noteworthy and statistically significant departures in the brains of the two Antarctic species are a reduction of the corpus cerebelli and an expansion.

---

**Figure 7.**

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of the mesencephalon and medulla (Table 1). Compared to Eleginops, both species also have a relatively smaller telencephalon, although this is significant only in D. mawsoni. When the two Antarctic species are compared, Pleuragramma has reduced olfactory bulbs and corpus cerebelli and an expanded mesencephalon relative to D. mawsoni. Thus the brain of Pleuragramma is more apomorphic or derived than that of Dissostichus.

Gross Morphology of Brains

The brains and cranial nerves of Dissostichus mawsoni (Fig. 6C,D) and D. eleginoides are identical in gross morphology and share the following features: proximal expansions of the olfactory nerves that are of greater diameter than the olfactory bulbs; sessile olfactory bulbs situated against the ventral telencephalon; a moderately-sized telencephalon with large and prominent dorsal medial lobes opposed against the midline; relatively large tecta and a caudally projecting corpora of the cerebellum; prominent eminentia granulares and crista cerebellares; large olfactory and optic nerves of similar diameter and well developed anterior and posterior lateral line nerves. When the brain of D. mawsoni is compared with that of Eleginops (Fig. 3), the increases in the relative sizes (weights) of the mesencephalon and medulla in D. mawsoni are not obvious to the unaided eye, however reductions in the relative sizes (weights) of the telencephalon and, especially, the corpus cerebelli are clearly evident. Nevertheless, the overall brain and cranial nerve morphology of D. mawsoni is similar to that of its non-Antarctic sister species Eleginops, and therefore can be considered a phylogenetically persistent morphology. However, unlike Eleginops (Fig. 3) and the phylogenetically basal bovichtids (Eastman and Lannoo, 2007), neither D. mawsoni nor any other member of the Antarctic clade possess fissuring or lobation of the corpus cerebelli.

In Pleuragramma antarcticum, on the other hand, the brain morphology (Fig. 6A,B) differs from that of both Eleginops and Dissostichus, and the differences between Pleuragramma and Dissostichus are as great as any interspecific differences we have encountered in our survey of nototheniid brain diversity. Both the diameter of the olfactory nerve and its proximal swelling are relatively smaller in Pleuragramma and, unlike any other nototheniid brain studied to date, the olfactory bulbs are slightly separated, or stalked, from the telencephalon to reveal the medial and lateral olfactory tracts. The stalking is not evident in small specimens and becomes evident at 125–150 mm SL. The optic is the largest cranial nerve. The mesencephalon is relatively larger than that of Dissostichus. The reduction of the corpus cerebelli to a small round upright lobe is an especially notable feature of the brain of Pleuragramma. Although visual comparison of the brain of Pleuragramma with Dissostichus (Fig. 6) gives the impression that Pleuragramma has hypertrophied octovalaterals, there is no significant difference in the relative weights of the medulla in the two species. Nevertheless, reduction of the corpus cerebelli renders the eminentia granularis prominent (Fig. 8D,F) and the crista cerebellaris form a conspicuous rim that caps the medulla (Fig. 8H) and that decussates across the midline to obscure most of the lumen of the fourth ventricle (Fig. 6B). The anterior and posterior lateral line nerves are the second largest cranial nerves.

Brain regions of early age class 0 postlarval Pleuragramma (10–15 mm SL) are differentiated rostrally but not caudally. The olfactory bulbs and telencephalon are small but recognizable in the interorbital area, the midbrain tectum is enormous and a small medulla is present in the rhombencephalon, however the corpus cerebelli, eminentia granulares and crista cerebellariss are not visible. Brains from age class 1 specimens are not included in our sample but those from juveniles of age classes 2–3 (60–85 mm SL) are adult, not juvenile, in their gross morphology with a characteristic small round corpus and prominent eminentia and crista.

Brain Histology

The brain histology of D. eleginoides and Pleuragramma reflect typical perciform patterns. Transverse sections through the caudal telencephalon at
the level of the anterior commissure (AC) (Fig. 7A,B) reveal clear dorsomedial (Dm), dorsolateral (Dl), dorsocentral (Dc) and dorsoposterior (Dp) lobes. Lobotomy is more pronounced in *D. eleginoides*. The ventral telencephalon, represented by the ventroposterior nucleus (VP), is well developed but less variable between species. In the diencephalon (Fig. 7C,D), the habenulae (Ha) are well developed, as is the dorsal medial nucleus of the thalamus (DM). The parvocellular nucleus of the preoptic region (PP), is extensive in both species, the magnocellular nucleus (PM) less so. The pretectal nucleus (NPTec) is large in both species. The rostral tectum (Tec) in both species is large, proportionally as large as in any other Antarctic notothenioid we have examined (Eastman and Lannoo, 1995).

Transverse sections through the rostral nucleus glomerulosus (Fig. 7E,F) again demonstrate the size of the tectal lobes in these species; in *D. eleginoides*, lobes expand laterally while in *Pleuragramma* they arch dorsally. The torus semicirculares (TS) are prominent, but not exceptional in size. The paired nucleus glomerulosus (G) are well defined. Inferior lobes are moderately large with well delimited nucleus glomerulosus (G) are well defined. Inferior lobes are moderately large with well delimited nucleus diffusus (ND) and lateral recesses (LR). In *Pleuragramma* at this level the saccus vasculosus (SV) forms a prominent ventral midline structure (Fig. 7F).

Farther caudally (Fig. 7G,H) the tectum, torus semicirculares and inferior lobes continue their prominence and the oculomotor nucleus (CN III) is present. However, the dominant feature at this level are the numerous large lobules of the valvula cerebellum (VCb). The valvula develops from an area near the base of the corpus cerebellum (CCb) and migrates forward, forming an “S” pattern as it occupies the medial portion of the tectal ventricle (see Fig. 3 for the adult morphology). In both species there is a rostral-caudal-rostral-caudal pattern to valvular development, unusual among not only perciforms but teleosts in general.

Sections through the caudal tectum and torus (Fig. 8A,B) reveal, in *D. eleginoides*, the rostral extreme of the corpus cerebellum (CCb) and the caudal extreme of the inferior lobes. Neither structure is visible at the comparable level in *Pleuragramma*. Both brains continue to exhibit the elaboration of the valvula. Sections through the body of the CCb and the central portion of the eminentia granulares (EG) at the level of the trigeminal motor nucleus (Vm) (Fig. 8C,D) demonstrate the comparable large size of these cerebellar structures in both brains. They also demonstrate the relative lateral compression of the *Pleuragramma* brain.

At the level of the caudal EG, their associated bundles of parallel fibers (crista cerebellares, CC; Fig. 8E,F) comprising the lateral line region are large, especially in *Pleuragramma*. Sections through more progressively caudal brain sections (Fig. 8G,H) continue to reflect large cristae. Figure 8E demonstrates the caudal extent of the corpus cerebelli in *D. eleginoides*, and all three caudal brainstem sections (Fig. 8D,F,H) demonstrate lateral compression in *Pleuragramma*.

### Retinal Histology

Figure 9 shows the histological appearance of 150 μm-long portions of the central retina. Table 2 provides data on retinal cell counts for both species of *Dissostichus* and *Pleuragramma* and a comparison with two non-Antarctic notothenioids including their sister species *Eleginops maclovinus*. The layering of the nototheniid retina is typical but its substance is relatively thin compared to the 500-μm maximum for fishes (Nicol, 1989). Rods are quantitatively dominant in the photoreceptor layer of all species and are especially evident between the small numbers of widely spaced cones (Fig. 9A,B) in *Dissostichus*. While *D. eleginoides* has single cones with oval-shaped ellipsoids 12–13 μm in diameter, *D. mawsoni* possesses more twin cones than single cones with the ellipsoids of the former measuring 10–12 μm. In *D. eleginoides* the outer segments of the photoreceptors are longer than those of *D. mawsoni*. All retinal layers of *D. mawsoni* contain fewer cells than those in *D. eleginoides*. The retina of *Pleuragramma*, on the other hand, is thick and more cellular, and in this respect is comparable to that of the non-Antarctic *Eleginops maclovinus* (Table 2). Layering is distinct and sublayering of the internal nuclear layer is present, with a clearly defined row of horizontal cells (Fig. 9F). The photoreceptor layer of *Pleuragramma* (Fig. 9C) is qualitatively different than that of *Dissostichus* because of the presence of side-by-side single cones with small ellipsoids of uniform width (≈ 5 μm). Rods are not as obvious but their proximal outer segments are visible between those of cones. The retinal pigment epithelium in *Pleuragramma* and both species of *Dissostichus* is sufficiently mobile that dispersion of pigment granules is evident as far centripetally as the junction between the inner and outer segments of the photoreceptors (Fig. 9D–F). While phyletically basal non-Antarctic species generally have thicker retinae and more retinal cells than Antarctic species, *Pleuragramma* is a noteworthy exception to the Antarctic pattern in having a well-developed retina. Their retinas have more cells than that of any other species of Antarctic nototheniod examined to date despite the fact that these other species are all sympatric with *Pleuragramma* (Eastman, 1988; Lannoo and Eastman, 2000; Eastman and Lannoo, 2003a,b, 2004).
Fig. 8. Transverse histological cross sections from caudal mesencephalon through medulla of (left column) *Dissostichus eleginoides* (SL = 53 cm) and (right column) *Pleuragramma antarcticum* (SL = 17 cm). Brain sections are presented at magnifications to best facilitate histological comparisons. Magnifications of pairs of equivalent sections differ by 1.2–2.0-fold (see later); refer to Figure 6 for accurate proportions of the brains. Magnifications: (A) x8; (B) x13; (C) x8; (D) x11; (E) x8; (F) x10; (G) x14; (H) x18. Key to abbreviations same as Figure 7.
Fig. 9. Transverse sections showing retinal histology of (A and D) *Dissostichus eleginoides* (SL = 76 cm), (B and E) *D. mawsoni* (SL ≈ 100 cm) and (C and F) *Pleuragramma antarcticum* (SL = 17 cm) with sections aligned along the plane of the external limiting membrane. Sections in top row stained with Gomori’s trichrome which highlights cone ellipsoids in the photoreceptor layer; bottom row stained with Bodian’s Protargol for visualization of nuclei in various layers of the retina. Magnification ×285. 1, retinal pigment epithelium; 2, outer segments of photoreceptors; 3, inner segments of photoreceptors (myoids and ellipsoids); 4, external limiting membrane; 5, external nuclear layer; 6, internal nuclear layer; 7, ganglion cell layer; 8, optic nerve fibers.

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DISCUSSION

Based on relative weights of brain regions and on morphology, and using the brain of the non-Antarctic sister group *Eleginops* as plesiomorphic, *Dissostichus* and *Pleuragramma* show loss of telencephalic and cerebellar mass and expansion of the mesencephalon and medulla. Nevertheless, in overall appearance the brain of *Dissostichus* is remarkably similar to *Eleginops* and therefore exhibits considerable phylogenetically persistent morphology. In comparing *Dissostichus* and *Pleuragramma*, there are a number of derived or apomorphic features in the brain of *Pleuragramma* including reduced olfactory nerves and bulbs, a reduced corpus cerebelli and an expanded mesencephalon. Although there is not a significant difference in the relative weights of the medulla in the two species, the relative prominence of the eminentia granularis and bulging cap-like appearance of the crista cerebellaris (Fig. 8H) are distinctive in *Pleuragramma*.

There are two other features that contribute to the morphological differences between the brains of *Dissostichus* and *Pleuragramma*, lateral compression in *Pleuragramma* and lobation in *Dissostichus*. Compression can easily be explained through two features of *Pleuragramma*: convergence on an anchovy/herring body shape and the relatively large brain in this small fish (i.e., a relatively large brain in a fish with a compressed body is likely to produce a compressed brain). In comparing *Dissostichus* and *Pleuragramma*, this is especially evident in Figures 7E versus 7F for the tectum and Figures 8E and 8G versus 8F and 8H for the medulla. *Dissostichus* are large fishes with a depressed head and a round trunk, features unlikely to alter brain shape. The second difference between these brains, a more prominent pattern of lobation in *Dissostichus*, is probably attributable to underlying histology, specifically to a reduction in cellularity of the neuropil in the nuclei and lobes in *Pleuragramma*. While certain features, such as the valvula cerebelli, eminentia granularis and crista cerebellares are highly lobated in *Pleuragramma* and equivalent in proportion to structures in *Dissostichus*, many structures, including the telencephalon, inferior lobes and corpus cerebelli are not (Figs. 7 and 8).

Are the Brain and Sense Organs of *Pleuragramma* Pedomorphic?

**Brain.** Persistence of the pelagic larval life style into adulthood is made possible by substantial pedomorphy, and this level of pedomorphy in notothenioids has only been documented in *Pleuragramma*. We have previously men-
tioned a number of pedomorphic body systems and also that the pelagic life style is itself pedomorphic and consistent with the heterochronic shift that may have resulted in the initial divergence of *Pleuragramma*. The brain is not grossly pedomorphic, although the lack of distinct loba
tion in the telencephalon, the relatively small inferior lobes, and the small round corpus cere
belli could possibly be considered pedomorphic given ontogenetic trajectories. However a similar
morphology in the corpus cerebelli is observed in a variety of sedentary benthic notothenioids (*Tremat
tomus scotti, Dolloidi Draco longidorsalis* and *Akaro
taxis nudiceps*) that are not as pedomorphic as
*Pleuragramma* (Lanno and Eastman, 2000; Eastman and Lanno, 2003a,b), and also in non-nototheon
ioids (Franz, 1911). Further, the relative lack of deep loba
tion in the telencephalon and the inferior lobes is not grossly obvious, nor unusual for percids.
We therefore conclude that pedomorphy is not the prime factor driving gross brain morphology in
*Pleuragramma*. Instead, the *Pleuragramma* brain reflects highly developed visual and lateral line sys
tems, as well as a sedentary lifestyle in the pelagic realm.

**Mechanosensory lateral line.** Individual
sense organs may or may not be pedomorphic. In
the case of the lateral line, superficial neuromasts are present at hatching in all teleosts and some persist throughout life; other neuromasts become enclosed in pored canals later in larval life or at transformation, depending on the group (Blaxter, 1988; Webb, 1999). In *Pleuragramma*, however, superficial trunk neuromasts do not induce forma
tion of bony canals, probably because of the general reduction in ossification associated with pelagic life, and thus the neuromasts are left in a pedomorphic state in adult fish. This heterochronic change has probably been detrimental to lateral line function because the filtering role of the canals has been lost (Coombs and Montgomery, 1994; Montgomery et al., 1994; Montgomery and Clements, 2000; Montgomery, 2000). However the large eminentia granulare
s and criptae cerebellae form part of an adaptive filter in the medulla that cancels low-frequency self-induced noise (Montgomery and Bodznick, 1994). Thus the superficial neuromasts of *Pleuragramma*
are pedomorphic due to incidental loss of the bony canals associated with skeletal pedomorphy, and the consequental neural disadvantage has been com
pensated for by central processing of mechanosen
sory information (Montgomery, 2000; Montgomery and Clements, 2000). The fact that *Pleuragramma* is a relatively inactive sit-and-wait zooplanktivore may also contribute to the effectiveness of this compensatory filtering mechanism.

**Eye and retina.** Although the eyes are large in larvae and continue to grow throughout life, eye diameter relative to body length shows negative allometry in teleosts (Nicol, 1989), and this is true
for notothenioids in general (Pankhurst and Mont
gomery, 1990). It is difficult to attribute the rela
tively large eye size in adult *Pleuragramma* to pedomorphy. After starting at about 7–8% of SL,
there are decreases in relative eye diameter in lar
vae of 12–25 mm SL and again at about 40–60
mm SL, but in specimens > 60 mm SL relative eye
diameter begins to increase reaching about 8–9%
of SL in adults (Hubold, 1985; Montgomery and Sutherland, 1997). Montgomery and Sutherland
(1997) note that uncoupling of visual and somatic
growth could be responsible for the periods in larval life when relative growth of the eye declines
(Pankhurst and Montgomery, 1994).

A pedomorphic retina is neuroanatomically simple and contains cone photoreceptors, the first photoreceptors to develop in most fish larvae
(Blaxter, 1988; Nicol, 1989; Webb, 1999; Fuiman,
2002). This is not what is seen in *Pleuragramma*. Instead the retina is complex with numerous rods,
many ganglion cells, a large number of total reti
cell nuclei (2-fold more than *D. mawsoni*) and the capacity for retinomotor movement (Table 2). All
represent departures from the larval condition and are suggestive of specialization for the adult habi
tat. There is, however, a possibility that individual cell types in the retina are pedomorphic. For
eexample, ultraviolet-sensitive single cones, thought to enhance the ability to detect and feed on zoo
plankton, are prominent in the retinae of many larval fishes, and some persist in adults of some
species (Webb, 1999). Such single cones have been identified in adult notothenioids on the basis of mor
phology (Miyazaki et al., 2001) but more sophisti
cated analyses revealed that the ultraviolet-sensi
tive short-wave sensitive pigment was not confined
to these cones (Pointer et al., 2005). Additional work on *Champsoscoephalus gunnari* has indicated that the full coding sequence of the putative ultraviolet-sen
sitive visual pigment gene (SWS1) was present in
the total retinal RNA of members of age classes 0–1
(Miyazaki et al., 2010), although it is not present
in adults (Pointer et al., 2005). There have been
no studies comparing photoreceptor and visual
pigment composition in the eyes of juvenile and
adult *Pleuragramma*.

**Brain and Retinal Morphology and Ecological Diversification: *Dissostichus Versus Pleuragramma**

**Olfactory bulbs and olfaction.** The olfactory
bulbs receive primary olfactory input from sensory
neurons with cell bodies located in the olfactory mucosa. With the exception of a minor projection
to the ventral telencephalon, primary olfactory fibers terminate exclusively in the olfactory bulbs
(Meek and Nieuwenhuys, 1998, p. 901). Thus the relative number of neurons devoted to this modal
ity can be inferred from the size of the bulb, and

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the size of the bulb serves as a proxy for the relative importance of olfaction. As in Eleginops, the olfactory bulbs in Dissostichus are large and represent phylogenetically persistent morphology. However they are significantly smaller on a relative weight basis in Pleuragramma (Table 1) but nothing is known about olfaction as related to life history in this species. Near the Falkland Islands and South Georgia, Dissostichus eleginoides exhibits scavenging behavior in following the odor plume emanating from squid and fish bait used in benthically deployed camera systems. However they rarely take the bait, possibly being deterred by the light of the camera flash or the lack of activity by the bait (Collins et al., 1999; Yau et al., 2001, 2002). In contrast D. eleginoides will enter bottom traps baited with fish and squid (Pilling et al., 2001), and both species are captured by the longline fishery on hooks baited with fish and squid and deployed at depths of 1,500–2,000 m (Eastman and DeVries, 2000; Pilling et al., 2001). It may be that the longline bait appears more realistic as it moves in the current. Thus although both species of Dissostichus are relatively active opportunistic predators on fish, cephalopods and larger shrimp and prawns (Pilling et al., 2001), they also possess the ability to track an odor plume emanating from squid and fish bait used in benthically deployed camera systems. However they rarely take the bait, possibly being deterred by the light of the camera flash or the lack of activity by the bait (Collins et al., 1999; Yau et al., 2001, 2002). In contrast D. eleginoides will enter bottom traps baited with fish and squid (Pilling et al., 2001), and both species are captured by the longline fishery on hooks baited with fish and squid and deployed at depths of 1,500–2,000 m (Eastman and DeVries, 2000; Pilling et al., 2001). It may be that the longline bait appears more realistic as it moves in the current. Thus although both species of Dissostichus are relatively active opportunistic predators on fish, cephalopods and larger shrimp and prawns (Pilling et al., 2001), they also possess the ability to track an odor plume to carrion. The significance of this behavior in providing food in the ability to track an odor plume to carrion. The and prawns (Pilling et al., 2001), they also possess predators on fish, cephalopods and larger shrimp Dissostichus in the current. Thus although both species of the longline bait appears more realistic as it moves in the current. Thus although both species of Dissostichus are relatively active opportunistic predators on fish, cephalopods and larger shrimp and prawns (Pilling et al., 2001), they also possess the ability to track an odor plume to carrion. The significance of this behavior in providing food in their regular diet is unknown. The only experimental study of olfactory behavior in notothenioids utilized Trematomus bernacchii, a species congeneric with Dissostichus and Pleuragramma which has a well-developed olfactory morphology similar to Dissostichus. Results indicated that only a combination of chemosensory and rheosensory information provided an adequate match to observed search tracks (Montgomery et al., 1999). Finally because Dissostichus is migratory, olfaction may also be involved in homing behavior and detection of potential mates on the spawning grounds via pheromones.

Mesencephalon, retina and vision. The mesencephalon includes a ventromedially located tegmentum and a more dorsal optic tectum and torus semicircularis. Both of the latter structures are involved in multimodal sensory integration and sensorimotor coordination (Meek and Nieuwenhuys, 1998). Most perciforms are visual specialists with a well-developed retinotopically mapped tectum (Demski, 2003) where information concerning movement, shape and color of objects are analyzed (Wullimann, 1998). Although vision is the most important sensory input to the tectum, it also receives mechanosensory input that has been first integrated by the torus (Meek and Nieuwenhuys, 1998). Dissostichus and Pleuragramma show no departure from the perciform norm of possessing large tecta and eyes, but we found that the relative weight of the mesencephalon of Pleuragramma was significantly larger than that of Dissostichus. However this is not necessarily attributable to the mass of mesencephalic structures per se because our divisions of the brain include the valvula of the cerebellum, which projects into the tectal ventricle, in the mesencephalic weight. Our histological analysis indicates that the valvula is well developed in both species. Like the tectum the valvula is an integrative center receiving a variety of afferent input including mechanosensory lateral line projections (Finger, 1983; Meek and Nieuwenhuys, 1998). The greater mesencephalic weight in Pleuragramma may simply reflect inclusion of a relatively greater amount of valvular tissue.

The retinal histology of the sister taxa Dissostichus and Pleuragramma encompasses the extremes seen in the Antarctic notothenioids. Both species of Dissostichus have retinae that are rod dominated in histological appearance, with low ratios of cones to rods and high convergence ratios of photoreceptors to ganglion cells (Table 2). Although nototheniid eyes are devoid of the extreme specializations seen in primary deep-sea species, the retina of Dissostichus bears some resemblance to scotopic retinas of these species in having a high degree of summation and good sensitivity (Munk, 1984). The retina of Pleuragramma, on the other hand, is remarkably similar to the photopic retina of the non-Antarctic Eleginops (Eastman and Lannoo, 2008) with a large number of total cells, including many rods (Table 2). Furthermore, the single cones are the same size, although Pleuragramma lacks the twin cones seen in Eleginops. The structure of the retina of Pleuragramma suggests that it is capable of functioning over wide ranges of depth and illumination. The high rod density increases the sensitivity (Warrant et al., 2003). Both the relatively large number of total photoreceptors and the small cones, relative to the 2-fold larger diameter cones in Dissostichus, enhance visual acuity (Nicol, 1989; Collin and Shand, 2003). The high ratio of cones: rods and low convergence ratio also suggest sufficient acuity for detecting small and moving prey.

Adult Pleuragramma are stratified by depth, with larger specimens living as deep as 400–700 m (Hubold and Ekau, 1987). In the presence of seasonal light they also exhibit diel vertical migration of as much as 350 m, moving to shallower depths at night and deeper during the day (Plötz et al., 2001; Fuiman et al., 2002; Lancraft et al., 2004; Robison, 2003). Robison's (2003) analysis of diel activity in Antarctic fishes led to the conclusion that the most likely explanation for its occurrence was avoidance of predation by visually-oriented predators like penguins and pinnipeds. Diel behavior is derived and specialized for a species in a benthic lineage and is convergent with that seen in true mesopelagic fishes such as myctophids. All these factors probably contribute to the relative uniqueness of its retina among Antarctic notothenioids. The divergent retinal histology of Dissostisi-
chus and Pleuragramma is not surprising given the long separation of these taxa, the differences in their ecology and the likelihood that retinal morphology is subject to strong selection pressure and diverges rapidly. In examining 40 nototheniid species we have found that retinal histology is evolutionarily labile and thus of little taxonomic and systematic value. In bathydraconid sister taxa, for example, retinal histology reflects habitat depth and is not tightly coupled to phylogeny (Eastman and Lannoo, 2003b).

**Corpus cerebelli and activity levels.** The corpus cerebelli is an especially variable region of the brain, and a large caudally projecting corpus, such as that in Eleginops and Dissostichus, is seen in many teleosts (Franz, 1911; Meek and Nieuwenhuys, 1998). The corpus cerebelli receives a variety of sensory inputs including visual and mechanosensory lateral line and is probably also involved in motor learning and coordination (Meek and Nieuwenhuys, 1998; Wullimann, 1998). The corpus cerebelli is significantly larger in the non-Antarctic Eleginops than in either species of Dissostichus. Eleginops is active (Vanella and Calvo, 2005) with a greater capacity for sustained labriform swimming and a more rapid escape response than most other notothenioids (Fernández et al., 1999). Furthermore, some populations of Eleginops are catadromous with spawning migrations in the Falkland Islands taking them as far as the shelf to waters 250 m deep (Brickle et al., 2005a,b).

Although not as active and aerobic as Eleginops, both species of Dissostichus retain a moderately large caudally projecting corpus as well as a migratory life style, as documented in the Introduction. In Pleuragramma, however, the corpus is significantly smaller and reduced to a round knob suggesting a less active life style. Although this may seem at odds with the apparent demands of a pelagic life, all evidence supports the notion that Pleuragramma is an inactive species. As detailed previously, Pleuragramma does not swim continuously and form dense schools. The amount of red muscle, gill morphometrics and blood parameters suggest a low level of activity, and this is born out by observations. Camera systems lowered through the water column from research vessels (J.T. Eastman, personal observation) and “critter cams” deployed on Weddell seals (Fuiman et al., 2002) indicate Pleuragramma exist as loose shoals (unstructured aggregations) with individuals estimated to be spaced 2–4 m apart at densities of 1 fish per 7–43 m³ (Fuiman et al., 2002). Their neutral buoyancy enables them to hang in the water, almost like a benthic fish rests on the bottom. Limited movement also allows effective utilization of their mechanosensory system to monitor the water column for vibratory disturbances produced by their zooplankton prey. Sedentary benthic notothenioids, including Pogonophryne scotti and Dolloiodraco longedorsalis, also have a small round corpus (Eastman and Lannoo, 1995, 2003a,b).

**Medulla and mechanosensory lateral line structures.** The eminencia granulares and crista cerebellares are mechanosensory lateral line associated areas of the medulla that are prominent in both Dissostichus and Pleuragramma. Primary mechanoreceptive input is via bipolar cells distributed in the lateral line nerves. These synapse in the medulla on secondary neurons forming the medial octavolateralis nucleus, situated immediately ventral to the crista cerebellares (McCormick, 1983). Although measurement of the relative size of the medial octavolateralis nucleus would provide a direct indicator of the degree of development of mechanosensation, the nucleus is complex, diffuse and cannot be clearly delineated in histological sections (Montgomery and Sutherland, 1997). Hence the sizes of the eminencia granulares and crista cerebellares are commonly taken as proxies for the degree of development of mechanosensation. This is a morphologically defensible approach because the crista cerebellares are composed of fibers with cell bodies located in the medial octavolateralis nucleus and fibers of granule cells in the eminencia granulares also contribute to the crista cerebellares (McCormick, 1983).

Although there is no difference between the relative weights of the medulla in D. mawsoni and Pleuragramma, in both species the medulla was significantly larger than in Eleginops, presumably because of the enlarged eminencia granulares and crista cerebellares in the Antarctic species. Montgomery has advanced the hypothesis that Antarctic notothenioids have experienced an ontogenetic shift in the development and use of visual and non-visual senses with larval fishes relying on vision whereas adults depend more on non-visual senses (Montgomery and Sutherland, 1997; Montgomery, 1997). Most notothenioids hatch in spring or early summer and their pelagic larvae therefore reside under photic conditions suitable for visual feeding. The ontogenetic shift to more reliance on the non-visual senses probably takes place during the first winter or later, depending on the species, and continues to be important under conditions of ice cover and low light (Montgomery, 1997). The adults of the nototheniid Pagotherinae, scotti have the ability to detect planktonic prey with their lateral line (Montgomery and Macdonald, 1987) but, as predicted by the ontogenetic shift hypothesis, the density of rods in their retina and spatial resolution are maximized at about 100 mm TL (Montgomery, 1997). Montgomery and Sutherland (1997) also used a series of 7–151 mm SL Pleuragramma as test subjects for the ontogenetic shift hypothesis. Using volumes computed from histological sections, they found that the optic tectum exhibited negative allometry.
with growth whereas the eminentia granulares and crista cerebellares continued increasing until at least 151 mm SL. Because *Pleuragramma* has a prolonged juvenile period, this ontogenetic shift does not take place until after the second winter of life at about 60 mm SL. Growth in relative diameter of the eye was uncoupled from somatic growth such that the eye continued to grow in specimens > 60 mm SL, but not at the rate of overall body growth.

We agree with Montgomery’s ontogenetic shift hypothesis with the caveat that *Pleuragramma* may not be a typical example of a notothenioid with decreased reliance on vision as an adult. Based on specialized retinal histology that is unique among Antarctic notothenioids, we suggest that vision in this species is important in adults to supplement the non-visual senses. The retina of *Pleuragramma*, with its numerous small cones and high cellularity, resembles that of the non-Antarctic *Eleginops*. The mean retinal cell count for the neutrally buoyant clade (*Pleuragramma* and both species of *Dissostichus*) is 2-fold greater (258 cells versus 126 cells) than in 18 species of the High Antarctic clade including artedidraconids, bathydraconids and channichthyids (Eastman and Lannoo, 2003a,b, 2004). It is not clear why this should be, as *Pleuragramma* are subject to the same unusual under-ice light regime, live at depths of several hundred meters and discriminally pick small and large zooplankton from the water column like many other High Antarctic notothenioids. But *Pleuragramma* are fundamentally different in their ecology than all other notothenioids, including *Dissostichus*, in that all stages of their life history, from egg to adult, play out in the water column. Furthermore the neutrally buoyant clade is as much as 15.6 million years (24.1 versus 8.5, Near, 2004) older than phylogenetically derived lineages such as the artedidraconids, bathydraconids and channichthyids (Near, 2004). Although *Pleuragramma* has been associated with the Antarctic environment for a longer period of time than sympatric High Antarctic species, they have not experienced the phyletic trend toward retinal simplification, with decreasing retinal thickness and cell number and loss of the choroid rete, seen in phylogenetically derived notothenioids.

**OVERVIEW AND CONCLUSION**

Diversification into the water column of the emerging Antarctic marine ecosystem was a major event in nototheniod evolutionary history. The neutrally buoyant clade is phylogenetically basal (Balushkin, 2000; Near et al., 2004; Sanchez et al., 2007; Near and Cheng, 2008) and was the first group of Antarctic notothenioids to appear, with the divergence of *Dissostichus* and *Pleuragramma* dated at 24.1 million years ago (Near, 2004). While it is paradoxical that a benthic lineage without a swim bladder would first occupy water column habitats, it is also a testimony to the prevalence of ecological selection in driving speciation (Schluter, 2009). There was little competition because a previous taxonomically diverse fish fauna had been mostly eradicated (Eastman, 2005). Moreover food was available in the water column as suggested by inferred divergence times of about 20 million years (Bargelloni et al., 2000b) for the Antarctic species of euphausiid krill (food for *Pleuragramma*) and 19.2 million years (Baker et al., 2006) for the High Antarctic Adélie penguin (*Pygoscelis adeliae*) which preys on *Pleuragramma*. The neutrally buoyant clade is not so close but monopolizes functional biodiversity in the water column of the high shelf. There is considerable adaptive disparity between *Dissostichus* and *Pleuragramma* as they have undergone morphological and ecological diversification in size, habitat depth, diet, activity level and tendency to migrate. They also occupy different trophic levels in the ecosystem. The case of *Dissostichus* and *Pleuragramma* is an exemplar of adaptive radiation theory and is consistent with empirical work that documents the rapid occurrence of substantial morphological and ecological responses when a clade enters a new habitat (Grant and Grant, 2008; Gavrilets and Losos, 2009; Losos, 2009).

To the question posed in the Introduction: how different are the brains and retinai of these sister species and what phylogenetic and ecological influences are reflected in brain and retinal anatomy and histology? Given the appearance of *Dissostichus* and *Pleuragramma* 24.1 million years ago and their divergent life histories, it is not surprising that there are brain and retinal differences involving sensory and integrative regions, phylogenetic persistence of some features, and regression or expansion of other features. Based on relative weights and using the non-Antarctic *Eleginops* for comparison, both *Dissostichus* and *Pleuragramma* have a relatively smaller corpus cerebelli but a relatively larger medulla. This reflects reduced activity levels of notothenioids in subzero temperatures and expansion of the mechanosensory lateral line system as a supplement to vision under conditions of reduced light. In a comparison of the two sister species, *Pleuragramma* has reduced olfactory bulbs and corpus cerebelli and an expanded mesencephalon relative to *D. mawsoni*. The reduction of the corpus to a small round knob is consistent with multiple physiological parameters and video observations suggesting it is relatively inactive in the water column. Because mesencephalic weights also include the valvula cerebelli, the relatively large value for *Pleuragramma* may be attributable both to its role in integration and sensorimotor coordination of information from the highly cellular duplex retina and to integration of signals.
from the well-developed octavolateralis system. The brain of *Dissostichus* displays considerable persistent morphology in its overall resemblance to that of *Eleginops*, especially the large olfactory bulbs and the relatively large caudally projecting corpus, and *Dissostichus* exhibits olfactory tracking ability and migratory behavior in common with *Eleginops*. The brain of *Pleuragramma*, on the other hand, is more apomorphic or derived than that of *Dissostichus*. Many body systems in *Pleuragramma* are pedomorphic but we found no evidence that pedomorphy has influenced gross brain morphology. The neumastoms without bony canals in *Pleuragramma* are, however, a pedomorphic feature. The retinæae of *Dissostichus* and *Pleuragramma* are highly divergent. As an interesting twist that does not necessarily imply phyletic persistence, the retina of *Pleuragramma*, with large numbers of cells and many cone photoreceptors, resembles *Eleginops* rather than the rod-dominated scotopic retina of *Dissostichus*.

The brains of *Dissostichus* and *Pleuragramma* have diverged substantially in the 24.1 million years since their separation. The influences of both phylogenetically persistent morphology and aspects of the habitat are apparent in both sensory and integration areas of their brains. In spite of the unusual Antarctic light regime, both species maintain well developed tecta and retinæae as is the norm for perciforms (Demska, 2003). Unlike African Great Lakes cichlids (van Staaed et al., 1994; Huber et al., 1997), there is also regression in some brain regions, most notably the olfactory bulbs and corpus cerebelli of *Pleuragramma*. Even though they are each other’s closest relative and sympatric in the water column, the magnitude of the differences between the brains and retinæae of *Dissostichus* and *Pleuragramma* are as great as any we have encountered among 30 other species of phylogenetically and ecologically diverse notothenioids. Early entry into a depauperate water column 24–25 million years ago allowed macrohabitat diversification, as predator and forage fish, respectively. *Dissostichus* and *Pleuragramma* each dominate a different level of the food web and substantial differences in brain morphology are to be expected, given that their general body morphology reflects the perimeters of notothenioid diversity.

**ACKNOWLEDGMENTS**

The authors are grateful to Danette Pratt for drawing and assembling all figures. Susan Johnson Lanno sectioned and stained the brains, and proofread the manuscript.

**LITERATURE CITED**


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habitat use, trophic patterns, and the evolution of brain
silverfish Pleuragramma antarcticum. In: Siegfried RW, Condy
PR, Lawns WM, editors. Antarctic Nutrient Cycles and Food
Sea, Antarctica. In: Kullander SO, Fernholm B, editors. Fifth
Congress of European Ichthyologists, Proceedings, Stockholm,
pp 391–396.
Hubold G, Tomo AP. 1989. Age and growth of Antarctic silver-
fish Pleuragramma antarcticum Boulenger, 1902, from the
southern Weddell Sea and Antarctic Peninsula. Polar Biol
9:205–212.
of brain morphology in teleosts: Brain and ecological niche.
Brain Behav Evol 69:78–86.
Johnston IA, Camm J-P, White M. 1988. Specialisations of
swimming muscles in the pelagic Antarctic fish Pleura-
Kellermann A. 1986. Geographical distribution and abundance
of postlarval and juvenile Pleuragramma antarcticum (Pisces,
Notothenioidei) off the Antarctic Peninsula. Polar Biol 6:111–
119.
Kiernan JA. 1990. Histological and Histochemical Methods:
Kotschal K, Palzenberger M. 1992. Neuroecology of cyprinids:
Comparative, quantitative histology reveals diverse brain
Kotschal K, van Staaden MJ, Huber R. 1998. Fish brains:
Evolution and environmental relationships. Rev Fish Biol Fish
eries 8:373–408.
Kunzmann A. 1990. Gill morphometrics of two Antarctic fish
species Pleuragramma antarcticum and Notothenia giberri-
La Mesa M, Eastman JT, Vacchi M. 2004. The role of notothe-
nioid fish in the food web of the Ross Sea shelf waters: a
Lancraft TM, Reisenbichler KR, Robison BH, Hopkins TL, Torres
JJ. 2004. A krill-dominated microeukton and macrozooplankton
community in Croker Passage, Antarctica with an estimate of
Passage, Antarctica with an estimate of fish predation. Deep-
Lapthinskaya V, Arkhipkin A, Brickle P. 2006. Distribution and
reproduction of the Patagonian toothfish Dissostichus eleginoides
of top predator foraging on fish in the pack ice of the southern
Losos JB. 2009. Lizards in an Evolutionary Tree: Ecology and
Adaptive Radiation of Anoles. Berkeley: University of Califor-
nia Press. 507 p.
McCormick CA. 1983. Organization and evolution of the octavo-
lateralis area of fishes. In: Northcutt RG, Davis RE, editors. Fish
Nieuwenhuys R, Ten Donkelaar HJ, Nicholson C, editors. The
Central Nervous System of Vertebrates, Vol. 2. Berlin and
Miller RJ, Evans HE. 1965. External morphology of the brain
Miyazaki T, Nakata K, Kasagi S, Iwami T, Yamauchi M, Kaw-
mura S. 2010. Molecular cloning of ultraviolet-sensitive visual
pigment in juvenile Champsosphasium gunnari (Channich-
Montgomery JC. 1997. An ontogenetic shift in the use of visual
and non-visual senses in Antarctic notothenioid fishes. In: Battaglini B, Valencia J, Walton DWH, editors. Antarctic Com-
munities: Species, Structure and Survival. Cambridge: Cam-
In: Davison W, Howard-Williams C, Broady P, editors. Antarc-
tic Ecosystems: Models for Wider Ecological Understanding.
Christchurch: New Zealand National Sciences. pp 103–
108.
Montgomery JC, Bodzick D. 1994. An adaptive filter that can-
cels self-induced noise in the electrosensory and lateral line
Montgomery J, Clements K. 2000. Disipation and recovery in
Montgomery JC, Macdonald JA. 1987. Sensory tuning of lateral
line receptors in Antarctic fish to the movements of plank-
Montgomery JC, Sutherland KBW. 1997. Sensory development of the Antarctic silverfish Pleuragramma antarcticum: a test
Montgomery J, Coombs S, Junnissen J. 1994. Form and function
relationships in lateral line systems: comparative data from six
species of Antarctic notothenioid fish. Brain Behav Evol
44:299–306.
Olfactory search tracks in the Antarctic fish Trematomus bernacchii.
Moreno C, Rueda T, Asencio G. 1986. Nicho trófico de Pleura-
gramma antarcticum en la región del estrecho Bransfield, con una
comparación cuantitativa con otras áreas del Oceano Antártico.
Inst Antárt Chileno Ser Cien No. 35:145–169.
Munk O. 1984. Duplex retina in the mesopelagic teleost Radici-
cephalus elongatus Osorio, 1917. Vidensk Meddr Dansk Natur
Foren 145:183–199.
fishes using a fossil-calibrated molecular clock. Antarct Sci
16:42–44.
SB, Kumar S, editors. The Timetree of Life. New York: Oxford
fishes (Teleostei: Acanthomorpha): Inferences from mitochon-
drial and nuclear gene sequences. Mol Phylogenet Evol
47:832–840.
Near TJ, Pesavento JJ, Cheng C-HC. 2004. Phylogenetic investi-
gations of Antarctic notothenioid fishes (Percomorpha: Notothe-
nioidae) using complete gene sequences of the mitochondrial
Near TJ, Russo SE, Jones CD, DeVries AL. 2003. Ontogenic shift in buoyancy and habitat in the Antarctic toothfish,
Dissostichus mawsonii (Percomorpha: Nototheniidae). Polar
Near TJ, Kendrick BJ, Detrich HW, III, Jones CD. 2007. Confir-
mation of neutral buoyancy in Aethotaxis mitopteryx DeWitt
Press. 308 p.
Northcutt RG. 1989. The phylogenetic distribution and innerva-
tion of craniate mechanoreceptive lateral lines. In: Coombs S,
Görner P, Münz H, editors. The Mechanosensory Lateral Line:
Neurobiology and Evolution. New York: Springer-
Verlag. pp 17–78.
Northcutt RG, Bevis WE. 1993. Cranial nerves of the coela-
canth, Latimeria chalumnae [Osteichthyes: Sarcopterygi-

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