Phyletic Divergence and Specialization for Pelagic Life in the Antarctic Nototheniid Fish *Pleuragramma antarcticum*

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**ABSTRACT.** Living free of the substrate and possessing distinctive morphology, *Pleuragramma antarcticum* is an arctic notothenid. Cladistic analyses indicate that *Pleuragramma* is one of the most phyletically derived species in the family. It is also distinctive in a number of features of its biology. I comment on phylogenetic and developmental aspects of these morphological and physiological features in *Pleuragramma*: skeletal and notochord, extent of red muscle, lipid storage, blood, retina, lateral-line, brain and gastrointestinal system. An entire suite of characters is unique to *Pleuragramma*, but individual features are convergent within other nototheniid clades living in the water column. Osteology provides the best documented evidence that paedomorphosis has been important in the evolution of *Pleuragramma*. *Comp. Biochem. Physiol. 118A;4:1095–1101, 1997. © 1997 Elsevier Science Inc.*

**KEY WORDS.** Antarctic, convergent evolution, heterochrony, Nototheniidae, paedomorphosis, pelagic, *Pleuragramma antarcticum*

**INTRODUCTION**

Consideration of the biology of the nototheniid fish *Pleuragramma antarcticum* was a major theme of the European Science Foundation sponsored workshop in Liège (21–23 September 1995), entitled "Relationships Linking Ecology, Life Style and Adaptive Evolution in Antarctic Fish." Recognition of the importance of *Pleuragramma* as a focus for future research stems from several aspects of its biology. Within a family of predominantly benthic fishes, *Pleuragramma* is an ecological novelty in having a life cycle that is entirely free of the substrate. Egg morphology and the relatively large size of the testes suggest that, unlike most other nototheniids, eggs are pelagic in *Pleuragramma* and spawning takes place in the water column (19). With streamlined external morphology, they depart considerably from other nototheniids in appearance as well as in a number of other morphological and physiological features. *Pleuragramma* is the major notothenid species by number and by biomass in the water column of most shelf areas of the Antarctic Ocean. Their overwhelming dominance has been especially well documented in the Ross (8) and Weddell (24,25) Seas. They have a circum-Antarctic distribution at depths ranging from 0 to 900 m (20) and are found in areas with and without sea ice cover. *Pleuragramma* is probably the key water column species in the food web of the Antarctic shelf (24), an area where krill are sparse (23). Finally, *Pleuragramma* is included in the most phyletically derived subfamily and is one of the most phyletically derived species in the family Nototheniidae (1,31).

The benthic mode of life is plesiomorphic among basal clades in both the suborder Notothenioidei and in the family Nototheniidae (14). Absence of a swim bladder, labriform locomotion, small amounts of axial red muscle and benthic feeding are additional plesiomorphic features of basal nototheniods. Although these features could be viewed as possible phyletic constraints, limiting the diversification of nototheniids into water column habitats, in the Southern Ocean they have not proven to be constraining under conditions of reduced competition from other fish groups. In the absence of a swim bladder, there are alternate methods for reducing density that do not involve continuous or intermittent swimming. Although only *Disostichus mawsoni* and *Pleuragramma* have been measured as being close to neutral buoyancy, the adults of about 50% of nototheniids from the Antarctic region exhibit evolutionary departure from ancestral benthic habitat (14). These species have undergone morphological and ecological divergence to occupy pelagic, semipelagic, cryopelagic and epibenthic habitats.

In the well-studied North American freshwater fauna, phyletic divergence is usually unaccompanied by ecological and morphological divergence (4,34). This generalization
does not universally apply to the Antarctic nototheniid fauna. Within the family Nototheniidae, for example, ecological diversification is frequently coupled with phylectic diversification (14). Here I explore the notion that Pleuragramma is distinctive in a number of features of its biology as well as being phylogenetically derived. I draw on a combination of my own published and unpublished observations as well as information from the literature. More specifically, I discuss the distinctive morphological and physiological characters of Pleuragramma and consider evidence that some of these characters may be paedomorphic.

**The Distinctive Suite of Characters for Pleuragramma**

**Relationships of Pleuragramma Within the Nototheniidae**

My hypothesis of phylectic relationships among nototheniids is based on the cladogram of Klingenberg and Ekau (31), the most fully resolved cladogram for the family (Fig. 1). Their cladistic analysis of morphological data indicates that Pleuragramma is one of the most phylogenetically derived nototheniids. Pleuragramma has not yet been included in molecular phylogenies of notothenioids; hence, the age of the pleuragrammin radiation has not been inferred from molecular data (2,3,37). In referring to members of the family Nototheniidae, I use the generic and subfamilial nomenclature of DeWitt et al. (10).

**Characters**

Table 1 summarizes the characters of Pleuragramma that I consider. Although some are autapomorphic for Pleuragramma, others may be synapomorphies for the entire subfamily. A complete analysis of these characters is not possible for the subfamily because little is known about these in Crotonethia and Gvozdana. Because there is a data base available for the species, I polarized characters using Trematomus bernacchii as the outgroup to the Pagothenia-Pleuragramminae clade (Fig. 1). With the possible exception of large superficial neuromasts, all characters of Pleuragramma (Table 1) are apomorphic with respect to the character state in T. bernacchii.

The distinctiveness of Pleuragramma is blurred by convergent trends toward habitation of the water column within other nototheniid clades (14). This trend is evident in all four subfamilies (Fig. 1). Although the entire suite of characters is unique to Pleuragramma, there is much convergence (homoplasy) in individual characters.

**Skeleton and Notochord**

The osteology of Pleuragramma has been more thoroughly studied than any other aspect of morphology (6,15,41–44). The skeletal system also provides the most definitive evidence of paedomorphosis. Nototheniids in general and pleuragrammins in particular show delayed ossification of the skeleton compared to other perciforms (43). The vertebrae of Pleuragramma are completely unconstricted (non-amphicoelous), centra are thin collars of bone around the notochordal foramina and vertebral processes are reduced. Pleuragramma also has a persistent notochord and this gelatinous larval structure fills the large notochordal foramina of adult vertebrae. Adults of some other nototheniid species have partially patent notochordal foramina (22), but in these species, unlike Pleuragramma, the foramina show an ontogenetic decrease in size (39). Specific changes in the visceral skeleton of clades inhabiting the water column involve consolidation in the number of bony elements, replacement of bone by connective tissue, lengthening of the jaws and reduction in the ascending process of the premaxillae that limits protraction (42). Furthermore, in Pleuragramma, the basioccipitals and exoccipitals ossify late, a possible autapomorphy for this species (44). Finally, as demonstrated by ashing, the definitive bones of Pleuragramma are less heavily mineralized than other nototheniids (15).

As a result of these changes, overall bone mass and density are reduced and the visceral skeleton becomes more suitable for pelagic feeding. Because density reduction and feeding are involved, these osteological modifications have probably been essential for diversification of Pleuragramma into a permanent water column habitat.

Because the chronology of differentiation in the axial skeleton is key to the unique morphology of Pleuragramma, it is likely that there has been modification of inductive or signaling influences on axial patterning by the homeobox family of genes. Large differences in adult morphology may be caused by small differences in genetic signals during development. The melding of the molecular and evolutionary biology of notothenioids is a fertile area for future research.

**Muscular System and Swimming**

With a compressed streamlined body, forked caudal fin and small pectoral fins, Pleuragramma is unlike most other nototheniids in external appearance. Pleuragramma also possesses an extensive red (slow) fibered lateralis superficialis muscle around the circumference of the trunk (6,15,29). Because this inserts on the bases of the caudal fin rays via tendons separate from those of the white myotomal musculature (14), Pleuragramma has a means of slow subcarangiform locomotion not involving the large mass of white muscle (14,29). The lateralis superficialis is usually better developed in larvae living in the water column and using subcarangiform locomotion (12,28). This is especially true in the case of the pelagic fingerling stage of Notothenia neglecta, a possible outgroup to Pleuragramma. It is therefore possible that an encircling lateralis superficialis and subcarangiform locomotion are paedomorphic characters in Pleuragramma.
Lipid Storage

The mechanism of lipid storage in Pleuragramma is unique among notothenioids and probably an autapomorphy for the species. Most lipid is contained in large sacs instead of in small (120 μm) adipose cells (15). Pleuragramma has subcutaneous lipid sacs (0.2–1.5 mm in diameter) along the sides of the body. A larger series of intermuscular lipid sacs (0.5–3.0 mm in diameter) is located deeper, adjacent to the midline vertical septum and proximal to the bases of the dorsal and anal fins. These are segmental and present at all vertebral levels. Aethotaxis has only adipose tissue in these locations.

Electron microscopy reveals that walls of intermuscular lipid sacs are composed of a complex of cells, similar to white adipocytes, arranged around the periphery of a large lipid droplet (16). This lipid is therefore an extracellular depot, possibly indicating that it is a passive buoyancy store rather than a metabolic reserve. The details of sac development and growth (whether isometric with body weight or length) are unknown. Studies of lipid sac development and growth and of the biochemical pathways and turnover of the lipids are required to clarify their origin and function.

Blood, Hemoglobin and Antifreeze

Pleuragramma has achieved near neutral buoyancy through static mechanisms rather than hydrodynamic lift that would require swimming. Although living in the water column, they are relatively inactive, do not possess large amounts of
TABLE 1. Distinctive characters of adult *Pleuragramma antarcticum*

<table>
<thead>
<tr>
<th>Character</th>
<th>Possibly paedomorphic</th>
<th>Convergent within nototheniids</th>
</tr>
</thead>
<tbody>
<tr>
<td>Permanent habitation of water column</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Pelagic eggs and spawning*</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Near neutral buoyancy</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Delayed skeletal ossification</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Low mineral content of skeleton</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Persistent and completely unconstricted notochord*</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Red fibered lateralis superficialis muscle completely encircling trunk*</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Subcarangiform locomotion</td>
<td>✓</td>
<td>-</td>
</tr>
<tr>
<td>Large intermuscular lipid sacs*</td>
<td>✓</td>
<td>-</td>
</tr>
<tr>
<td>Low levels of typical nototheniid antifreeze glycopeptide*</td>
<td>✓</td>
<td>-</td>
</tr>
<tr>
<td>Possession of a novel antifreeze glycopeptide*</td>
<td>✓</td>
<td>-</td>
</tr>
<tr>
<td>Three hemoglobin components*</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Photoceptors of retina dominated by single cones</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Large superficial neuromasts on head and trunk</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Hypertrophied eminentia and crista of brain*</td>
<td>✓</td>
<td>-</td>
</tr>
<tr>
<td>Small corpus cerebelli of brain</td>
<td>✓</td>
<td>-</td>
</tr>
<tr>
<td>Three pyloric cea*</td>
<td>✓</td>
<td>-</td>
</tr>
<tr>
<td>Extensive peritoneal melanism</td>
<td>✓</td>
<td>-</td>
</tr>
</tbody>
</table>

Except for large superficial neuromasts, all characters are apomorphic when polarized relative to *Trematomus bernacchi*. Asterisk indicates autapomorphic (uniquely derived or diagnostic) characters for *Pleuragramma*. Check marks indicate characters that may be paedomorphic in *Pleuragramma* and also characters that are convergent in other water column clades of nototheniids. See text for references.

red muscle, a substantial aerobic capacity or an enhanced scope for activity (29). In fact, studies of the physiological properties of the blood of *Pleuragramma* and the closely related pleurogrammin *Aethotaxis* suggest that metabolic and activity levels are low in these species when compared with other nototheniids (32,33).

Most nototheniids have one major and one minor hemoglobin component in the approximate proportions 95:5 (11). The recent report of a third component in *Pleuragramma* makes this species unique in the family and the suborder (40). All components are functional and possibly reflect adaptation to pelagic life.

The blood and body fluids of *Pleuragramma* are fortified with antifreeze glycopeptides identical to those of other nototheniids, although concentrations are lower and ontogenetically variable (45,46). Lower concentrations imply that adults of *Pleuragramma* are not completely protected from freezing in habitats with temperatures of less than −1.9°C, a common occurrence in shelf waters. There are indications that *Pleuragramma* possesses an additional “novel” anti-freeze glycopeptide with different freezing behavior (45,46).

Retina

Retinal histology reveals that *Pleuragramma*, and some other water column nototheniids, have rods and cones, but the cones are single cones instead of the twin cones common in outgroups like bovichtiids, *Notothenia* and some *Trematomus* (13). In the developing teleost retina, cones are formed before rods and twin cones are formed by fusion of single cones (35). Single cones could be a paedomorphic feature, but retinal histology in a developmental series of *Pleuragramma* is necessary to supply a definitive answer.

Lateral Line

Most species in the *Eleginopinae* and *Nototheniinae* have a complete or nearly complete cephalic lateral line system (1,27). Phyletically derived species living in the water column, especially *Pagotenia* and the pleurogrammins, have interrupted canals, enlarged canals with prominent pores and free neuromasts (7,26,27). *Pleuragramma* is most specialized with respect to the gross morphology of the lateral line. The traditional view holds that much of the canal system on the head has been replaced by superficial neuromasts (9). Although there have been no developmental studies, an alternative hypothesis involving paedomorphosis, suggests that the superficial neuromasts are persistent larval structures that have not induced the formation of canals. Although not studied specifically in *Pleuragramma*, the large free neuromasts in the ventral trunk line of other nototheniids are thought to have arisen by paedomorphosis. They are, however, probably non-adaptive as far as lateral line function is concerned (5).

Brain

Peripheral lateral line morphology and the static mechanisms of buoyancy are reflected in the brain of *Pleuragramma*. When brain diversification of 32 species in the suborder is considered, *Pleuragramma* emerges as one of three nototheniids having distinctive brains (18). This designation is based on measurements of relative brain areas and a suite of qualitative brain characters. *Pleuragramma* has hypertrophied lateral line regions, specifically the eminentia granularis of the cerebellum and crista cerebellaris of the rhombencephalon. Based on the large size of these structures, *Pleuragramma* is probably a lateral line specialist. This is noteworthy among notothenioids because brain diversi-
fication in the suborder has usually not resulted in hypertrophied sensory modalities.

*Pleuragramma* also possesses a small round corpus cerebelli, an indication of an inactive life style involving little rapid movement and non-migratory behavior. Because they are close to neutral buoyancy, *Pleuragramma* is capable of remaining stationary, monitoring the water for perturbations caused by swimming zooplankton.

Although there is evidence of paedomorphosis in the brain of salamanders (38), this phenomenon has not been studied in the central nervous system of notothenioids.

**Gastrointestinal System**

With three pyloric cece, *Pleuragramma* is unusual among notothenioids in having the fewest cece and in showing no intraspecific variation in this trait (17). Three cece is an autapomorphy for *Pleuragramma*; *Eleginops* has 4, trematomids 6–7 and *Aethotaxis* 7–9.

All pleuragrammids show extensive peritoneal melanism involving infiltration of melanosomes into the mucosal linings of portions of the oral and gill cavities, the parietal peritoneum and the tunica serosa of the esophagus, stomach and rectum (17). Melanism is most pronounced in *Aethotaxis*, which lives somewhat deeper than *Pleuragramma*, and probably serves to screen bioluminescence of gut contents. This is a convergent trend, evident in at least four other nototheniid clades.

**CONCLUSIONS**

**Heterochrony**

With the reintegration of evolution and development, the study of heterochrony is at the forefront of modern evolutionary biology (21). Heterochronic processes involve changes in the timing of developmental events and, in the case of paedomorphism, adults of a taxon retain traits that characterize the juveniles of outgroups. Heterochrony may also be responsible for macroevolutionary changes seen in the origination of higher taxa (21).

Most nototheniid larvae are pelagic (30,36), and paedomorphosis may have played a role in the evolution of *Pleuragramma* and other nototheniid clades (1). It may be that species had more adaptive potential to occupy the pelagic realm by extending the larval phase and retaining some larval characteristics in the adult rather than by further development of the adult stage. The specialization of *Pleuragramma* was probably linked to permanent habitation of the water column and the diversification of other clades to feeding in the water column.

With the exception of osteology (43,44), the timing of the development of various systems and organs has not been examined in *Pleuragramma* or in other nototheniids. Voskoboynikova (43) considers delayed ossification “a mechanism of paedomorphic evolution,” and her work is the most extensive and best documented example of heterochrony in nototheniids. Additionally, Klingenberg and Ekau (31) infer from their analysis of adult trematomids and *Aethotaxis* that the morphometric differences reflecting various degrees of adaptation to life in the water column are established in larval life. As the proceeding survey of organ systems has shown, there are possible, but as yet incompletely studied, instances of persistent larval traits in the muscular system, retina and lateral line of adult *Pleuragramma*. These topics could be considered as part of an agenda for future research on heterochrony in nototheniids.

**Convergence in Habitation of the Water Column**

*Pleuragramma* is a member of the most highly derived clade and may be the most phylogenetically derived species in the family Nototheniidae. Unlike the situation in some other fish groups, this phyletic divergence has been accompanied by considerable morphological and ecological divergence. This is probably because *Pleuragramma* was diversifying into a pelagic habitat with little competition from non-nototheniid fish groups. An apparent phyletic constraint, the absence of a swim bladder, was overcome by a suite of density-lowering modifications that allowed habitation of the water column. The same can be said for modes of locomotion, feeding and reproduction that, in the plesiomorphic condition, were oriented toward the substrate. Finally, contained in the suite of characters unique to *Pleuragramma* are a number of individual characters that are convergent (homoplastic) within other nototheniid clades. The explanation for this is that the overall nototheniid radiation has encompassed several independent diversifications into water column habitats in the Southern Ocean.

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**References**


