

# Nervous and Sensory System Correlates of an Epibenthic Evolutionary Radiation in Antarctic Notothenioid Fishes, Genus *Trematomus* (Perciformes; Nototheniidae)

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**ABSTRACT** The perciform suborder Notothenioidei consists of 120 species, with 94 confined to the Antarctic Region of the Southern Ocean. On the Antarctic shelf, this phyletic radiation has been accompanied by a substantial morphological and ecological diversification towards a pelagic existence. For example, the primarily benthic genus *Trematomus* contains an epibenthic radiation that includes *T. loennbergii*, *T. lepidorhinus*, and *T. eulepidotus*. By comparing these epibenthic species with three congeneric benthic species (*T. scotti*, *T. pennellii*, and *T. bernacchii*) we tested three null hypotheses regarding brain variation in Antarctic trematomids: 1) that there is no difference in brain morphology among the six species; 2) that phylogenetic and ecological factors do not influence brain morphology; and 3) that peripheral sensory struc-

tures do not influence brain morphology. We rejected each of these hypotheses, leading us to conclude that *Trematomus* brains vary interspecifically, between benthic and epibenthic species, and with a species' depth distribution. Further, we conclude that brain variation is correlated with differences in peripheral sensory systems and motor activity. Specifically, epibenthic *Trematomus* have larger percentages of their brain volume devoted to lateral line mechanoreceptive and motor (cerebellar) structures. Species living at greater depths have low ratios of cones:rods in the retina and larger olfactory structures. *J. Morphol.* 245:67–79, 2000. © 2000 Wiley-Liss, Inc.

**KEY WORDS:** brain morphology; adaptive radiation; pelagization; interspecific variation; buoyancy adaptations

Because the notothenioid fishes of the Antarctic shelf form an adaptive radiation (Eastman and Clarke, 1998; Johns and Avise, 1998), they offer excellent opportunities to study the effects of ecological variation on the evolutionary diversification of nervous and sensory systems (Eastman and Lannoo, 1995; Lannoo and Eastman, 1995; Montgomery and Macdonald, 1998; for a general discussion see Lauder and Liem, 1983a,b; Albert et al., 1998). The perciform suborder Notothenioidei includes eight families and 120 species; all but 26 of these species are confined to the Antarctic Region (Eastman, 1993). This phyletic diversification has been accompanied by a substantial morphological and ecological diversification. Although lacking a swimbladder, some notothenioid clades underwent a pelagic diversification centered on reduction of total body density and the acquisition of morphologies associated with swimming and feeding in the water column.

Within the family Nototheniidae, about 50% of the Antarctic species, including representatives from at least eight genera, exhibit some form of pelagic existence, including pelagic, semipelagic, cryopelagic, or epibenthic life styles (Eastman, 1993; Klingen-

berg and Ekau, 1996). For example, the primarily benthic genus *Trematomus* contains an epibenthic radiation that includes *T. loennbergii*, *T. lepidorhinus*, and *T. eulepidotus*. These epibenthic species are streamlined and possess modifications for life in the water column, as suggested by morphometric measurements (Ekau, 1988, 1991). While benthopelagic might seem a suitable term for fishes living near the sea floor, this designation applies only to species living at depths beyond the edge of the continental shelf (Marshall, 1979). It also invites comparison with phyletically distant, nonperciform groups living over the continental slope. The Antarctic shelf is deeper than elsewhere in the world; in the

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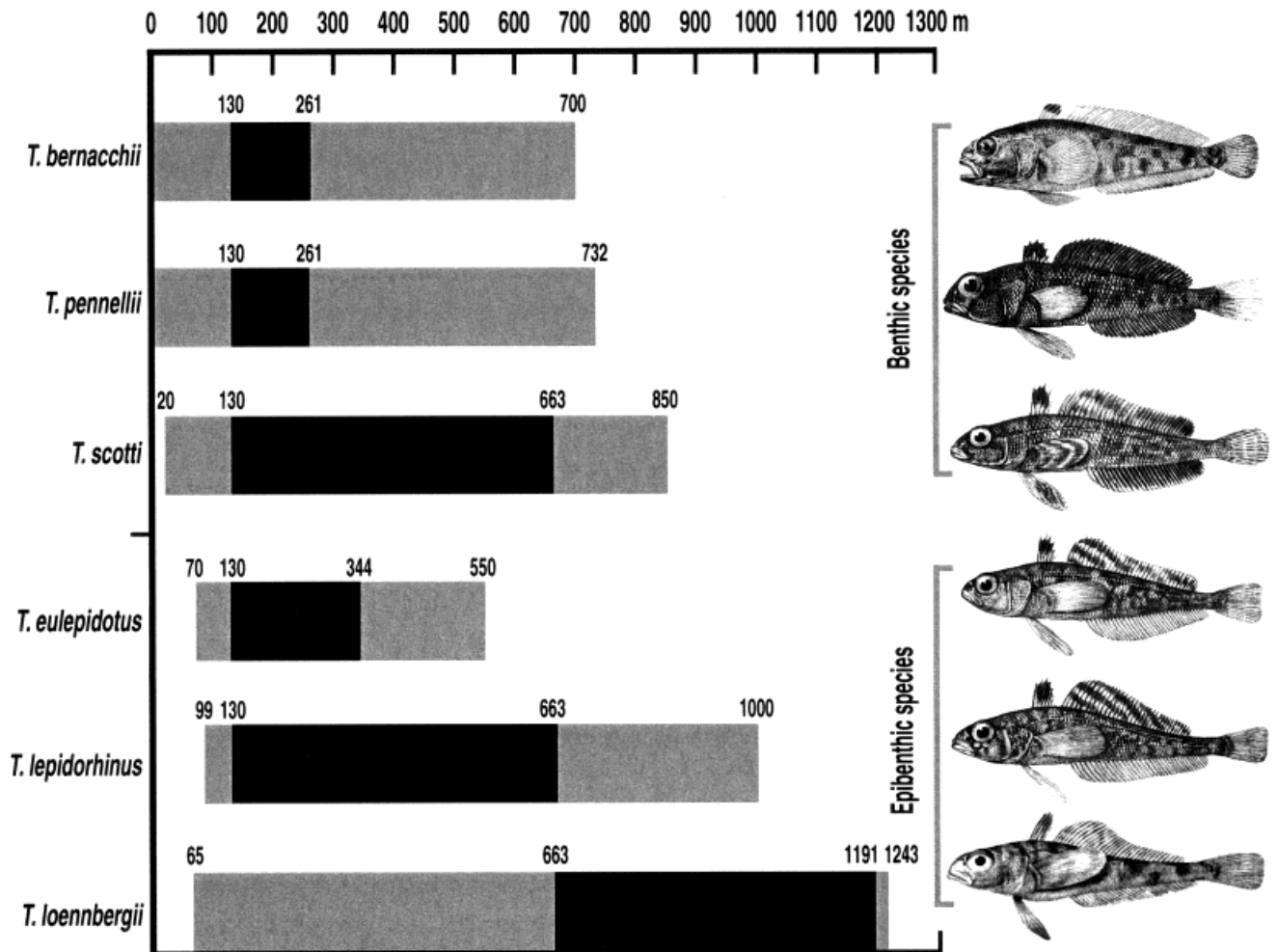


Fig. 1. Depth distribution in meters (m) and body morphology of six species of benthic and epibenthic *Trematomus*. Horizontal bars represent known depth ranges, with gray portions from the literature (DeWitt et al., 1990; Gutt and Ekau, 1996) and black portions based on collections made during cruises 96-6 and 97-9 of the RVIB *Nathaniel B. Palmer* in the Ross Sea (Eastman and Hubold, 1999).

Ross Sea the shelf averages 500 m in depth (Vanney et al., 1981) vs. 130 m for other continents (Kennett, 1982). Other estimates place the average depth at eight times the world average (Anderson, 1999). The fish fauna, however, is primarily coastal in origin and composition (Eastman, 1993).

Epibenthic species, as exemplified by *Trematomus loennbergii*, are not neutrally buoyant, but do have lower percentage weights in sea water than all species except the pelagic nototheniids, such as *Dissostichus mawsoni* and *Pleuragramma antarcticum* (Eastman and DeVries, 1982). Epibenthic species spend more time in the water column than benthic species, although they frequently perch on and hide in sponges, and may feed in the water column as well as on the substrate (Ekau and Gutt, 1991; Gutt and Ekau, 1996). Underwater video footage confirms that epibenthic *Trematomus* swim slowly within one meter of the bottom (Ekau and Gutt, 1991). When

held in aquaria they show more spontaneous swimming activity than benthic trematomids. Unlike benthic species, epibenthic *Trematomus* can be induced to swim in a respirometer (Wohlschlag, 1964).

The epibenthic trematomids have a circum-Antarctic distribution and occur sympatrically in the large shelf areas of the Weddell and Ross Seas. They are ecologically important as inferred from their dominance in collections and on underwater video footage from these areas. For example, *Trematomus eulepidotus* is the second most abundant species collected during bottom trawling in the Weddell Sea, and composes 11% of the fish biomass on the eastern shelf (Kock et al., 1984; Ekau, 1990; Hubold, 1991). *Trematomus lepidorhinus* and *T. eulepidotus* are among the five most frequently identified species in underwater video observations in the Weddell Sea (Ekau and Gutt, 1991). In the Ross Sea, *T. eulepidotus* is the third most abundant species, represent-

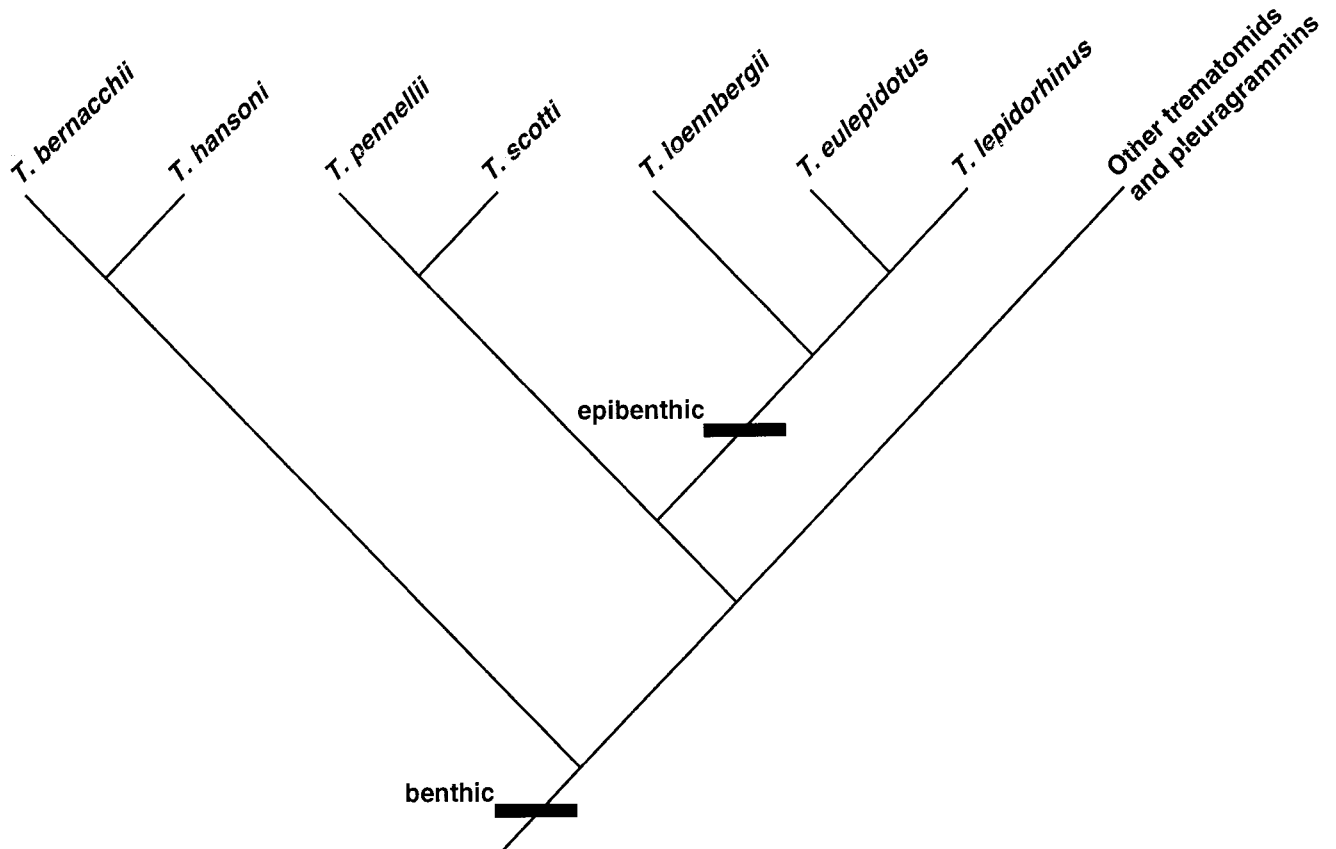


Fig. 2. Cladogram of hypothesized relationships among some species of *Trematomus*. Distribution of epibenthic and benthic lifestyles is mapped on this cladogram derived from morphological data (tree B1 of Klingenberg and Ekau, 1996).

ing 8.7% of the catch by numbers (Eastman and Hubold, 1999). The epibenthic species exhibit graded and somewhat disjunct depth distributions, with *T. eulepidotus* most common in shallow water, *T. loennbergii* in deep water, and *T. lepidorhinus* ranging from shallow to moderately deep water (Fig. 1).

Among trematomids, the suite of characters associated with epibenthic life is sufficiently distinctive that the epibenthic species cluster together in dendrograms of morphological and morphometric similarity (Ekau, 1988, 1991). Furthermore, the epibenthic lifestyle has a single origin in the common ancestor of *Trematomus loennbergii*, *T. lepidorhinus*, and *T. eulepidotus* (Fig. 2). Because all surrounding nodes are assigned a benthic lifestyle, parsimony methods unequivocally map the origin of the epibenthic lifestyle on the branch giving rise to this clade (Klingenberg and Ekau, 1996). Based on molecular sequence data, the estimated average age of the trematomid radiation is 3.4 million years (Ritchie et al., 1996).

Our objective is to examine the effects of pelagization on the central nervous systems of epibenthic trematomids. Cladograms based on both morphological (Klingenberg and Ekau, 1996) and molecular

(Ritchie et al., 1996, 1997) data indicate that the epibenthic trematomids form a monophyletic group separate from the three species of benthic trematomids that serve as outgroups for our comparison (Fig. 2). The brain of one of our outgroup species, *Trematomus bernacchii*, has been previously described, including a low-resolution atlas (Eastman and Lannoo, 1995). Dorsal and ventral views of the *T. bernacchii* brain are included here as a guide to brain regions (Fig. 3). Retinal histology has also been studied in some of the six species (Eastman, 1988). Visual and lateral line function have also been examined in some of the trematomids and in the closely related *Pagothenia borchgrevinki* (Pankhurst and Montgomery, 1989; Coombs and Montgomery, 1994a,b; Montgomery et al., 1994; Janssen, 1996; Baker and Montgomery, 1999).

We tested three null hypotheses. Hypothesis 1: there is no difference in brain morphology among the six species of *Trematomus* examined. Hypothesis 2: phylogenetic and ecological factors do not influence brain morphology. Hypothesis 3: peripheral sensory structures do not influence brain morphology. Rejecting all three hypotheses, we conclude that *Trematomus* brains vary interspecifically, vary between benthic and epibenthic species, and vary with

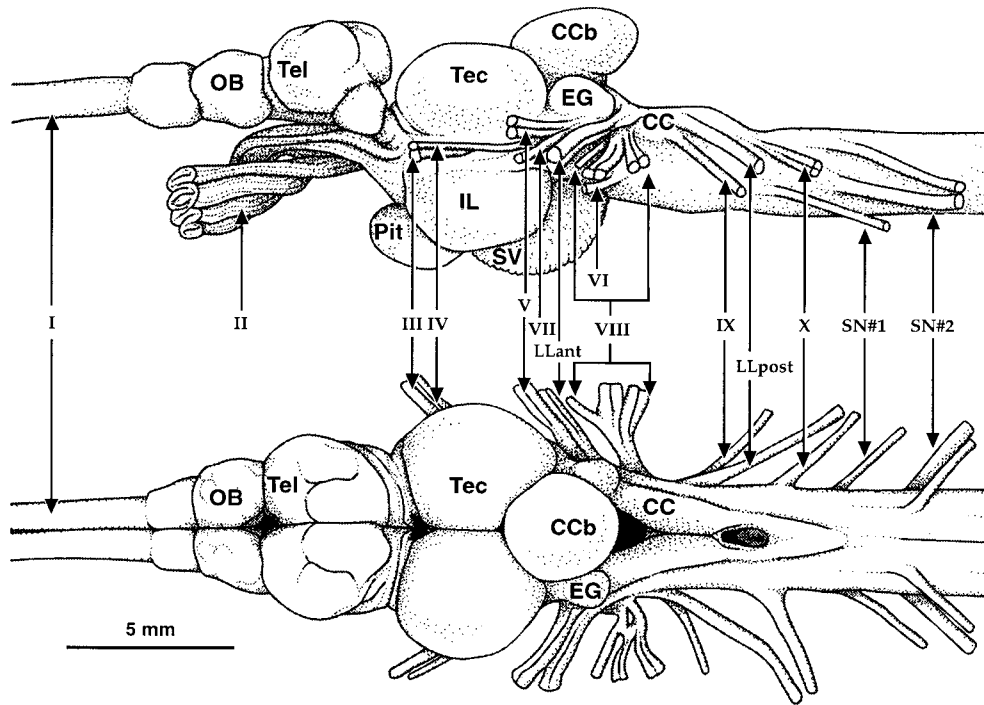


Fig. 3. Lateral and dorsal illustrations of the brain of *Trematomus bernacchii* showing major brain structures; modified from Eastman and Lannoo (1995). CC, crista cerebellaris; CCb, corpus division of the cerebellum; EG, eminentia granularis; IL, inferior lobe of the diencephalon; LL ant, anterior lateral line nerve; LL post, posterior lateral line nerve; OB, olfactory bulb; Pit, pituitary gland; SV, sacculus vasculosus; SN #1, first spinal nerve; SN #2, second spinal nerve; Tec, optic tectum; 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.

depth distribution. Furthermore, a component of brain variation is correlated with differences in peripheral sensory systems and motor activity that are associated with life in the water column.

## MATERIALS AND METHODS

We conducted bottom trawling during cruises 96-6 (11 Dec. 1996 to 8 Jan. 1997) and 97-9 (20 Dec. 1997 to 10 Jan. 1998) of the RVIB (Research Vessel Ice Breaker) *Nathaniel B. Palmer* in the southwestern Ross Sea. The trawls used were a 9.1 m long, 7.6 m effective width Marinovich Gulf Coast style flat trawl—a type of otter trawl—and a Blake trawl with a frame measuring 1.5 m wide by 0.5 m high. Towing speed was 2.0–3.0 knots for a duration of 30–60 min. Species were identified using taxonomic keys and the scientific nomenclature of DeWitt et al. (1990). A total of 474 *Trematomus* specimens were collected as follows: *T. scotti* (291), *T. eulepidotus* (85), *T. lepidorhinus* (35), *T. pennellii* (28), *T. loennbergii* (32), and *T. bernacchii* (3).

For this study, we used 37 fish: six specimens each of *Trematomus scotti*, *T. eulepidotus*, *T. pennellii*, *T. loennbergii*, and *T. bernacchii*, and seven specimens of *T. lepidorhinus*. To control for ontogenetic variation, we used the largest adult specimens in our collection. In these species it has been shown that larval development is more important in determining morphology than is allometric growth in juveniles and adults (Klingenberg and Ekau, 1996). Interspecific allometric variation was controlled in part because five of the six species examined have

similar adult sizes; the benthic *T. scotti* tends to be smaller. We chose to use two, independent methods of measuring brain morphology: gross brain measurements and histological analyses. These techniques are detailed below.

## Gross Brain Anatomy

We used 30 fish for gross brain analyses. These specimens were either immersion-fixed in 10% formalin and stored in 70% ethanol, or perfusion-fixed as detailed below. For each of the six species, we chose five adult fish and removed, then cleaned their brains by stripping the meninges and cranial nerves. For each brain, we measured—under a microscope using a dial calipers—lengths, widths, and heights of each of the following structures: olfactory bulb, telencephalon, optic tectum, corpus cerebellum, telencephalon, eminentia granulares, crista cerebellares, and inferior lobes (Fig. 3). To correct for size, we measured total brain length (from rostral telencephalon to obex) of each brain and divided this value into the measurement for each structure. We then multiplied together the measurements for each structure to arrive at a size index (a rough estimate of volume) for each structure. We averaged indices for each brain region across the five specimens in each species, then made comparisons across species (Table 1).

## Histology

All fish used for histological analyses were fixed by transcathal perfusion of Bouin's fixative onboard

TABLE 1. Indices of brain region size based on measurements of external brain features in six Antarctic *Trematomus* species

Species*	Benthic				Epibenthic	
	TBE	TPE	TSC	TEU	TLE	TLO
Olfactory bulb	3.9	4.0	2.4	3.3	5.4	4.8
rank	4	3	6	5	1	2
Telencephalon	11.0	15.1	11.2	9.0	14.6	10.0
rank	4	1	3	6	2	5
Tectum	19.0	37.0	25.6	31.3	21.4	15.0
rank	5	1	3	2	4	6
Inferior lobes	7.4	12.4	8.8	6.8	7.6	5.6
rank	4	1	2	5	3	6
Corpus cerebellum	6.8	10.8	6.7	9.4	13.2	8.1
rank	5	2	6	3	1	4
EG + CC	1.6	1.9	1.7	2.9	2.4	1.9
rank	6	3	5	1	2	3

\*Abbreviations for species are as follows: TBE, *Trematomus bernacchii*; TPE, *T. pennellii*; TSC, *T. scotti*; TEU, *T. eulepidotus*; TLE, *T. lepidorhinus*; TLO, *T. loennbergii*.

Indices were calculated by dividing each absolute linear dimension (length, width, height in mm) by brain length, multiplying each of these numbers by 10, and multiplying each of the three linear dimensions for each brain region to estimate volume. Indices are then ranked across species, from highest (1) to lowest (6). Within benthic and epibenthic groups, species are listed in order of increasing depth preference (Fig. 1). Among brain regions, EG + CC designates eminentia granularis plus crista cerebellaris, the lateral line region.

ship according to procedures described previously (Eastman and Lannoo, 1995) and summarized briefly here. After anesthetization in a 1:1,000 concentration of 3-aminobenzoic acid ethyl ester (MS-222, Sigma, St. Louis, MO), the heart and bulbous arteriosus were exposed. Notothenioid saline solution (O'Grady et al., 1982) was prepared, adjusted with NaCl to a concentration of 600 mOsm liter<sup>-1</sup>, maintained at ambient sea water temperature (-1.5°C), and transcardially perfused. Saline was followed by Bouin's fixative. During this perfusion the gills were periodically irrigated with subzero seawater.

For histological analyses, we examined the fixed brains of one specimen each of three benthic *Trematomus* species (*T. bernacchii*: TBE 88-5; *T. scotti*: TSC 13-8; and *T. pennellii*: TPE 88-7) and four specimens of three epibenthic *Trematomus* species (*T. loennbergii*: TLO 30-7; *T. eulepidotus*: TEU 13-1; and *T. lepidorhinus*: TLE 13-8, TLE 46-14). Brains were removed, dehydrated in alcohol, cleared in Hemo-De, and embedded in paraffin according to standard procedures (Kiernan, 1990). Embedded brains were cut in the transverse plane on a rotary microtome to produce sections 10–12 µm thick. Sections were mounted on slides, dried, deparaffinized, stained with hematoxylin and eosin, dehydrated, and coverslipped using Permount as the mounting medium. We viewed sections using either a Nikon SMZ-U dissecting microscope or a Zeiss Jenalumar compound microscope and took photographs using Kodak T-Max 100 black and white film.

We also cut histological sections of the retina from one or two specimens of each of the six *Trematomus* species. We took samples from the central retina adjacent to the optic nerve of the left eye. We employed the protocol outlined above except that sections were cut at 7 µm. Sections were stained with

hematoxylin and eosin, periodic acid-Schiff, or Bodian's Protargol (Clark, 1981) for 24 h at 50°C.

To determine brain volumes, brains were removed from the following specimens: *Trematomus bernacchii* (TBE 88-2; SL = 206 mm), *T. scotti* (TSC 46-10; SL = 130 mm), *T. pennellii* (TPE 88-4; SL = 205 mm), *T. loennbergii* (TLO 20-20; SL = 193 mm), *T. eulepidotus* (TEU 1-3, SL = 198 mm), and *T. lepidorhinus* (TLE 58-14; SL = 163 mm). After each brain was removed it was trimmed rostrally to include the olfactory bulbs and caudally at the obex; the cranial nerve roots and meninges were removed. Brains were then immersed in 70% ethanol in a 10 ml in 1/10 ml serological pipette and the displaced volume determined.

From each brain about 150 sections, evenly spaced between the rostral-most cellular portion of the olfactory bulbs and the obex, were identified. This resolution meant that either every sixth (*Trematomus scotti*) or every eighth (the remaining species) section was sampled. Each section was scanned into and stored on a Power Macintosh G3 personal computer. Brain structures were identified as follows: olfactory bulbs, telencephalon, pituitary, optic tectum, inferior lobes, valvula cerebellum, corpus cerebellum, saccus vasculosus, eminentia granularis, and crista cerebellaris. Areas of brain regions present in each section were measured. After all sections were entered and areas of all brain regions summed, the percentage of each brain region was then calculated from the brain total. Because our samples were taken from equally spaced sections, our percentages based on area are equivalent to percentages based on volumes. For our analysis, we considered olfactory bulb volume to be a measure of the olfactory region, the tectal volume to be a measure of the visual region, and the volume of the eminentia granularis and the crista cerebellaris to-

TABLE 2. Volumes of brain regions represented as percentages of total brain volume for six Antarctic *Trematomus* species

Species*	Benthic				Epibenthic	
	TBE	TPE	TSC	TEU	TLE	TLO
Olfactory bulb rank	2.8	1.7	2.3	2.7	4.0	4.8
	3	6	5	4	2	1
Telencephalon rank	14.7	13.6	18.5	11.0	13.4	18.2
	3	4	1	6	5	2
Tectum rank	16.4	16.9	18.4	20.1	15.5	13.1
	4	3	2	1	5	6
Inferior lobes rank	11.3	11.3	15.3	7.6	8.6	9.2
	2	2	1	6	5	4
Cerebellum rank	9.0	7.1	7.6	10.4	14.0	9.1
	4	6	5	2	1	3
EG + CC rank	2.0	2.2	2.6	4.0	3.9	3.8
	6	5	4	1	2	3

\*Abbreviations for species are as follows: TBE, *Trematomus bernacchii*; TPE, *T. pennellii*; TSC, *T. scotti*; TEU, *T. eulepidotus*; TLE, *T. lepidorhinus*; TLO, *T. loennbergii*.

Percentages are ranked across species, from highest (1) to lowest (6). Within benthic and epibenthic groups, species are listed in order of increasing depth preference (Fig. 1). Among brain regions, EG + CC designates eminentia granularis plus crista cerebellaris, the lateral line region.

gether to be a measure of the lateral line region. To facilitate interpretation, percentages were then ranked across species (Table 2).

## RESULTS

When viewed either grossly (Fig. 4) or quantified (Tables 1, 2), there were differences in brain proportions, and these are fairly obvious. Results from both gross and histological analyses demonstrate that these interspecific differences are greater than intraspecific differences. We examine this interspecific variation according to brain region.

### Olfactory Bulbs

In all species the olfactory bulbs are sessile and the transition from bulb to nerve is marked by an expansion of the olfactory nerve. In *Trematomus scotti* the olfactory nerves run in an over-and-under—right nerve dorsal—rather than the usual side-by-side orientation seen in the other five species (Fig. 4). By both gross and histological measurements, epibenthic *T. lepidorhinus* and *T. loennbergii* have the largest olfactory bulbs (Tables 1, 2). The size of the olfactory bulbs in *T. eulepidotus*, the remaining epibenthic species, is unremarkable and falls within the range of the benthic species.

### Telencephalon

The telencephalon of each species is characterized by a prominent Dm (dorsal medial subdivision of the telencephalon) and Dp (dorsal posterior subdivision of the telencephalon) lobes (Figs. 3, 4). Proportions of these structures vary across species. There is little correlation between telencephalic size and benthic or epibenthic habitats (Tables 1, 2). In both analyses, *Trematomus eulepidotus* has the smallest

telencephalon, and a benthic species (either *T. scotti* or *T. pennellii*) has the largest telencephalon. But when compared with other brain regions, this relationship between neural structure and habitat type is weak.

### Optic Tectum

Tectal volumes vary widely, up to 50% within the genus (Tables 1, 2; Fig. 4). Tectal variation is related to depth preferences and retinal morphology. For example, *Trematomus eulepidotus*, a shallow water epibenthic species, has 1/5 (20%) of its total volume devoted to the tectum (Table 2). In contrast, *T. loennbergii*, the deepest water epibenthic species, has only about 1/8 (13%) of its total brain volume devoted to the tectum (Table 2). Histologically, the tectum of *T. eulepidotus* is shaped differently than in the five remaining *Trematomus* (Fig. 5A,B). The generalized condition in *Trematomus* is for each tectal hemisphere to be spherically shaped (Fig. 5A). In *T. eulepidotus*, the paramedian portions of the dorsal surface are elongate and flattened, probably adding to the brain volume of this structure (Fig. 5B). Additionally, the midline region of contact between the two lobes, dorsal to the torus longitudinalis, is greater.

Tectal size is not related to benthic or epibenthic habitation, but rather to the habitation of shallow water (Tables 1, 2). In both gross and histological analyses, the benthic *Trematomus pennellii* and *T. scotti*, and the epibenthic *T. eulepidotus* have the three largest tecta. These are all species found at relatively shallow depths (Fig. 1). Conversely, by both gross and histological measures, the deep-water *T. loennbergii* has the smallest tectum. Tectal size is also related to cellular and functional features of the retina (see below).

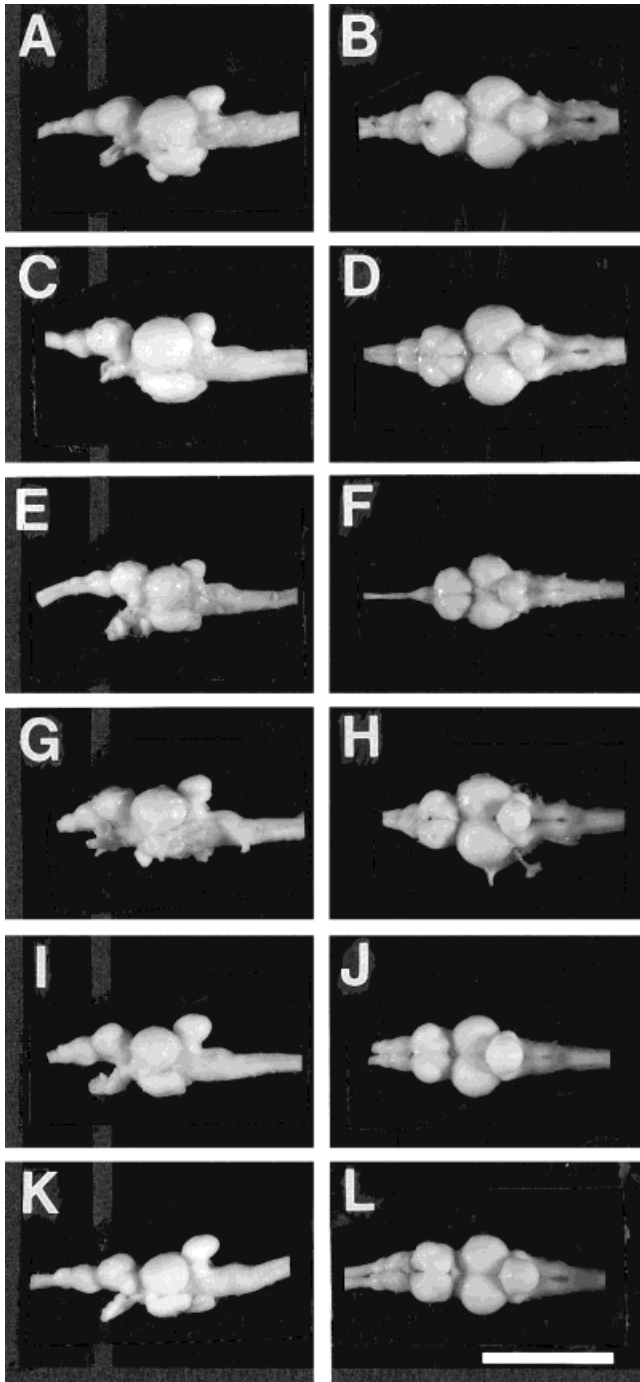


Fig. 4. Lateral (left column) and dorsal (right column) photographs of the brains of the six species of *Trematomus* considered here. **A,B:** *T. bernacchii*. **C,D:** *T. pennellii*. **E,F:** *T. scotti*. **G,H:** *T. eulepidotus*. **I,J:** *T. lepidorhinus*. **K,L:** *T. loennbergii*. Scale bar = 1 cm.

### Inferior Lobes

The diencephalic inferior lobes form the largest structures on the ventral surface of the brain (Fig. 3). Curiously, the inferior lobes vary widely, with the benthic species tending to have proportionally larger inferior lobes than epibenthic species (Tables 1, 2).

### Cerebellum

The cerebellum is traditionally regarded as the organ of locomotion, but its functions are poorly understood. It is generally larger in species that are more mobile. In our analysis we have two measures of the cerebellum. Our gross brain measurements give us an index for the corpus cerebellum, our histological analysis measures both the corpus and the valvula cerebella. In both analyses, there is a tendency for the epibenthic species to have larger cerebella (Tables 1, 2). In our gross brain analysis, epibenthic species had three of the four largest cerebella. In our histological analysis, the epibenthic species had the three largest cerebella (although the cerebella of the epibenthic *Trematomus loennbergii* and the benthic *T. bernacchii* were similarly sized; Table 2).

### Lateral Line System

Our analysis of the lateral line system combines measurements of its cellular structure, the eminentia granularis—which is also considered to be a component of the cerebellum—and its axonal structure, the crista cerebellaris. In both gross brain and histological analyses, epibenthic species have the largest lateral line regions (Tables 1, 2). By these measures, the benthic *Trematomus bernacchii* has the smallest lateral line region; about half the size of *T. eulepidotus*, the epibenthic species with the largest lateral line region.

### Notable Neurohistological Features

Antarctic notothenioids and scorpaeniform liparids are unique among vertebrates studied to date in having the ependymal walls of their third ventricles expanded (Eastman and Lannoo, 1995, 1998; Lannoo and Eastman, 1995). Degree of expansion correlates inversely with ambient temperatures. Among the *Trematomus* species observed here, one (*T. scotti*) exhibits a small type 5 expansion (after Lannoo and Eastman, 1995), the other five exhibit a type 4 expansion (Fig. 5C,D). The type 4 expansions also vary, with *T. bernacchii* and *T. lepidorhinus* having weak midline contact and *T. pennellii*, *T. loennbergii*, and *T. eulepidotus* having midline adhesions.

### Testing the Hypotheses

Together, these results lead us to reject the first null hypothesis, that there are no interspecific differences in brain morphology. In our analysis, every brain region varies. Variation occurs across the genus, both within and among benthic and epibenthic clades.

The second hypothesis—that phylogenetic and ecological factors do not influence brain morphology—is also rejected. In three of the six brain

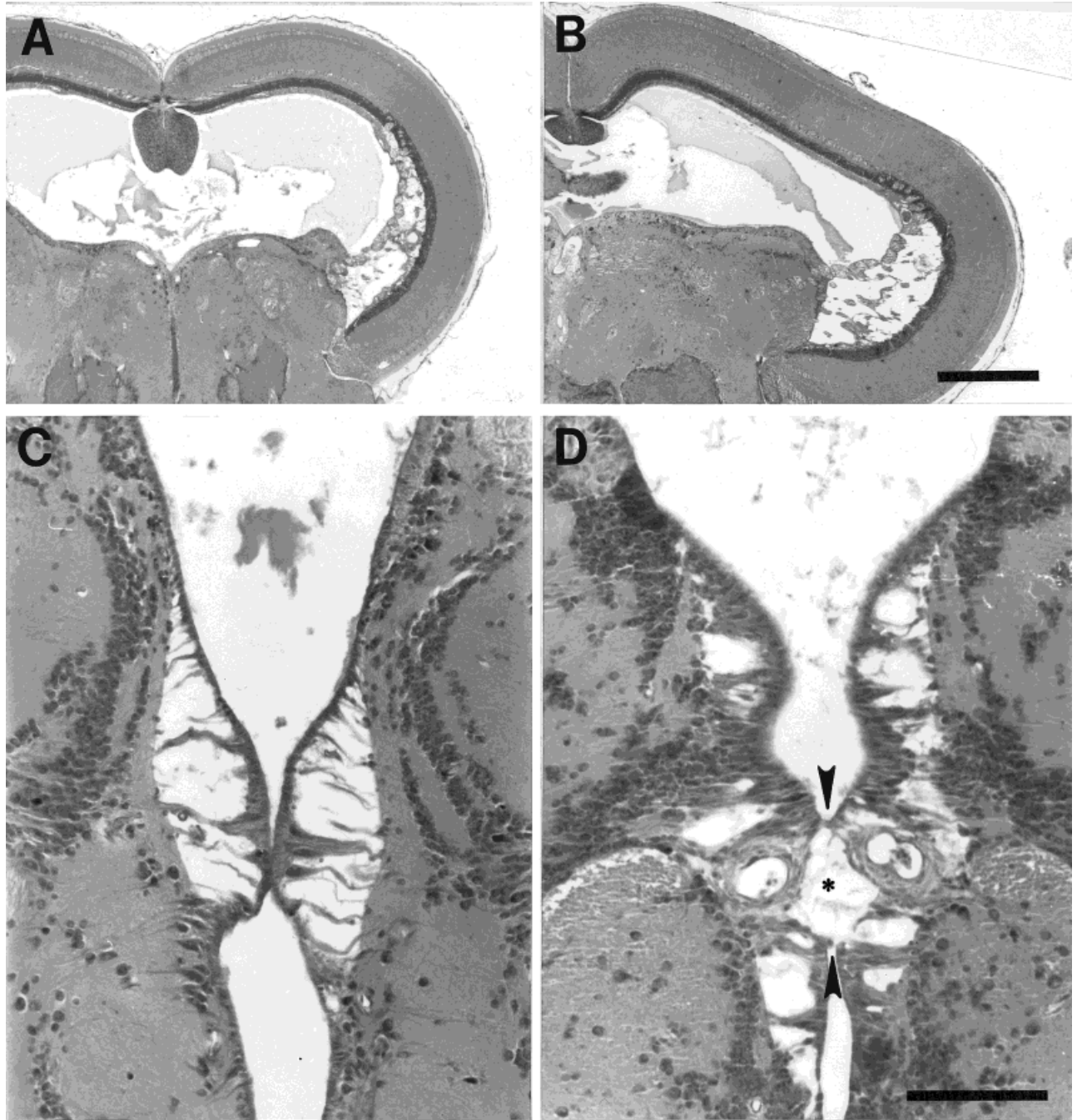


Fig. 5. Histological variation in the brains of some of the six species of *Trematomus*. **A:** The optic tectum in *T. lepidorhinus*, showing the usual, spherical shape seen in most species. **B:** The flattened tectal lobes seen in *T. eulepidotus*. **C:** Subependymal expansions in the caudal third ventricle of *T. lepidorhinus*, showing the type 4 expansion seen in most species. **D:** Subependymal expansions in *T. scotti*, showing the type 5 expansion observed uniquely in this species. Arrowheads indicate dorsal and ventral connections that delimit the secondary ventricular lumen (asterisk). Scale bars: **A,B** = 1,000  $\mu\text{m}$ ; **C,D** = 100  $\mu\text{m}$ .

regions, the epibenthic species each had either larger or smaller percentages than the benthic species. In at least one of these five regions—the cerebellum—large size is correlated with mobility, an ecological factor. Two other senses, vision and olfaction, vary with depth.

To test the third hypothesis, that peripheral sensory structures do not influence brain morphology, we evaluated the morphology of two sensory systems: vision, represented by the retina, and lateral line mechanoreception. Details of the two sensory systems are given in the subsections below. We note

TABLE 3. Cell counts and ratios in central area of retina for six Antarctic *Trematomus* species<sup>1</sup>

Species	Cones	Rods	Cones + rods	Ratio cones:rods <sup>2</sup>	Cells in internal nuclear layer	Ganglion cells	Convergence ratio (cones + rods: ganglion cells) <sup>3</sup>
<b>Benthic</b>							
<i>T. bernacchii</i>	7	47	54	1:7	67	6	9:1
<i>T. pennellii</i>	10	45	55	1:5	98	9	6:1
<i>T. scotti</i>	7	37	44	1:5	56	8	6:1
<b>Epibenthic</b>							
<i>T. eulepidotus</i>	7	58	65	1:8	62	7	9:1
<i>T. lepidorhinus</i>	9	95	104	1:11	94	9	12:1
<i>T. loennbergii</i>	4	166	170	1:42	67	6	28:1

<sup>1</sup>Counts are mean number of nuclei for three replicates in an area of 100  $\mu\text{m}$  along the various layers of one Bodian-stained histological section viewed at  $\times 1,000$ .

<sup>2</sup>Values for cone:rod ratios in notothenioids (modified from Eastman, 1988): high (1:2–4), moderate (1:5–11), and low (1:14–57).

<sup>3</sup>Values for convergence ratios in notothenioids (Eastman, 1988): high (58:1), moderate (30–12:1), and low (10–5:1).

here that variation in brain structure (Tables 1, 2) is not independent of variation in peripheral sensory structures (Tables 3, 4), thus the third hypothesis is also rejected.

**Retinal histology.** With a photoreceptor layer consisting of both cones and rods, the notothenioids examined to date have retinas similar to perciform fishes from coastal habitats elsewhere in the world (Eastman, 1988). The epibenthic and benthic trematomids are no exception; neither group possesses a retinal histology distinctive to that lifestyle. Cones and rods are present in all six species examined here, with cones qualitatively dominant in sections of all retinæ except *Trematomus loennbergii*, where rods predominate (Fig. 6). Both single and twin cones are present, with single cones most prominent in *T. eulepidotus* and *T. loennbergii* and twin cones in *T. scotti* and *T. lepidorhinus*. The size of the cone ellipsoids is markedly reduced in *T. loennbergii*. Outer segments are also longer and thinner in this species (Fig. 6D).

The retina of the epibenthic but shallow-living *Trematomus eulepidotus* is similar to the cone dominated retinas of the three benthic species. In the epibenthic species the number of rods increases with

increasing depth of occurrence (Table 3). They are most prominent in deep-living *T. loennbergii* and, to a lesser extent, in *T. lepidorhinus*. In these deep-dwelling species the thickness and cell counts for the external nuclear layer, made up of rod and cone nuclei, are two to three times that of species from shallower depths (Fig. 6). *Trematomus loennbergii* has more rods than *T. lepidorhinus* because the external nuclear layer of *T. loennbergii* contains six to eight rows of nuclei while this layer in *T. lepidorhinus* contains four to six rows (Fig. 6C,D). With the exception of *T. loennbergii*, there is little variation in retinal cell counts among the six species (Table 3). Cone:rod ratios are moderate in all species but low in *T. loennbergii*. Convergence ratios are low in all species but moderate in *T. loennbergii* and *T. lepidorhinus*.

**Lateral line system.** Variation in the lateral line periphery is correlated with the volume of the eminentia granulares and the crista cerebellares (Tables 2, 4). In general, benthic species have a mean of about 60 neuromast pores while epibenthic species have a mean of about 75, a difference of 25%. This variation is not constant across lateral line regions (Table 4). For example, numbers of cephalic pores do

TABLE 4. *Trematomus* trunk and cephalic lateral line counts from DeWitt et al. (1990)

Species*	Benthic			Epibenthic		
	TBE	TPE	TSC	TEU	TLE	TLO
Dorsal lateral line	26–41	30–38	10–23	42–48	39–49	41–47
Middle lateral line	Pored scales			Tubed scales		
Preopercular-mandibular	11	10	10	10	10	10
Infraorbital	8	7	7	7–8	6–8	7
Supraorbital	4	4	4	4	4	4
Coronal Commissure	1	1	1	1	1	1
Temporal	5–6	5–7	5–6	5–6	5–6	5–6
Supratemporal	5	3	3	3	3	3
Total	60–76	60–70	40–54	71–80	69–81	71–78

\*Abbreviations for species are as follows: TBE, *Trematomus bernacchii*; TPE, *T. pennellii*; TSC, *T. scotti*; TEU, *T. eulepidotus*; TLE, *T. lepidorhinus*; TLO, *T. loennbergii*.

Within benthic and epibenthic groups, species are listed in order of increasing depth preference (Fig. 1). DeWitt et al. (1990) do not give middle lateral line counts for the benthic species, but note that benthic species have pored scales, while epibenthic species have tubed scales.

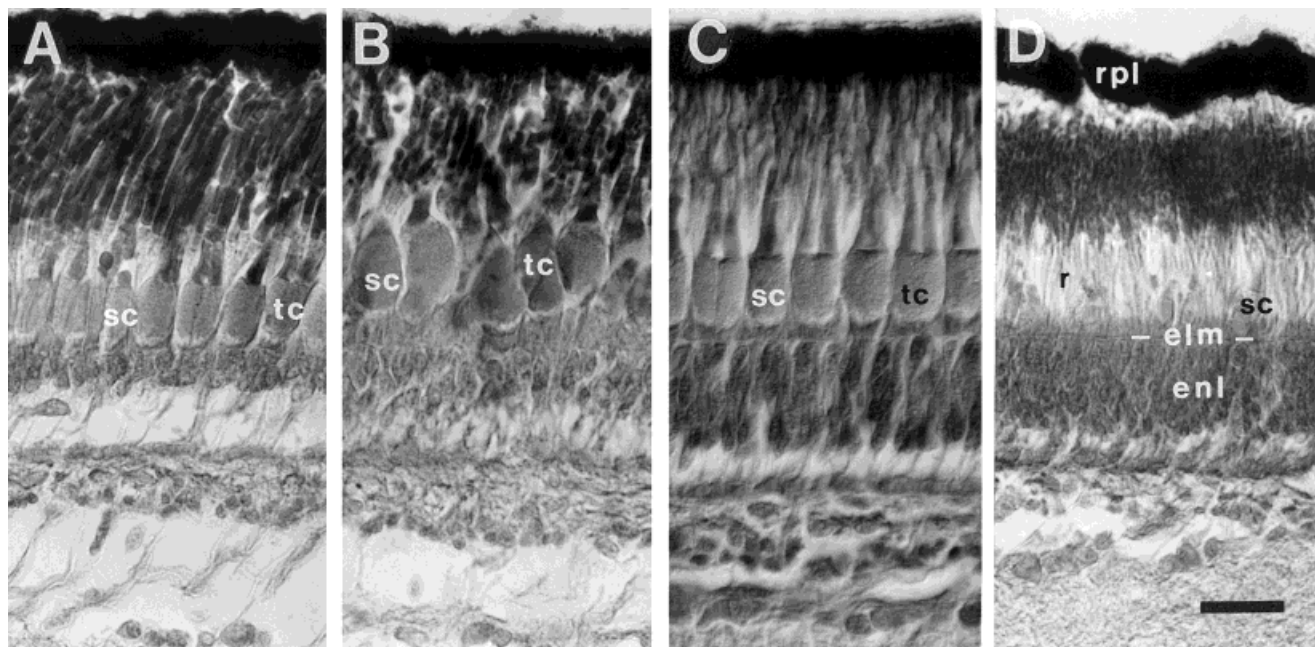


Fig. 6. Retinal histology depicting influence of habitat depth on photoreceptor layer of benthic (A) and epibenthic (B–D) species of *Trematomus*. Species are arranged in order of habitat depth from shallow (A) to deep (D). A: *T. scotti*. B: *T. eulepidotus*. C: *T. lepidorhinus*. D: *T. loennbergii*. Photos aligned horizontally along external limiting membrane. Abbreviations in D hold for all micrographs. Periodic acid-Schiff technique. elm, external limiting membrane; enl, external nuclear layer; rpl, retinal pigment layer; r, rod photoreceptors; sc, single cone; tc, twin cone. X450. Scale bar = 25  $\mu$ m.

not vary greatly. On the trunk, however, epibenthic species have more neuromasts in the upper lateral lines. In the middle lateral line there is an additional morphological difference. Along this line, epibenthic species have scales with tubular openings, while benthic species have scales with open pores.

## DISCUSSION

We tested three null hypotheses regarding brain variation in Antarctic trematomids. The first hypothesis was that there is no difference in brain morphology among the six species of *Trematomus* examined. The second hypothesis was that phylogenetic and ecological factors do not influence brain morphology. The third hypothesis was that peripheral sensory structures do not influence brain morphology. We rejected each of these hypotheses, and instead conclude that *Trematomus* brains vary interspecifically, vary between benthic and epibenthic species, and vary with a species' depth distribution.

The assumption that differences in brain structures are reflected by differences in peripheral structures or a resulting behavior has been examined by Kotrschal et al. (1998) and found to be generally true, especially for closely related taxa. These authors conclude that differences in demand tend to alter the number and size of neuronal features rather than their connectivity, and thus the relative size of brain regions is indicative of their importance

to an animal. Phylogeny is also known to be an important determinant of brain morphology. Relative sizes, positions, and fusions of brain lobes have been used as characters in the phylogenetic analysis of higher level clades within the Osteoglossiformes, Gadiformes, Synbranchiformes, and Gymnotiformes (Lauder and Liem, 1983a,b; Albert et al., 1998).

## Variation Between Benthic and Epibenthic Species

We show that a certain amount of brain variation is correlated with differences in peripheral sensory systems and the motor system. A comparison of brain regions among trematomid species shows that epibenthic *Trematomus* have larger percentages of their brain volume devoted to primary sensory and motor functions. These regions include lateral line mechanoreceptive, and visual sensory structures, as well as the cerebellum, the brain region considered to coordinate motor activities (e.g., Paulin, 1993; Tables 1, 2).

The increase in lateral line representation appears to occur as a result of increases in the number of canal neuromasts along the body (Tables 1, 2). This could be a true adaptation. Perhaps pelagic fishes are more vulnerable to predators than benthic species, and increases in trunk neuromasts add sensitivity to the caudal portion of the animal (see also Janssen, 1996). In contrast, increased lateral line scale counts might not be an adaptation, but instead

be an epiphenomenon. For example, an increase in trunk neuromasts could be the result of body elongation associated with streamlining for life in the water column, or of the presence of smaller, but more numerous, scales. Furthermore, loss of lateral line canals and similar response properties of superficial neuromasts may be associated with a paedomorphic trend in notothenioids that is nonadaptive for the lateral line (Coombs and Montgomery, 1994a,b). As exemplified by *Trematomus eulepidotus*, epibenthic trematomids exhibit other paedomorphic features such as a slower rate of osteological development (Voskoboynikova, 1994).

This analysis assumes that the sensory epithelium of each neuromast contains the same number of hair cells, and that superficial neuromast numbers are about equal across species. The fact that among benthic species *Trematomus scotti* has a larger percentage of brain volume associated with the lateral line system but fewer neuromast pores indicate that these assumptions may not hold. Indeed, Janssen (1996) shows that *T. bernacchii* has wider neuromast canals, larger pores, and larger supraorbital neuromasts than *T. pennellii*, and is more sensitive to mechanical stimuli. Furthermore, canal and superficial neuromasts have different sensitivities. Montgomery and Coombs (1992) characterize canal neuromasts as being most sensitive to constant acceleration stimuli while superficial neuromasts are most sensitive to constant velocity stimuli. The canal neuromasts are probably more concerned with feeding behavior, whereas the superficial neuromasts mediate rheotaxis (Baker and Montgomery, 1999). It is likely that the neuronal circuits required for determining acceleration (change in velocity) are more complex than those simply required to determine velocity.

The morphology of the trunk lateral line is paradoxical in two ways. First, according to Klingenberg and Ekau (1996; characters 27 and 28), within the nototheniids, tubed scales are plesiomorphic. Yet, among the *Trematomus* species considered here, generalized benthic species have pored scales while derived epibenthic species have tubed scales—an arrangement reversed from predictions. Second, among nototheniids lower density, including reduction in bone mass, is associated with pelagization (Eastman and DeVries, 1982). From this one could deduce that to reduce bone mass, epibenthic *Trematomus* would have pored, rather than tubed, scales. Yet they do not—a second morphological arrangement reversed from predictions. In this sense they are less pedomorphic than are benthic *Trematomus*.

Had we made predictions about differences between the brains of epibenthic and benthic species, cerebellar size would have been considered. Large cerebella are associated with increased mobility both in elasmobranchs and teleosts (Northcutt, 1989). When morphometric measurements are used in clustering and ranking trematomids on a benthic

to pelagic scale, the epibenthic species are clearly distinguished as pelagic from all other species in the genus (Ekau, 1988, 1991). Our observation that epibenthic species have larger cerebella is consistent with these data and with the generalization about activity patterns and cerebellar size. However, another nototheniid, *Pleuragramma antarcticum*, is neutrally buoyant and lives pelagically in the water column, but has an extremely small cerebellum (Eastman and Lannoo, 1995). Neutral buoyancy in *P. antarcticum* is attributable to the static mechanisms of skeletal reduction and lipid deposition rather than dynamic mechanisms requiring continuous swimming (Eastman and DeVries, 1982). Although *P. antarcticum* lives in the water column, diversification in this phyletically derived species has been toward inactivity. Its cerebellar size is consistent with this activity pattern.

### Variation With Depth Distribution

The visual and olfactory systems vary less with benthic or epibenthic habitation than they do with a species' depth distribution. For example, species living at the greatest depths have smaller optic tecta (*Trematomus loennbergii*, *T. lepidorhinus*; Tables 1, 2). Among species living at less than 400 m, tectal percentages do not vary with depth preferences, although the species with the largest tecta are within this group.

Complicating the relationship between depth and tectal size is the relative number of cones to rods in the retina. This reflects the well-documented trend among fishes that cone-dominated retinas are found in shallow-living species and rod-dominated retinas are found in species from deeper water. Rods are responsible for scototopic vision, whereas cones are more important in phototopic vision and are also the receptors for color vision (Nicol, 1989).

As with tectal size, differences in the proportions of cones to rods, especially among the epibenthic species, reflect habitat depth rather than phylogeny or epibenthic lifestyle. Among these six species of shelf-dwelling *Trematomus*, the break point or critical depth where large numbers of rods begin to appear, although cones are still obvious in histological sections, is 800–1,000 m, with *T. lepidorhinus* the exemplar (Table 3). *T. loennbergii* is the only trematomid known to have a rod-dominated retina. *T. loennbergii*, and, to a lesser extent, *T. lepidorhinus* have low cone:rod ratios and moderate convergence ratios of photoreceptors to ganglion cells. Furthermore, these two species have more cells in the external nuclear layer (rod and cone nuclei) than in the internal nuclear layer (Table 3). This is a characteristic of the retinae of deep-sea fishes with a high degree of summation (Munk, 1984). These features increase retinal sensitivity under low light intensity, and reflect habitat depth, not lifestyle. Although Walls (1942) mentions that twin cones are

more prominent in species from shallow water, we found them in all trematomids, including *T. loennbergii*.

Comparison of the retinas of *Trematomus scotti* and *T. lepidorhinus* suggests that the documented depth distribution, which is nearly identical (Fig. 1), may be misleading. Both species have cone-dominated retinas (Fig. 6), but the retina of *T. lepidorhinus* also contains large numbers of rods, suggesting that this species is more eurybathic. Collection records may be biased toward that part of the population living in shallow water. Inference from retinal histology suggests that this species lives at greater depths than indicated in most collection records.

Depth-related gradients in sensory development are well documented among mesopelagic, bathypelagic, and benthopelagic marine fishes. For example, with increasing depth vision becomes less important and chemo- and tactile sensations gain prominence (Montgomery and Pankhurst, 1997; Kotrschal et al., 1998). Although modest in the shallower depths of the Antarctic shelf, this phenomenon is evident in *Trematomus*. The species with the smallest optic tecta (*T. lepidorhinus* and *T. loennbergii*) have the largest olfactory bulbs. Kotrschal et al. (1998) also note a correlation between the size of the olfactory complex and the telencephalon, a relationship our analyses did not reveal. Montgomery et al. (1999) have shown that benthic *T. bernacchii* use olfactory cues in combination with rheosensory information to locate the source of olfactory plumes. It is likely that all *Trematomus* use their olfactory systems in similar ways, although some species may be more reliant on this modality. Vision and olfaction are reciprocally developed in *T. lepidorhinus* and *T. loennbergii*, while vision and lateral line mechanoreception are not. As in deep-sea fishes, mechanoreception may be an adjunct to vision (Montgomery and Pankhurst, 1997).

A depth of 1,000 m is considered the break point for delimiting fish faunas of the deep sea (Montgomery and Pankhurst, 1997). Although one of the epibenthic trematomids inhabits depths of 1,200 m, the brain and sensory system morphology we have documented is modest. The extreme specializations of deep-sea fishes are lacking, and probably not to be expected in this coastal perciform group. Most deep-sea fishes are nonperciforms, with long evolutionary histories in the relatively stable habitat provided by these depths (Montgomery and Pankhurst, 1997; Montgomery and Macdonald, 1998). The Antarctic shelf has experienced a nearly complete replacement of its fish fauna in the past 40 million years (Eastman, 1993; Eastman and Clarke, 1998). Furthermore, it has been a dynamic environment subject to major glaciological events during the Pliocene and possibly as recently as the Pleistocene (Anderson, 1999). The brain and sensory diversification we see among the benthic and epibenthic *Trematomus*

species has likely taken place within 3.4 million years, the estimated age of this radiation (Ritchie et al., 1996).

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