

A comparative analysis of the feeding apparatus in pomacanthids, with special emphasis of oesophageal papillae in *Genicanthus personatus*

J. C. HOWE

Auburn University Marine Extension and Research Center, 4170 Commanders Drive,
Mobile, Alabama 36615, U.S.A.

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Of the pomacanthids examined in the present study (22 species; seven genera), only *Genicanthus* (eight species) had unique oesophageal papillae. The papillae of the masked angelfish, *Genicanthus personatus* are arranged in a radial fashion, finger-like or polypoid in shape, very abundant, fill the lumen, and vary considerably in length (0.38–2.40 mm) and width (0.12–1.18 mm). The surface pores (2.8–45.2 µm in diameter) of each papilla are part of the gastric or mucus-secreting oesophageal glands as determined by histological examination. Preliminary stomach content analyses revealed that *G. personatus* consumes a variety of animal and plant material, including algae, copepods, diatoms, and eggs, but dominated in volume by plant material. The oesophageal papillae may constitute a morphological specialization of the digestive tract at the genus level. This may enable *Genicanthus* spp. to utilize and process a food source not readily available to other pomacanthid species. Additional studies are necessary to determine other ecological, behavioural, social, and morphological variables that separate this large and diverse group of fishes ecologically.

Key words: diet; oesophageal papillae; gastrointestinal tract morphology; *Genicanthus personatus*; Pomacanthidae.

I. INTRODUCTION

Gause's Principle states that two species cannot coexist in the same ecological niche (Odum, 1953). Much research has been conducted investigating the mechanisms of coexistence among coral reef fishes (Anderson *et al.*, 1981; Sale & Williams, 1982; Doherty & Williams, 1988). The simplest hypothesis to explain the distribution of fishes is that it is completely random, with each species equally likely to occur at any site (Sale & Williams, 1982). This hypothesis though, has been shown to be incorrect by Anderson *et al.* (1981). Consequently, of the many parameters limiting the abundance of reef fishes, food and space have been considered to be the most important (Doherty & Williams, 1988). For example, Jones (1968) studied the variables separating acanthurids ecologically; most important were: habitat preference, foraging methods, diet, and morphological specializations for feeding. Similarly, Reese (1975) investigated the behavioural and ecological separation of chaetodontids. He concluded that diet, social behaviour, habitat, and size of the home range were most important. Comparable studies have not been conducted for pomacanthids, but a similar set of variables may separate the ecological requirements of the species in this large and diverse family of fishes. One factor which may differ in part between the pomacanthids is diet. *Centropyge* spp. are herbivorous and feed exclusively on

algae growing on the substratum. Some of the larger pomacanthids (e.g. *Apolemichthys*, *Chaetodontoplus*, *Holacanthus*, *Pomacanthus*, and *Pygoplites* spp.) are omnivorous, feeding primarily on sponges and/or tunicates, supplementing their diet with bottom-living algae, eggs, gorgonians, hydroids, and zoantharians. Unlike the first two classes of pomacanthids that forage near or on the substratum, *Genicanthus* spp. commonly aggregate well above the bottom, feeding on plankton, supplemented with benthic algae, bryozoans, and tunicates (Randall, 1975, 1976; Tinker, 1978; Carlson, 1982; Allen, 1979; Randall, pers. comm.).

In 1987 during a necropsy of four *Genicanthus personatus* (Randall, 1975) from Midway Island, previously undocumented oesophageal papillae were observed. The function and number of species possessing these papillae are the bases for the present study. The following items were examined: (1) the gross anatomy of the digestive tract; (2) the histological structure of the digestive tract; (3) the ultrastructure of the oesophageal papillae; (4) diet; and (5) the digestive tract of seven other pomacanthid genera, of the acanthurid, *Acanthurus thompsoni* (Fowler, 1923) and of the lutjanid, *Caesio cuning* (Bloch, 1791).

II. MATERIALS AND METHODS

A total of four *Genicanthus personatus* from Midway Island and 14 representatives of the seven other known *Genicanthus* species from the Bernice P. Bishop Museum, the California Academy of Sciences, and the Australian Museum were examined for the presence of oesophageal papillae. All other specimens examined are part of the National Museum of Natural History collection.

The four Midway specimens were preserved in a 10% buffered formalin solution, their entire digestive tracts removed and photographed. Cross sections (2 mm thick) of the anterior, middle, and posterior sections of the oesophagus were dehydrated through an ethanol series. Each tissue sample was critical point dried with liquid CO₂, serving as the transitional fluid using a Denton Vacuum DCP-1 Critical Point Dryer. This method did not significantly alter oesophageal morphology, as determined by comparison with untreated samples using high powered light microscopy. After critical point drying, each sample was mounted on aluminium stubs and sputter coated with palladium-gold. Coated samples were observed with a Cambridge Scientific Instruments S-100 scanning electron microscope at the Scanning Electron Microscope Laboratory, U.S. Museum of Natural History, Washington, D.C. A total of 77 micrographs were taken of the oesophageal papillae at an accelerating voltage of 15 and 20 kV.

For histological examination, cross-sections of the oesophagus, stomach, and both the small and large intestine were dehydrated through a graded ethanol and histosolv (xylene substitute) series and embedded in paraffin. The samples were sectioned (8 µm) using a microtome and then stained with a modified Trichrome stain.

The stomach contents of the Midway fish were examined. The pulverized condition of the food precluded analyses by weight, volume, or by enumeration of each food item. Consequently, the percentage of all specimens containing each food was determined.

Statistical analyses were conducted using the Statistical Analysis System (SAS), Version 6.03. A general linear model (GLM) was used to test correlations between the mean proportional length (e.g. length of uncoiled intestine/standard length) of the small intestine, large intestine, and total gastrointestinal (GI) tract and the feeding mode (herbivorous, omnivorous, and planktivorous). The GLM procedure was appropriate since normality was not assumed and the data sets were not balanced. The non-parametric Wilcoxon Rank Sum Test was used to test the significance of differences between the means of two populations, since normality was not assumed, and the sampled populations were continuous and the samples independent. For both

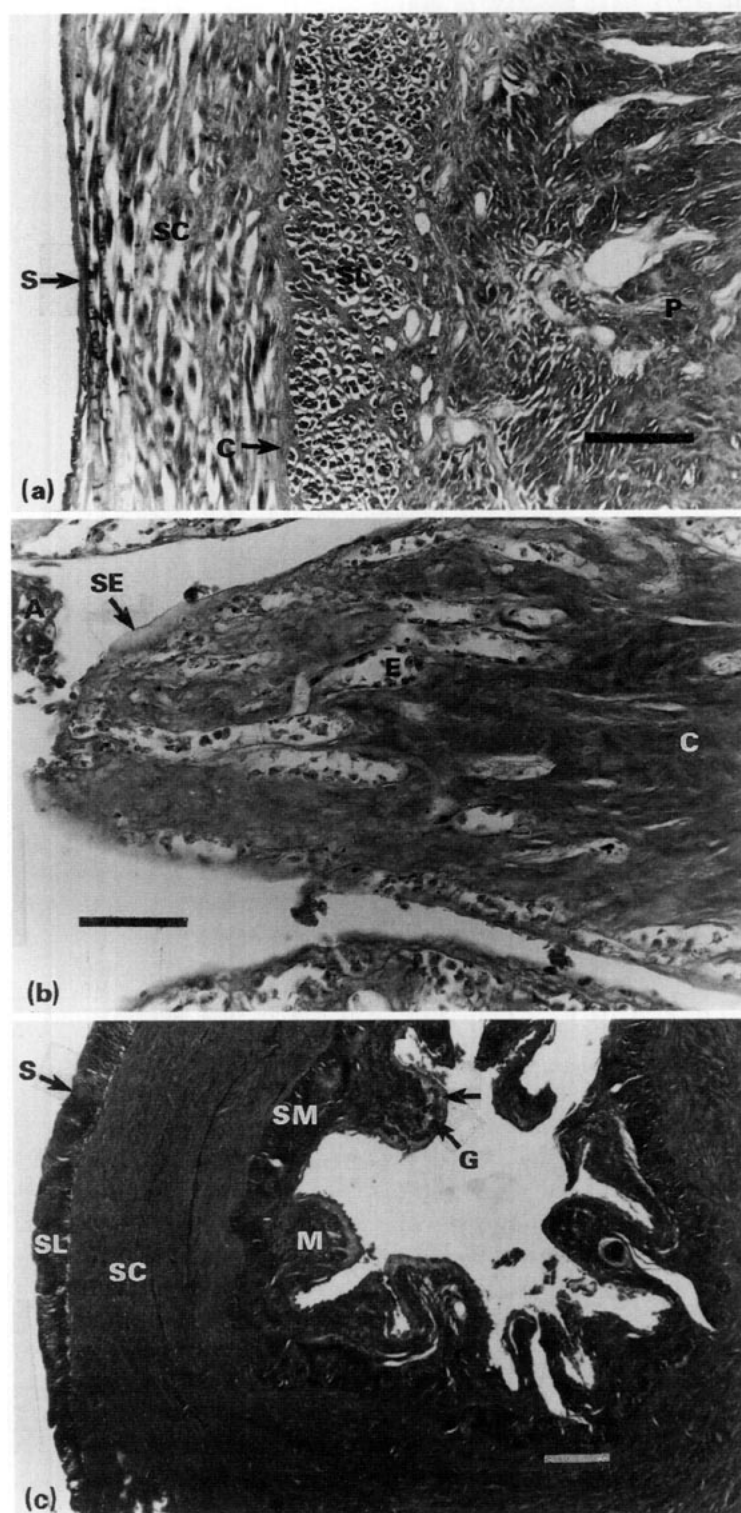
TABLE I. The mean proportional length [length of GI component/standard length (S.L.)] of the small intestine (SI), large intestine (LI), and total gastrointestinal tract (GI) by species according to feeding mode

Species	n	S.L. (mm)	Feeding mode	Mean proportional length		
				SI	LI	GI
<i>Centropyge bispinosus</i>	2	60.7, 64.9	Herbivore	5.22	0.39	5.75
<i>Centropyge flavissimus</i>	2	59.9, 77.8	Herbivore	3.68	0.34	4.17
<i>Centropyge multifasciatus</i>	3	57.4-72.9	Herbivore	1.64	0.33	2.20
<i>Centropyge vrolik</i>	2	72.4, 72.8	Herbivore	3.03	0.28	3.58
			Mean values =	3.20	0.33	3.73
<i>Apolemichthys xanthurus</i>	2	70.3, 102.0	Omnivore	3.63	0.31	4.14
<i>Chaetodontoplus mesoleucus</i>	2	72.2, 89.7	Omnivore	1.99	0.33	2.63
<i>Holacanthus tibicens</i>	2	69.4, 76.7	Omnivore	2.61	0.40	3.31
<i>Holacanthus venustus</i>	1	56.3	Omnivore	2.29	0.35	2.89
<i>Pomacanthus arcuatus</i>	2	85.8, 120.7	Omnivore	2.95	0.55	3.77
<i>Pomacanthus imperator</i>	2	69.8, 91.2	Omnivore	2.45	0.38	3.11
<i>Pomacanthus maculosus</i>	2	75.2, 85.1	Omnivore	2.27	0.35	2.83
<i>Pomacanthus paru</i>	2	77.3, 112.0	Omnivore	3.56	0.55	3.91
<i>Pomacanthus semicirculatus</i>	2	108.2, 125.3	Omnivore	1.08	0.41	1.97
<i>Pygoplites diacanthus</i>	2	83.1, 117.7	Omnivore	2.73	0.34	3.33
			Mean values =	2.57	0.40	3.20
<i>Genicanthus bellus</i>	1	99.3	Planktivore	2.16	0.29	2.79
<i>Genicanthus caudovittatus</i>	1	102.0	Planktivore	1.67	0.37	2.43
<i>Genicanthus lamarck</i>	2	80.1, 120.8	Planktivore	2.14	0.34	2.70
<i>Genicanthus melanospilos</i>	4	68.2-90.6	Planktivore	1.58	0.30	2.31
<i>Genicanthus personatus</i>	7	123.8-160.1	Planktivore	2.33	0.38	3.13
<i>Genicanthus semifasciatus</i>	4	99.7-190.3P	planktivore	2.16	0.31	2.90
<i>Genicanthus spinus</i>	1	176.1	Planktivore	2.01	0.23	2.75
<i>Genicanthus watanabei</i>	1	111.6	Planktivore	1.70	0.36	2.36
			Mean values =	2.05	0.33	2.78

the GLM procedure and the Wilcoxon Rank Sum Test, the 0.05 level of significance was used.

III. RESULTS

There was a significant correlation in the mean proportional length of the small intestine, large intestine, and total gastrointestinal tract between the three classes of pomacanthids based on feeding mode ($P < 0.05$ GLM) (Table I). There was a significant difference in the mean proportional length of the small intestine between the omnivorous and planktivorous species and between the herbivorous and planktivorous species ($P < 0.05$ Wilcoxon Rank Sum Test). There was a significant difference in the mean proportional length of the large intestine between the herbivorous and omnivorous species and between the omnivorous and planktivorous species ($P < 0.05$). Only between the omnivorous and planktivorous species was there a significant difference in the mean proportional length of the gastrointestinal tract ($P < 0.05$).



MORPHOLOGY

In *G. personatus*, the oesophagus is a relatively large and thick-walled organ. The anterior portion of the stomach is thin-walled and sac-like, becoming progressively thicker posteriorly, ending in seven pyloric caecal lobes followed by the small and large intestine. The latter is sac-like and thick-walled. In adult females with well-developed ovaries, a layer of fatty tissue ran along the small intestine and stomach.

Although the basic anatomy of the GI tract varied considerably, only *Genicanthus* spp. exhibited oesophageal papillae. To date, all eight known species of *Genicanthus* have been found to contain oesophageal papillae.

HISTOLOGY

The serosa of the oesophagus is made up of a thin layer of simple squamous epithelial tissue followed by a thick muscularis composed of a single layer of striated circular and longitudinal muscle [Fig. 1(a)], the two layers separated by a thin layer of connective tissue. A distinct submucosal layer was not observed. The papillae which comprise the mucosa portion of the oesophagus, are composed of connective tissue [Fig. 1(b)]. Although no mucus or goblet cells were associated with the papillae, oesophageal glands were interspersed throughout each papilla [Fig. 1(b)], which was enclosed by a thin layer of squamous epithelium [Fig. 1(b)].

The serosa of the stomach consists of epithelial tissue followed by a thinner muscularis as compared to the oesophagus [Fig. 1(c)]. The muscularis is arranged opposite that of the oesophagus with smooth longitudinal muscle outside the smooth circular muscle [Fig. 1(c)]. The latter is considerably thicker than the longitudinal layer, probably due to its involvement in contractions and peristalsis. The submucosa is made up of primarily connective tissue followed by the mucosa, where now goblet and/or mucus cells appear [Fig. 1(c)]. The lining of both the small and large intestine is similar to that of the stomach.

ULTRASTRUCTURE

The oesophagus of *G. personatus* specimens preserved shortly after being collected, revealed papillae arranged in a radial fashion, very abundant, and filling the lumen [Fig. 2(a)]. The larger papillae are conical in shape, while some of the smaller ones are forked or polypoid [Fig. 2(b)]. Whether these small papillae remain polypoid as they develop is not known, but large polypoid papillae were never observed. The papillae vary from 0.38 to 2.40 mm in length and 0.12 to 1.18 mm in width. Those in the anterior portion of the oesophagus are smaller and more abundant than those in the mid and posterior sections. The latter appear similar to each other in both size and abundance. The large papillae are oriented or curved slightly in a posterior direction relative to the oesophagus. The smaller papilli in the anterior section are perpendicular to the

FIG. 1. The digestive tract of *G. personatus*: (a) cross-section of the oesophagus, S, serosa; SC, striated circular muscle; SL, striated longitudinal muscle; C, connective tissue; P, papillae; modified Trichrome stain; scale bar, 0.2 mm. (b) Cross-section of an oesophageal papilla, A, an artifact resulting from histological sectioning; C, connective tissue; E, oesophageal gland; SE, squamous; a piece of tissue epithelium; modified Trichrome stain; scale bar, 0.2 mm. (c) Cross-section of the stomach, S, serosa; SL, smooth longitudinal muscle; SC, smooth circular muscle; SM, submucosa; M, mucosa; G, goblet/mucus cells; modified Trichrome stain; scale bar, 0.25 mm.

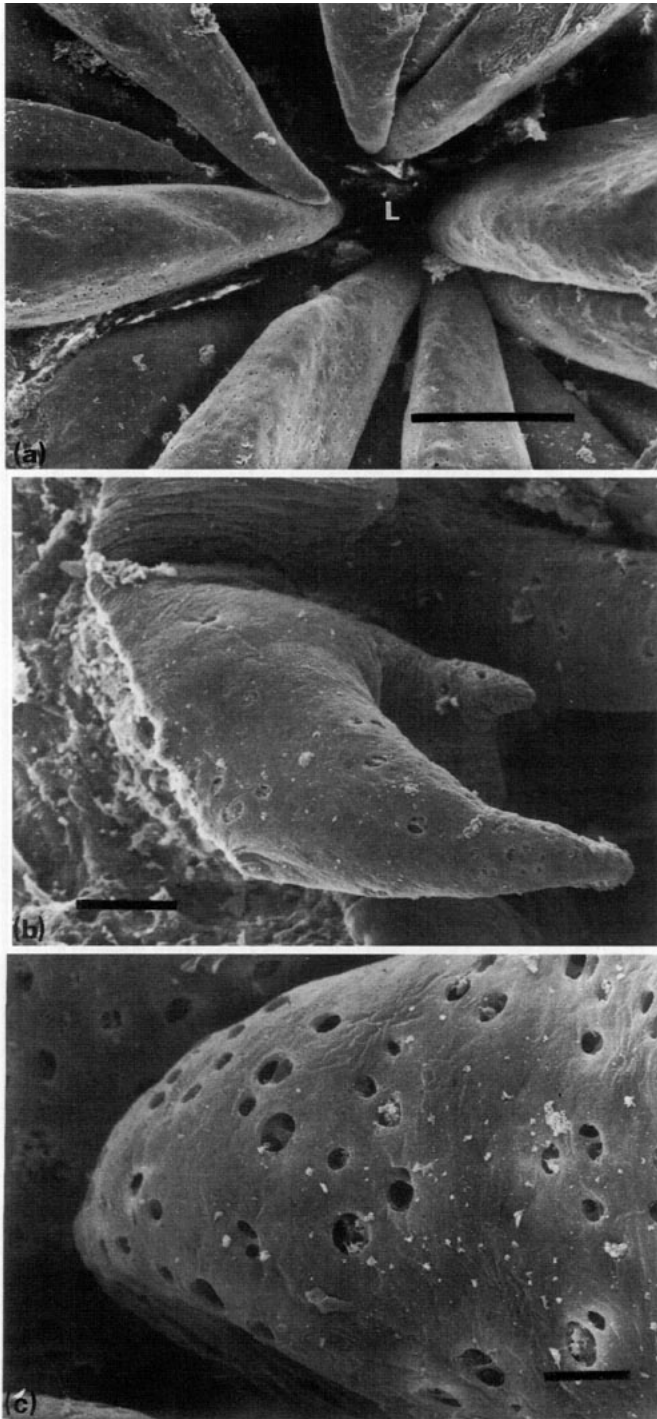


FIG. 2. Oesophageal papillae of *G. personatus*: (a) cross-section of the oesophagus, L, lumen; scale bar, 1 mm. (b) A polypoid oesophageal papilla; scale bar, 100 μ m. (c) Pores of the oesophageal glands; scale bar, 50 μ m.

oesophageal wall. The size or arrangement of the papillae does not differ between mature male and female specimens.

Evenly distributed pores, 2.8–45.2 μm in diameter (most <25 μm) penetrated the wall of each papilla [Fig. 2(c)] regardless of papilla size or position within the oesophagus. These pores are part of the oesophageal glands, and did not differ in size or density between the sexes regardless of age, or position within the oesophagus.

DIET

Food particles were homogeneous throughout the length of the GI tract. *Genicanthus personatus* consumed both animal and plant material (Table II), including algae, copepods, diatoms, and eggs, but plant material dominated by volume. Echinoderms and sponges were represented only by spicules.

IV. DISCUSSION

In 20 different acanthurids, Jones (1968) discovered that grazers had the longest, browsers an intermediate, and zooplankton feeders the shortest gastrointestinal tract. The pomacanthids in the present study have similar diets (Allen, 1979) to the acanthurids examined by Jones (1968), so it was expected that their gastrointestinal length would reflect foraging method/diet similarly. There was a statistical difference between the omnivores and planktivores in the lengths of the small intestines, large intestines, and the total gastrointestinal tract, but not between the herbivores species and either the omnivores or planktivores. However, the type of preservative, length of preservation, and age of the specimen might explain this in part. For example, specimens shrink in formalin and ethanol, but more so in ethanol (Engel, 1974; Fowler & Smith, 1983; Glenn & Mathias, 1987; Hay, 1982; Kruse & Dalley, 1990; Stobo, 1972; Theilacker, 1980), and may change in body proportions when transferred to isopropanol. Unfortunately, no studies have tested the long term effects (>11 mo) of preservation on tissue shrinkage. These sources of error are minimized when specimens are dissected and measured in the field. Secondly, age may affect the results: do pomacanthids change diet with age? If so, does the gastrointestinal tract alter histologically and/or morphologically? Such questions need answering to understand better the ecological separation of pomacanthids based on diet and foraging methods.

Of the 20 acanthurids examined by Jones (1968), only two, *Acanthurus thompsoni* and *Naso hexacanthus* (Bleeker, 1855), are considered zooplanktivores. Instead of the longitudinal folds in the lining of the oesophagus and cardiac stomach typical of the other species, both *A. thompsoni* and *N. hexacanthus* have regular rows of thorn-like papillae (Jones, 1968). However, the papillae of *Genicanthus personatus* are arranged radially filling the entire lumen, and are considerably larger and finger-like. Pointing posteriorly, they may keep food items moving down the oesophagus and reduce food loss by regurgitation (Frazier, pers. comm.). Since the papillae have no cornified tip as do those of turtles, it is unlikely that they impale and/or shred large food items, but may impale soft, gelatinous prey. With no blood vessels or capillaries, the papillae are unlikely to take up nutrients, but they may process noxious prey items (i.e.

TABLE II. GI contents of four *Genicanthus personatus* specimens (S.L. 152–175 mm)

Food item	Percentage of fish containing each item
Algae fragments	
Colonial	100
Filamentous	100
Unicellular	100
Bryozoan fragment	25
Crustacea	
Copepoda	100
Decapoda	25
Fragments	75
Ostracoda	25
Detritus	75
Diatoms	
<i>Nitzshia</i> spp.	100
Unidentified	100
Dinoflagellates	25
Echinodermata	
Spicules	100
Unidentified larva	25
Egg	100
Fish scales	
Ctenoid	25
Cycloid	25
Hydrozoa	
Siphonophore (?)	25
Hydromedusa	25
Polychaeta	
Trochophore larvae	25
Porifera	
Calcareous sponge spicules	100
Radiolarians/Radiolarian spines	100
Urochordata	
<i>Doliolum</i> spp. (?)	25
Unidentified	25

spiny and stinging zooplanktors), so protecting the oesophagus from physical and immunological damage (Frazier & Polunin, pers. comm.). For example, all sea turtles, some of which feed heavily on jellyfish, have oesophageal papillae (Frazier, pers. comm.), and these papillae may 'disarm' or discharge the nematocysts prior to disassimilation in the stomach.

Among non-pomacanthid species, *Caesio cuning* has oesophageal papillae that most resemble those of *G. personatus*, being arranged radially, filling the lumen of the oesophagus, pointing posteriorly, and largest in the mid-oesophageal region. These differ in being proportionally as large or larger than those of *G. personatus*, and are not smooth and finger-like, but have four flattened sides that come to a point (like a whittled stick). The presence of oesophageal papillae in *C. cuning* coincides with their midwater zooplanktivory (Carpenter, 1988).

The particle size/consistency of food items throughout the gastrointestinal tract (oesophagus to the intestines) was similar, suggesting that most trituration and catabolic activity may occur in the pharyngeal apparatus and oesophagus. Histological and SEM examinations revealing abundant gastric and/or mucus-secreting oesophageal glands support this idea. In addition, goblet or mucus cells associated with the stomach mucosa indicate catabolic activity. However, since the food consistency in the intestines does not differ from that in the oesophagus, the catabolic activity in the stomach would appear to be negligible.

The oesophageal papillae appear to be a generic morphological specialization of the *Genicanthus* gastrointestinal tract which enables use of food unavailable to other pomacanthids, and distinguishes them ecologically. Additional field work is necessary to better understand the diet of all *Genicanthus* species and what role(s) the papillae play. Large scale studies are necessary to determine other ecological, behavioural, social, and morphological variables that separate this large and diverse group of fishes ecologically.

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