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THE CEPHALIC LATERALIS SYSTEM OF CARDINALFISHES (PERCIFORMES: APOGONIDAE) AND ITS APPLICATION TO THE TAXONOMY AND SYSTEMATICS OF THE FAMILY

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ABSTRACT

The Apogonidae is one of the most speciose coral reef fish families. Members of this family are found on every coral reef in all tropical and subtropical waters worldwide and yet, despite this apparent ubiquity, the systematic relationships of its species are poorly understood. Few studies have attempted to address the question of the family's evolutionary history and, as a result, little is known about the evolution of this major group of coral reef fish. This dissertation addresses this shortcoming by using characters derived from the skeleton, external morphology, and cephalic lateralis system to produce a cladistically derived hypothesis of the evolutionary relationships among the genera and subgenera of the family Apogonidae. The cephalic lateralis of the type species of each apogonid genus and subgenus was described and illustrated, and comments were made on the variability of this system within the supra-specific taxon to which the species belongs. The cephalic lateralis of apogonids is a highly diverse system; much variation exists within and among the family's genera and subgenera. Cladistic analyses resulted in a number of well-resolved, but not well-supported (as indicated by the consistency and retention indices), equally parsimonious cladograms. Homoplasies aside, all of the cladograms suggest that the apogonid genera *Apogon* sensu lato and *Pterapogon* sensu lato are not monophyletic as they are currently defined. The results of this research highlight the need for revision of the family's classification in order more accurately reflect the group's phylogenetic history.

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CHAPTER 1. INTRODUCTION TO THE APOGONIDAE

The Apogonidae, commonly known as cardinalfishes, constitute one of the largest coral-reef fish families. The family occurs on all coral reefs worldwide, reaching its greatest diversity on the reefs of the Indo-Pacific (Randall et al., 1990a; Allen and Robertson, 1994; Allen and Morrison, 1996; Bellwood, 1996; Sale, 2002). Cardinalfishes are also found in a wide range of non-reef habitats, from the deep ocean to the estuaries and freshwater streams of numerous oceanic islands (Springer, 1982; Tinker, 1982; Gon, 1986; Potter et al., 1990). Although members of the family are found in a diversity of habitats, individual species are restricted to relatively narrow ecological zones (Randall et al., 1990a; Allen and Robertson, 1994; Allen and Morrison, 1996). Cardinalfishes are generally nocturnal, hiding by day and emerging at night to feed. Therefore, a visual reef survey during daylight hours underestimates the great numbers of individuals that may be present (Vivien, 1975; Chave, 1978; Greenfield and Johnson, 1990; Böhlke and Chaplain, 1991; Marnane, 2000; Greenfield, 2003).

Cardinalfishes are characterized by having two separate dorsal fins, the first with 6-8 spines, and the second with one spine and 8-14 rays; an anal fin with two spines, only the first of which is on the first pterygiophore; scales that are ctenoid, cycloid, or absent; seven branchiostegal rays; and usually 24 vertebrae, 10 pre-caudal and 14 caudal (Nelson, 1994). Their common name suggests that they display the red coloration of a cardinal's vestments; and such is true for many of the earliest described apogonid species (Burgess and Axelrod, 1973; Hoover, 1993; Allen and Robertson, 1994; Allen and Morrison, 1996). However, as our knowledge of the family has grown, as has the list of its species, this name has become a less than accurate qualifier of the family's color. A wide range of colors, including yellow, brown, black, and white, are also displayed by apogonids (Randall et al., 1990a). Cardinalfishes are relatively small. A few species reach a maximum total length near 20 cm, but most grow to only about 10 cm (Randall et al., 1990a; Allen and Robertson, 1994).

In spite of their small size, cardinalfishes play a significant role in the food chains of coral reef ecosystems (Vivien, 1975; Shao and Chen, 1986). Their importance is based on a combination of their large numbers and relatively rapid turnover rate (Burgess and Axelrod, 1973). Apogonids are carnivores; most species consume zooplankton or benthic Crustacea, although small fishes may also be eaten (Hobson, 1974; Vivien, 1975; Shao and Chen, 1986; Allen and Morrison, 1996; Kume et al., 1999). Within the reef ecosystem, cardinalfishes function not only as predators, but also as prey for the reef's larger piscivorous fishes, and are thus integral in the transfer of nutrients between trophic levels (Vivien, 1975; Chave, 1978; Marnane, 2000). Marnane (2000) has shown that cardinalfishes tend to use a single location as their diurnal resting position throughout their lifetime. He also demonstrated that cardinalfishes have the ability to return selectively to their hiding locations if experimentally displaced distances up to 2 km away. This behavioral persistency, particularly when the group's typically high densities are taken into consideration, results in cardinalfishes providing a substantial and reliable source of energy and nutrients for a reef's piscivore and detritivore communities (Marnane, 2000).

Mouth brooding has been documented in all apogonid species for which their reproductive behavior has been investigated (Barlow, 1981; Leis and Rennis, 1984). This behavior is rare among marine fishes, with the Opistognathidae and the Arridae being the only other marine families known to exhibit this behavior (Randall et al., 1990a; Randall, 1998). During spawning the female releases a large egg mass consisting of hundreds or even thousands of eggs (Garnaud, 1962; Neira, 1991; Allen, 1993). Immediately following fertilization, the male scoops the egg mass into its mouth, where it is retained until hatching. The larvae of most cardinalfishes measure 2-4 mm and are planktonic for a number of weeks before settlement and transformation to the juvenile stage (Randall et al., 1990a; Allen and Morrison, 1996). *Pterapogon kauderni* Koumans, 1933 is unique among apogonids in that the embryos develop directly into juveniles; the free-living larval stages are bypassed and the embryos hatch, measuring about 6 mm at post-flexion stages (Vagelli, 1999). As would be predicted from this pattern of development, *P. kauderni* produces much larger, although fewer, eggs than do most other apogonid species (Garnaud, 1962; Charney, 1976; Neira, 1991; Allen, 1993; Vagelli, 1999). A few other apogonids, e.g., *Apogon rueppellii* Günther, 1859, *Cheilodipterus macrodon* (Lacepède, 1802), and *Vincentia conspersa* (Klunzinger, 1872), are also characterized by low fecundity and large egg size, suggesting that they may also exhibit direct development, but no studies have tested this hypothesis (Vagelli, 1999).

Numerous studies have been done on apogonid taxonomy (Smith, 1961; Randall et al., 1985; Fraser, 1998; Gon, 2000, and additional references within this chapter), ecology (Hobson, 1974; Vivien, 1975; Chave, 1978; Greenfield, 2003), reproductive biology (Garnaud, 1950; Fishelson, 1970; Smith et al., 1971; Charney, 1976; Usuki, 1977; Kuwamura, 1983, 1985; Okuda, 1999a, 1999b; Kume et al., 2000; Okuda, 2001; Kume et al., 2002; Kolm, 2002; Lahnsteiner, 2003), and life history (Leis and Rennis, 1984; Neira, 1991; van Zwieten, 1995; Kume et al., 1998). But few studies have attempted to address the question of the family's evolutionary history. As a result, little is known about the evolution and phylogenetic relationships of this major group of coral reef fish.

This dissertation addresses this shortcoming by using data derived from the cephalic lateralis system, in conjunction with preexisting morphological and osteological data (Fraser, 1972), to produce a cladistically derived hypothesis of the evolutionary relationships among the genera and subgenera of the family Apogonidae. Chapter 2 presents detailed descriptions of the cephalic lateralis system of each genus and subgenus in the family. Chapter 3 presents the results of the cladistic analysis of the data matrix derived from Fraser's (1972) data. Chapter 4 presents an examination of evolutionary trends across the cephalic lateralis systems of the examined taxa and the results of the cladistic analysis of the combined data matrix composed of Fraser's (1972) morphological and osteological data and the characters generated from the examination of the fishes' cephalic lateralis systems. Chapter 5 concludes the dissertation with a summary of the conclusions drawn, their broader implications, and recommendations for future work. The results of this evolutionary study of the Apogonidae not only increase our knowledge of the cephalic lateralis and its morphology in the family but also suggest that the current classification of the apogonid genera is an inaccurate representation of the family's evolutionary history.

Apogonid Classification and Phylogeny

The Apogonidae belong to the superorder Acanthopterygii, which are characterized by the presence of (1) a maxillo-rostroid ligament, (2) a large, median supraoccipital bearing a spina occipitalis, (3) a modification of the posttemporalepioccipital association, such that the dorsal limb of the posttemporal is tightly bound to the neurocranium by connective tissue fibers, and (4) the presence of an ethmovomerine complex formed from the articulation of anterior extensions of the lateral ethmoids and the lateral processes of the vomer (Stiassny, 1986). The Acanthopterygii encompass three series, the Mugilomorhpa, Atherinomorpha, and Percomorpha, and 13 orders (Nelson, 1994). Various suggestions have been made about the interrelationships among the superorder's major taxa, including disagreement on the composition of the various series. Placement of the orders Stephanoberyiformes, Zeiformes, and Beryciformes within the Acanthopterygii is uncertain; they are either positioned as basal to the Percomorpha (Johnson and Patterson, 1993) or included within the Percomporpha as its more primitive lineages (Stiassny and Moore, 1992; Nelson, 1994).

The Apogonidae belong to the percomorph order Perciformes. The Perciformes are the most diverse order of fishes and largest order of vertebrates. The position of the Perciformes within the Percomorpha is uncertain, as are the relationships among the higher taxa within the order. Johnson and Patterson (1993) presented evidence that the Perciformes may represent an unnatural taxon as it is currently defined, and may be monophyletic only if its limits are expanded to include the orders Scorpaeniformes, Pleuronectiformes, and Tetraodontiformes. The Perciformes currently contains 18 suborders and 148 families (Nelson, 1994). The Apogonidae, with more than 250 species, is the eighth most speciose family in the order (Randall et. al., 1990a; Allen and Robertson, 1994; Nelson, 1994; Allen and Morrison, 1996). The Apogonidae is placed into the largest perciform suborder, the Percoidei. It has been suggested that the Percoidei represent the group from which all other perciform groups are derived (Nelson, 1994). The monophyly of a number of the suprafamilial perciform taxa is uncertain, as many of the order's suborders, super-families, and families are defined on the basis of plesiomorphic characters (Johnson, 1984; Nelson, 1994).

The 23 apogonid genera are placed in two subfamilies, the Apogoninae and the Pseudaminae (Table 1). Johnson (1993) identified five characters shared by the fishes in the Apogonidae. Three of these characters are related to the unusual configuration of the dorsal gill-arch elements in apogonids. These are: 1) the absence of a direction articulation between the second epibranchial and second pharyngobranchial; 2) the third epibranchial is expanded and the fourth is narrow; and 3) the fourth upper pharyngeal toothplate is small and lacks a fourth pharyngobranchial cartilage. Johnston noted that among the percoid fishes with two separate dorsal fins, the distal radial associated with the last spine of the first dorsal fin in apogonids is comparatively short; so short, that the proximal-middle element nearly contacts the base of the spine. The last shared character Johnston identified is the presence of horizontal and vertical rows of superficial neuromasts, associated with the lateralis system, on the head and body of apogonids. This regular arrangement of sensory papillae had previously been thought to characterize only the pseudamine apogonids. Johnson observed their existence in a number of apogonine genera, and suggested it as a unifying character for the family.

Table 1. Classification of the Apogonidae and geographic ranges of apogonid genera and subgenera. The data presented are largely based on Fraser (1972, 1973), Randall et. al. (1985), Randall and Smith (1988), Fraser and Struhsaker (1991), Gon (1993, 1996), Nelson (1994), Baldwin and Johnson (1999), Vagelli and Erdmann (2002), and Gon and Randall (2003).

Taxon	Geographic Ranges
Class Actinopterygii	
Superorder Acanthopterygii	
Order Perciformes	
Suborder Percoidei	
Family Apogonidae	
Subfamily Apogoninae	
Genus *Apogon* Lacepède, 1801	
Subgenus *Apogon* Lacepède, 1801	Circumtropical and -subtropical
Subgenus *Brephamia* Jordan & Jordan, 1922	Philippine Islands to Indonesia
Subgenus *Jaydia* Smith, 1961	Indo-west Pacific
Subgenus *Lepidamia* Gill, 1863	East Africa to Philippine Islands
Subgenus *Paroncheilus* Smith, 1964	Gulf of Guinea to western tropical Atlantic
Subgenus *Pristiapogon* Klunzinger, 1870	East Africa to Hawaii
Subgenus *Pristicon* Fraser, 1972	Australia to Marshall Islands
Subgenus *Ostorhinchus* Lacepède, 1802	East Africa to Hawaii
Subgenus *Yarica* Whitley, 1930	Indonesia to Philippine Islands
Subgenus *Zapogon* Fraser, 1972	Caribbean Sea and Hawaii
Subgenus *Zoramia* Jordan, 1917[b]	East Africa to Guam
Genus *Apogonichthys* Bleeker, 1854[a]	East Africa to Hawaii
Genus *Archamia* Gill, 1863	Indo-Pacific

Table 1. Continued.

Taxon	Geographic Ranges
Genus *Astrapogon* Fowler, 1907	Western Tropical Atlantic
Genus *Cercamia* Randall & Smith, 1988	Eastern Central Pacific
Genus *Cheilodipterus* Lacepède, 1801	Indo-Pacific
Genus *Coranthus* Smith, 1961	Indo-West Pacific
Genus *Foa* Jordan & Evermann, 1905	East Africa to Hawaii
Genus *Fowleria* Jordan & Evermann, 1903	East Africa to Marshall Islands
Genus *Glossamia* Gill, 1863	Australia and New Guinea
Genus *Holapogon* Fraser, 1973	Gulf of Oman and the southern Arabian coast
Genus *Lachneratus*Fra ser & Struhsaker, 1991	Hawaii to Indian Ocean
Genus *Neamia* Smith & Radcliffe, 1912	East Africa to Philippine Islands
Genus *Phaeoptyx* Fraser & Robins, 1970	Gulf of Guinea to western tropical Atlantic
Genus *Pterapogon*	
Subgenus *Pterapogon* Koumans, 1933	Banggai Islands
Subgenus *Quinca* Mees, 1966	Australia
Genus *Rhabdamia*	
Subgenus *Bentuviaichthys* Smith, 1961	Indo-Pacific
Subgenus *Rhabdamia* Weber, 1909	East Africa to Marshall Islands
Subgenus *Verulux* Fraser, 1972	East Africa to Marshall Islands
Genus *Siphamia* Weber, 1909	East Africa to Marshall Islands
Genus *Sphaeramia* Fowler & Bean, 1930	East Africa to Philippine Islands
Genus *Vincentia* Castelnau, 1872	Southern Australia to Tasmania
Subfamily Pseudaminae	
Genus *Gymnapogon* Regan, 1905	East Africa to Marshall Islands
Genus *Paxton* Baldwin & Johnson, 1999	Northwestern Australia
Genus *Pseudamia* Bleeker, 1865	Indo-Pacific
Genus *Pseudamiops* Smith, 1954	East Africa to Hawaii

However, the validity of the presence of superficial neuromasts as a character uniting the apogonids is questionable. My research shows that superficial neuromasts are absent from some apogonids and their homology is questionable among those species that do possess them. As Johnson (1993) stated, free neuromasts associated with the lateralis system are present in many apogonine genera in addition to the pseudamine genera. They are not, however, present in all apogonine genera, nor are they present in the grid-like pattern characteristic of the pseudamine genera and therefore cannot be considered among the synapomorphies uniting the family. The size, shape, and distribution of these papillae also suggest that they may not be homologous among all apogonid taxa, although detailed observation of the ontogeny of the system is necessary to confirm this hypothesis.

Although the characters identified by Johnson (1993) have been referred to as synapomorphies of the Apogonidae, they are not unique to the family, as each of them is shared with at least one other perciform family (Baldwin and Johnson, 1999). These characters, in light of the dearth of information regarding the evolutionary relationships among the perciform families, have been used to help identify groups with potential evolutionary ties to the Apogonidae. Species in the family Kurtidae share four of the apogonid synapomorphies, including the three characteristics unique to the dorsal gill arch configuration and the presence of a crosshatch pattern of sensory papillae on the head and body (Johnson, 1993). Johnson (1993) also suggested that similarities exist in the microstructure of apogonid and kurtid eggs, further supporting a hypothesized close evolutionary relationship between the taxa. The eggs of both groups possess filaments around the micropyle that function to bind the eggs into a mass, thereby facilitating the oral brooding that is characteristic of apogonids and the attachment of the egg mass to the supraoccipital hook in kurtids.

The presence of two spines in the anal fin has also been used, because it is less common in percoid fishes than the typical three-spine morphology, to either unite various taxa within the Apogonidae or to suggest relationships between other groups and the Apogonidae (Smith, 1961; Tominaga, 1968; Fraser, 1972). On the basis of this character, the Epigonidae had been included within the Apogonidae, but as a separate subfamily, the Epigoninae (Smith, 1961; Fraser, 1972; Johnson, 1984; Gon, 1985). However, examination of internal morphology revealed that the association between the anal-fin spines and their supporting pterygiophores is different in these two groups and thus, this character state is not homologous in these taxa (Johnson, 1984; Baldwin and Johnson, 1999). In percoids possessing three anal-fin spines, the first two spines are in supernumerary association with the first pterygiophore, and the third spine is in serial association with the same pterygiophore. In epogonines, the first two anal-fin spines are also in supernumerary association with the first pterygiophore, but the third fin-element has not developed into a spine. In contrast, only the first anal-fin spine in apogonids is in supernumerary association with the first pterygiophore. The second anal fin spine is serially associated with the first pterygiophore, suggesting that the first anal fin spine of primitive percoids has been lost in this group. Thus, the two-spined condition of the anal fin in these two groups is a product of convergence, and not shared ancestry (Johnson, 1984).

As is the case with the higher perciform taxa, the evolutionary relationships among the apogonid species are also poorly understood. Fraser (1972) completed what is to date, the most comprehensive osteological study of the family. His study preceded the widespread acceptance and use of cladistic methods to elucidate phylogenetic history. He anticipated that a greater understanding of the phylogenetic relationships within the Apogonidae would result from detailed study of previously hypothesized natural groupings. He suggested that osteological characters would be the best source of phyletic information. By comparing apogonid, lower percoid, and beryciform osteological units, he hypothesized apogonid evolutionary history and character transformation. Although his work to establish the evolutionary history of osteological units via comparison with outgroup forms appears cladistic in nature, he did not apply cladistic methods to analyze his data. In terms of inter-familial relationships, Fraser ascertained differences between apogonid and beryciform osteology and hypothesized that the beryciform character states were more ancestral.

Fraser did not always, however, accurately determine the intra-familial polarity of evolutionary change when more than one state existed for a given character. Although he used beryciform osteological data and meristics to define primitive character states, he did not always adhere to the suggested trends when providing direction to character evolution. For example, if the serrated condition of the opercle and preopercle in berycoids is assumed to be primitive, a smooth opercle and preopercle should be considered more derived. Fraser assigned the correct polarity to the loss of opercular spination but incorrectly assigned the polarity of preopercular serration. He designated contradictory conditions, the loss of serrations on the preopercular edge and the gain of serrations along the preopercular ridge, as derived (Gon, 1996).

Instead of using cladistic methodology to estimate the degree of relatedness among genera, Fraser based his hypothesized intergeneric relationships on the degree of physical similarity between taxa. He referred the apogonid genera to two phenetic groups on the basis of the following characteristics: retention or loss of the basisphenoid, presence or absence of the supramaxilla, morphology of the caudal fin, and degree of cryptic coloration. Within these groups, Fraser placed the genera in the direction of one of the two extremes, between the more "advanced" and "primitive" genera with which they shared the largest number of characters. He then collated these sequences into a phenogram. Interpretational difficulties, such as character reversals, parallel evolution of hypothetically advanced characters, and independent losses of characters within multiple lineages, plagued Fraser's resultant phylogeny. He found that the evolutionary path was more obvious for some character sets than for others; and often, character sets suggested conflicting evolutionary histories.

The failure to define taxa on the basis of synapomorphic characters lies at the root of Fraser's problematic analysis. This is particularly apparent in the large and diverse genus *Apogon* Lacepède, 1801. Fraser defined the genus based on the following characters: five free hypurals, three epurals, a well-developed basisphenoid, a serrate posterior preopercular edge, no supramaxilla, ctenoid scales, a shelf on the third infraorbital, a complete pored lateral line, nine segmented second-dorsal fin rays, and eight segmented anal fin rays. These characters are symplesiomorphic in nature (Gon, 1995). The first eight character states are shared with the berycoids and primitive percoids, and Fraser was unsure of the degree of primitiveness of the last two characters.

The probability of creating unnatural (i.e., non-monophyletic) taxa and taxonomic-hierarchies increases when plesiomorphic characters are used to define them. In such a classification, when a character undergoes a change in multiple taxa, it often appears anomalous in the evolutionary scheme, and a mosaic distribution of character states results. Such is the case for the genus *Apogon.* Four subgenera do not conform to the distinguishing characters of the genus: *Yarica* species retain the supramaxilla; *Paroncheilus* species have cycloid scales; *Zoramia* species have lost the infraorbital shelf; and species in *Brephamia* have incomplete lateral lines. Although Fraser did not address this weakness of his defining character set, he recognized that even after his revisionary work, *Apogon* might still represent an unnatural taxon.

Fraser determined the subgeneric classification of *Apogon* using the same characters he used to distinguish the apogonid genera. He divided the genus into 10 subgenera: *Apogon*, *Brephamia*, *Lepidamia*, *Nectamia*, *Paroncheilus*, *Pristiapogon*, *Pristicon*, *Yarica*, *Zapogon*, and *Zoramia.* When evaluated within the context of the genus, eight of the subgenera may be defined by one unique character. *Apogon* is the only subgenus with no uroneurals. *Brephamia* is the only subgenus with an incomplete lateral line. *Lepidamia* has much smaller scales, and thus a significantly higher number of them in the lateral line, than do other *Apogon* subgenera. *Paroncheilus* is characterized by the presence of cycloid, not ctenoid, scales. *Pristiapogon* is the only subgenus with the intercalary facet barely on the otic bulla. The presence of a supramaxilla distinguishes *Yarica. Zapogon* possesses a smooth ceratohyal. *Zoramia* is distinguishable by the significantly longer first-dorsal fin spines. *Pristicon* and *Nectamia* are the only two subgenera not defined by one unique (within *Apogon*) character. The two subgenera are distinct from other *Apogon* subgenera because they lack the previously mentioned unique characters, and possess two or three predorsals and one pair of uroneurals. The number of epipleurals distinguishes them from each another: *Pristicon* has epipleurals on all but the last pair of ribs, whereas *Nectamia* has epipleurals on all but the last two pairs of ribs.

The characters used to define a genus should be different from those used to diagnose its subgenera; and the states of the generic characters should be consistent within each subgenus. Thus, the generic characters have no taxonomic utility at the subgeneric level. So although it is possible to distinguish between the proposed *Apogon* subgenera, it is not possible to say that they are all groups of the same taxonomic rank. Nor is it possible, because of the weak definition of *Apogon* itself, to conclusively state that they are all subgenera of this genus.

Despite these problems, Fraser's work has been heavily relied upon as a source of information for defining and distinguishing apogonid genera and subgenera. The classification has remained as defined by Fraser, with little modification through the subsequent years. In order to expedite species identification, authors have created diagnostic keys using external characters to distinguish the genera and subgenera, always citing Fraser's work as the source of osteological and internal character data, notably swim bladder morphology (Fraser and Lachner, 1985; Fraser and Struhsaker, 1991; Gon, 1995; Gon and Randall, 2003).

Much of the work since Fraser's (1972) study has been committed to revising the taxonomy of the species in the family. Nomenclatural difficulties plague the Apogonidae. Many of the species and genera were described in the 1800s, and either descriptions or illustrations were inaccurate or voucher material has either been lost or is in poor condition, thus making identification difficult, if not impossible. Fraser acknowledged the necessity of further taxonomic analysis at the species level, acknowledging that supra-specific relationships will not be understood until the taxonomy of the species is better known.

Some taxonomic difficulties have been resolved, resulting in changes to Fraser's (1972) classification of *Apogon*. Randall et al. (1990b) removed *Apogon aureus* (Lacepède, 1802) from synonymy with *Apogon fleurieu* (Lacepède, 1802) and recognized them both as valid species. Previously, upon the basis of an inaccurate specific description, *A. fleurieu* had been placed in the Oplegnathidae (Whitley, 1959). Gon (1987) recognized the original illustration of *A. fleurieu* as an apogonid and placed it in *Nectamia*, synonymizing it with *A. aureus*. The recognition of *Apogon fleurieu* as a valid taxon resulted in *Ostorhinchus* Lacepède, 1802, replacing *Nectamia* Jordan, 1917[b], as a subgenus of the genus *Apogon*.

Gon (1995) reevaluated the subgenus *Lepidamia* and considered it to include four species: *Apogon kalosoma* Bleeker, 1852[a], *Apogon multitaeniatus* Cuvier in Cuvier & Valenciennes, 1828, *Apogon natalensis* Gilchrist & Thompson, 1908, and *Apogon omanensis* Gon & Mee in Gon, 1995. He did not add any new characters to the subgeneric description and referenced Fraser (1972) for osteological and swimbladder data. He did, however, use cladistic methods in his analysis. He argued that small scale-size is a derived character state in the Apogonidae, and is thus an autapomorphy that separates *Lepidamia* from the remaining *Apogon* subgenera. Gon used meristic data and color characters to create a cladogram depicting the relationships among the *Lepidamia* species. He stated that his phylogenetic hypothesis was supported by the generalizations that rare (in frequency of occurrence) characters tend to be derived and that small geographic distributions are characteristic of derived taxa.

Gon (1996) further revised the genus *Apogon* by removing *Jaydia* from synonymy and elevating it to subgeneric status. *Jaydia* was originally introduced by Smith (1961) to accommodate two species he believed did not belong in *Apogon*. Fraser (1972) did not believe sufficient differences existed to distinguish *Jaydia* from *Apogon*, or at least to warrant its generic recognition, and synonymized the two genera. Gon (1996) recognized six characters supporting the monophyly and recognition of *Jaydia* as a subgenus, four of which represent unique characters or character states within the genus *Apogon*. *Jaydia* species are characterized by one of three preopercular serration patterns: a weakly serrate preopercular edge and a smooth to weakly serrate ridge; a serrate preopercular edge and ridge; or a smooth preopercular edge and ridge. The latter two patterns are unique (within *Apogon*) to this subgenus. A second distinguishing characteristic is the presence of a rounded caudal fin in adult *Jaydia*. In all other *Apogon* subgenera, adults retain the emarginately shaped caudal fin from their earlier life history stages. Gon considered the rounded caudal fin shape to be derived, as did Fraser (1972), who cited it as a diagnostic character for the hypothetically advanced genera *Astrapogon*, *Pseudamia*, and *Pseudamiops*. The position of the longest dorsal-fin spine is also unique in *Jaydia*. In *Jaydia*, it rests on the third pterygiophore; in all other apogonids it rests on the second pterygiophore. Gon considered this a synapomorphic character for the group. Also, all *Jaydia* species possess or have secondarily lost (according to Gon's phylogenetic analysis) light organs associated with the intestine (Iwai and Asano, 1958; Haneda et al., 1969a, b; Haneda et al., 1970; Herring and Morin, 1978). *Jaydia* species are not the only apogonids to possess light organs, but they are the only ones to employ a luciferin-luciferase mechanism for light production. The other bioluminescent cardinalfish species use bacteria for their light production (Iwai and Asano, 1958; Haneda et al., 1969a, b; Herring, 1982). Gon recognized this character as a fourth synapomorphy uniting the group. Gon validated the elevation of *Jaydia* to subgeneric status on the basis of these derived characters.

Antithetically, Gon identified an additional character that suggests that defining *Jaydia* as a subgenus of *Apogon* results in an unnatural, i.e., polyphyletic, generic taxon. Apogonids exhibit all stages of the reduction and loss of the eighth first-dorsal fin spine and its supporting elements. During the last stage of this progression, the eighth distal and ninth basal pterygiophores fuse. All *Jaydia* species have lost the eighth first-dorsal-fin spine, but only one species exhibits fusion of the eighth and ninth pterygiophores. Examination of species from other *Apogon* subgenera (*Nectamia*, *Apogon*, and *Pristiapogon*) indicates that the pterygiophore elements are at least partially fused in other *Apogon* species. Because the fusion of these two elements is a final step in the loss of the eighth first-dorsal spine, the fused condition is considered derived. Gon suggested that the prevalence of the primitive, i.e. un-fused, state in *Jaydia* implies that the subgenus cannot be nested within the genus *Apogon.* Gon suggested that further phylogenetic analysis of *Jaydia* might lead to the reinstitution of the group's full generic status.

Fraser (2000) later questioned the validity of *Jaydia*, stating that all of the group's diagnostic, "synapomorphic" characters grade into those of other *Apogon* subgenera, particularly the subgenus *Ostorhinchus*. Fraser discussed numerous *Apogon* species that challenged the definition of *Jaydia*. Each species, while clearly belonging in another *Apogon* subgenus, shared at least one of the diagnostic characters Gon used to define *Jaydia*. Fraser suggested that perhaps defining the taxon solely on the basis of the luciferin-luciferase bioluminescence system would lead to monophyly.

Additional work has led to the refinement of *Apogon* subgeneric characters and consequently to the removal of species from the various subgenera, and their return to *Apogon* sensu stricto. For instance, Fraser (1972) had previously placed *Apogon unicolor* Döderlein in Steindachner & Döderlein, 1883 in the subgenus *Pristicon*. He later removed this species and placed it back in *Apogon* (*Apogon*) on the basis of the presence of a ventral fleshy, unossified flap on the preopercle; small body scales; and a black stomach and intestine (Fraser, 1998). Fraser stated that he believed *Apogon unicolor* might represent another, yet undescribed, lineage within the genus *Apogon*.

Fraser (1998) augmented his 1972 study by publishing notes on the distribution of a number of character states across the *Apogon* subgenera. He divided the subgenera into phenetic groups on the basis of the number of first-dorsal fin spines. Species of *Apogon*, *Zapogon*, *Paroncheilus*, *Pristicon*, *Yarica*, *Brephamia*, and *Zoramia* have six first-dorsal spines. *Lepidamia* and *Pristiapogon* species have seven first-dorsal spines. Species of *Ostorhinchus* may have six, seven, or eight first-dorsal spines. He also examined the distribution of the degree of preopercular-margin ossification and serration across the subgenera. The six-spined species may be further subdivided into three phenetic groups. *Apogon* and *Zapogon* species have a preopercle with an unossified ventral margin and a serrate vertical edge. The preopercle of *Paroncheilus* species has a partially ossified ventral edge and a serrate vertical edge. The remaining six-spined *Apogon* species have preopercula with ossified, serrate ventral and vertical edges. Fraser's (1998) data in combination with Gon's (1996) analysis of preopercular ridge and edge serration has led to additional distinguishing characteristics for the *Apogon* subgenera. *Pristicon* may be further distinguished from *Ostorhinchus* on the basis of the degree of preopercular serration. *Pristicon* species have a completely serrate preopercle, including a serrate ridge, whereas, *Ostorhinchus* species have a preopercle with a serrate edge and a smooth ridge. Although detailed character analyses and examination of character-state distributions have led to an increase in the amount of knowledge available, thereby facilitating species identification, little systematic headway has been made from the additional information, as cladistic methods have not been applied to data analysis.

Taxonomic revision has proven to be a daunting task, as a lack of definable, non-variable characteristics precludes accurate species identification. Apogonid species are often distinguished by coloration. Although characteristic color markings may identify species relatively easily when the animal is fresh, they usually fade rapidly after collection and leave the taxonomist with few clues to the fishes' identity (Smith, 1961; Greenfield, 2001). Color patterns may also vary during the different stages of a fish's development. Fraser et al. (1999) noted an instance of taxonomic confusion resulting from a species being described on the basis of juvenile color patterns.

Despite their inherent weaknesses, color patterns continue to be widely used in apogonid taxonomy. Gon and Randall (2003) recently organized the thirteen species of the genus *Archamia* into six phenetic groups on the basis of the color patterns of living specimens. The *macroptera* group, which includes*A. macroptera* (Cuvier in Cuvier &

Valenciennes, 1828), *A. biguttata* Lachner, 1951, and *A. fucata* (Cantor, 1849), is characterized by the presence of 20-23 narrow, vertical, curved orange lines on the body. The *lineolata* group, which includes *A. lineolata* (Cuvier in Cuvier & Valenciennes, 1828) and *A. flavofasciata* Gon & Randall, 2003, is characterized by the presence of 7-13 narrow, dusky yellow to dark brown bars on the body. The *zosterophora* group, which includes *A. zosterophora* (Bleeker, 1856[a]) and *A. ataenia* Randall & Satapoomin, 1999, is diagnosed by the presence of two narrow orange bars on the opercle. The *buruensis* group, which includes *A. buruensis* (Bleeker, 1856[b]), *A. bilineata* Gon & Randall, 2003, *A. mozambiquensis* Smith, 1961, and *A. pallida* Gon & Randall, 2003, is characterized by one or two orange to dark brown stripes on the body. *Archamia bleekeri* (Günther, 1859) forms a monotypic group characterized by a small caudal spot on an otherwise unmarked body. *Archamia leai* Waite, 1916 also forms a monotypic group, characterized by the presence of 3-5 dusky to dark brown bars that increase in width posteriorly. Aspects of the species' color patterns were used not only to organize the species into these phenetic groupings, but additional color pattern characteristics were also used to distinguish among the species within each group. The authors' detailed descriptions of the variations in color patterns, particularly the nocturnal fading of key color markings, the fading of key characteristics in preserved specimens, and the variation between adult and juvenile color patterns underscore the limitations of using color pattern to define and identify species. Gon and Randall (2003) presented circumstances, for almost all species, in which color pattern alone failed to provide an infallible suite of characters for distinguishing the species' identity among its morphologically and meristically similar *Archamia* congeners.

In addition to difficulties associated with using color patterns to diagnose and identify species, meristic characters are often stable and do not differ among closely related species. One example of just such a complicated species identification is found within the *Apogon* subgenus *Pristiapogon* which contains three morphologically similar species: *Apogon taeniopterus* Bennett, 1836, and a sympatric species pair composed of *Apogon exostigma* (Jordan & Starks in Jordan & Seale, 1906) and *Apogon abrogramma* Fraser & Lachner, 1985. It was long believed that *A. taeniopterus* formed a sympatric species pair with *Apogon menesemus* Jenkins, 1903. Fraser and Lachner (1985) distinguished *A. menesemus* from *A. taeniopterus* on the basis of two characters: the degree of completeness of a black bar in the caudal fin and different numbers of pectoral fin rays. However, Randall (1998) documented a population of *A. taeniopterus* from Pitcairn Island with a color pattern identical to *A. menesemus,* including the complete bar across the caudal fin. Randall also discovered that the data documenting the presence of 13 pectoral fin rays in *A. taeniopterus* and 14 fin rays in *A. menesemus* were erroneous. The pectoral fins of both species have 13 rays. *Apogon menesemus* was subsequently relegated to synonymy with *A. taeniopterus*. *Apogon taeniopterus* differs only in color pattern from the *A. exostigma* and *A. abrogramma* species pair. Meristic and morphometric measurements do not differ significantly among the species. *Apogon exostigma* and *A. abrogramma* also differ only in their color patterns. *Apogon abrogramma* lacks a spot on the caudal peduncle just dorsal of the lateral line, which is present in *A. exostigma.* Geographic variation exists, however, in the development of the caudal spot in *A. exostigma*, and the caudal spot ranges from intense to obscure. This color variation, in conjunction with the overlap in meristic and morphometric measurements that occurs, inhibits conclusive species identification of faded and preserved *A. exostigma* and *A. abrogramma* specimens (Fraser and Lachner, 1985).

Another group of species whose identities have been frequently confused is *Apogon coccineus* Rüppell, 1838, *Apogon crassiceps* Garman, 1903, *Apogon doryssa* (Jordan & Seale, 1906), and *Apogon erythrinus* Snyder, 1904 (Smith, 1961; Shen and Lam, 1977; Shao and Chen, 1986; Greenfield, 2001). These four species superficially resemble one another in size, shape, and lack of color pattern and pigmentation on the scales. *Apogon erythrinus* has been synonymized with *Apogon crassiceps* and *Apogon coccineus* (Smith, 1961; Shen and Lam, 1977; Randall et al., 1990a; Greenfield, 2001). Until recently the species have been distinguished on the basis of differences in the number of gillrakers and proportional length measurements of the body and fins; however, these characteristics are ambiguous because intra-specific variation is known to occur within the geographic range of several of the species. For example, it was possible to distinguish *Apogon crassiceps* and *Apogon doryssa* on the basis of morphometric variation. But *Apogon erythrinus* exhibited sufficient morphological variation over its entire geographic range to cover all these differences (Shen and Lam, 1977). It was thought that specimens of *A. erythrinus* from the Red Sea attained a larger average size, had a greater number of gillrakers, and had shorter fin spines than did specimens taken east of the Philippine Islands (Lachner, 1953; Smith, 1961). Unequivocal identification of species from this group was considered difficult, if not impossible.

Recent work has distinguished and validated these species (Greenfield, 2001). *Apogon doryssa* is distinguished from the other species by its significantly longer second-dorsal fin spine, triangular-shaped head, unique nasal configuration, and slender caudal peduncle (Lachner, 1953; Shen and Lam, 1977; Masuda et al., 1984; Greenfield, 2001). Greenfield (2001) recognized that the remaining species fall into two phenetic groups. These groups he referred to as the *Apogon erythrinus* complex and the*Apogon crassiceps* complex. The members of these complexes share the following characteristics: six first-dorsal fin spines, 8-9 dorsal soft rays, 7-8 rays in the anal fin, 16 or fewer total gillrakers on the first gill arch, 13-14 pectoral-fin rays, and two predorsals (Greenfield, 2001).

Greenfield (1994) revised the definition of *Apogon erythrinus*, listing it as a species endemic to the Hawaiian Islands and Johnston Atoll. Prior to this, *A. erythrinus* had been considered to have a large geographic distribution and a broad character definition. Detailed morphological examination has shown that "*Apogon erythrinus*" is in fact a group of closely related species, Greenfield's *Apogon erythrinus* complex. As defined by Greenfield, this complex encompasses four species: *Apogon erythrinus, Apogon indicus* Greenfield, 2001, *Apogon marquesensis* Greenfield, 2001, and *Apogon susanae* Greenfield, 2001. These species share two characteristics. The skin at the end of the snout, near the anterior nostril, is not formed into a flap but is smooth, and there are two full scales between the lateral line and the second and third spines of the first dorsal fin. In contrast, species in the *crassiceps* complex have a free-edged flap of skin near the anterior nostril and a single, large, full scale between the lateral line and first dorsal fin. The *crassiceps* complex includes not only *Apogon crassiceps* and *Apogon coccineus* but also a number of other *Apogon* species historically confused with *Apogon erythrinus*.

Despite the taxonomic confusion that has been resolved during the past several decades, little headway has been made toward understanding the evolution of the apogonid family as a whole. This may be partially attributed to a lack of characters needed to resolve the relationships among such a large and diverse group of organisms. It has been suggested, that for highly diverse taxa, their evolutionary history and taxonomy can best be understood by conjoining the analysis of complex character sets, such as the body and cephalic lateralis system, with the analysis of simpler characters of reduction and loss provided by the skeleton (Miller and Wongrat, 1979). Thus describes one of the primary objectives of this study: to examine the cephalic portion of the lateralis system in apogonids and to develop a suite of characters that, when combined with Fraser's (1972) osteological data and analyzed using cladistic methodologies, are capable of producing a reliable hypothesis of the evolutionary relationships among the genera and subgenera of the family Apogonidae.

The Lateralis System and Its Previous Utilization in Fish Systematics

Until the mid-1800s, the lateral line system was considered the organ responsible for producing the mucous coating of fishes (Dijkgraaf, 1989). However, in 1850, Franz Leydig (1850) discovered that the canals functioned as sensory organs rather than mucus-producing organs. During the next two decades, Franz Eilhard Schulze (1861, 1870) made observations of the microstructure of the sensory cells associated with the lateralis system and observed that impacting water caused a deflection of the cells' cupulae. He suggested that water movement, including that generated from the transmission of low-frequency sound waves, relative to the fish could function as a stimulus for the system. As a result of morphological and embryological investigations of the system, it was concluded, without physiological support, that the lateralis system's primary function was as a receptor of low-frequency sound. This belief continued through the second half of the 19th century (Dijkgraaf, 1989). In 1933, Dijkgraaf described in his dissertation the lateral line as sense of touch at a distance (Dijkgraaf, 1934). Research has continued to support this function, and has refined the limits of the system's perceptibility to include only those relative movements between the fish and its surroundings that occur at close distances (Kalmijn, 1989; Platt et al., 1989). The information received by the lateral line system underlies various behaviors of particular importance to nocturnal coral reef fish species like cardinalfish, including schooling behavior (Partridge and Pitcher, 1979; Partridge, 1981), obstacle avoidance (Von Campenhausen et al., 1981), and prey detection (Coombs and Janssen, 1988).

The functional unit of the lateralis system is the neuromast. Each neuromast is composed of a base of support cells and mantle cells, a number of sensory epithelia hair cells, and the entire neuromast is covered by a gelatinous cupula (Coombs, et al., 1989). A single neuromast of *Apogon cyanosoma* Bleeker, 1853 has been found to contain up to 1,500 hair cells (Rouse and Pickles, 1991). Ciliary bundles are attached to the apical ends of the hair cells. Each ciliary bundle consists of a number of stereocilia of graded lengths. The stereocilia are arranged in length, from the shortest to the tallest, with the tallest being positioned adjacent to a stereocilium. The axis along which the stereocilia are arranged determines the direction of sensitivity of a given hair cell. Hair cells with opposite directional sensitivities are arranged together in neuromasts such that each neuromast has a single axis of best sensitivity (Coombs et al., 1989). Neuromasts in fishes are located either along the base of canals (canal neuromasts) or are free on the surface of the skin (superficial neuromasts or sensory papillae). Cardinalfishes have both types of neuromasts. It is the pattern of distribution of the superficial neuromasts of the cephalic portion of the lateralis system that is the focus of this dissertation.

Use of characters of the cephalic lateralis system, particularly the patterns of the sensory papillae, in taxonomic designation is not a new concept in ichthyology. The systematic utility of these characters has been known and used, at least for gobiids, since Sanzo (1911) published his paper touting the importance of the sensory papillae patterns in goby systematics. Within the past two decades gobioid systematists have used cheek papillae patterns to investigate a variety of systematic questions ranging in scope from species identification to the construction of hypotheses of evolutionary relationships.

Miller (1998) created a key distinguishing three species of West African *Eleotris* on the basis of a set of characters from the lateral-line system. Initially, identification was based upon the number of lateral-line scales only. Although a practical method of identification, in terms of field utility, it did not always yield conclusive species identifications as scale counts overlapped; however, when the lateral-line scale count was used in conjunction with characters from the head lateral line system, species identification was unambiguous.

Miller et al. (1989) used established keys to identify an unknown gobioid from western Africa as the Indo-Pacific eleotrid *Prionobutis koilomatodon* (Bleeker, 1849). At that time, *Prionobutis* included three species: *P. koilomatodon*, *P. dasyrhynchus* (Günther, 1868), and *P. microps* (Weber, 1907). Further investigation of *Prionobutis* demonstrated a marked contrast between the well-developed suborbital transverse papillae pattern of *P. koilomatodon* and the greatly reduced suborbital papillae pattern present in the other *Prionobutis* species. Miller et al. (1989) noticed that the papillae pattern of *P. koilomatodon* was very similar to that of species in the genus *Butis* Bleeker, 1856[b] and subsequently transferred *P. koilomatodon* to *Butis*. Thus, they were able to clarify the issue of generic placement of these species by using characters of the cephalic lateralis system.

Characters of the cephalic lateralis have proven useful beyond the realm of species level taxonomy. A number of these characters have been suggested as supporting the monophyly of several supra-generic taxa. Winterbottom and Burridge (1992, 1993a, 1993b) used cheek sensory papillae patterns to divide the goby genus *Priolepis* into two phenetic groups: those with a transverse pattern of papillae and those with a reduced transverse pattern of papillae. They hypothesized that the latter condition was derived from the former, and thus, the species group characterized by a reduced sensory papillae pattern formed a monophyletic group. McKay and Miller (1997) used characteristics of the cephalic lateralis canals and sensory papillae patterns to show affinities among a group of genera, the European sand gobies. Pezold (1993) reported the presence of a unique supraorbital canal morphology in the species assigned to the Gobiinae. He suggested that the presence of a single interorbital pore in the anterior interorbital space combined with the termination of the supraorbital canal adjacent to the posterior nostril (as opposed to termination adjacent to the anterior nostril in most other gobioids) was synapomorphic for the subfamily. The monophyly of this subfamily, as defined by these cephalic lateralis characters, continues to be accepted (Nelson, 1994).

Gill et al. (1992) discussed the difficulty in generating sufficient numbers of characters necessary for cladistic analyses of large numbers of taxa. They presented the cephalic lateralis as a potential source of a large number of readily available characters for such analysis. In order to refute the common criticisms against using cephalic lateralis characters to hypothesize evolutionary relationships and to demonstrate their utility for such purposes, they generated a number of data sets based on osteological, morphological, and cephalic sensory papillae pattern characters. These data sets, individually and in various combinations, were then subjected to phenetic analysis. The classifications generated were then compared to classifications produced by descriptive taxonomy, based primarily on osteological characters, and by multivariate analysis of morphometric data. All three approaches yielded the same groupings and intra-group relationships. The classification based on the phenetic analysis of the papillae pattern data showed the same relationships as did the classifications derived from similar analyses of osteological and/or morphological characters. Thus, the analysis supported the assertion that papillae patterns can be used to hypothesize phylogenetic relationships.

Parin and Astakhov (1982) assessed the structure of the cephalic lateralis system of beloniform fishes in the light of what was then the group's accepted classification. Their research focused primarily on the connectivity and complexity, specifically the degree of branching and perforation, of the cephalic lateralis canals, as opposed to the sensory papillae patterns commonly employed in gobiid taxonomy. They found that characters of the cephalic lateralis system were diagnostic at taxonomic levels from suborders to genera and subgenera. Previously, characters of the cephalic lateralis system had been used to diagnose the Beloniformes (Rosen, 1964; Gosline, 1971) and as components of generic diagnoses for taxa in the Exocoetidae and Belonidae (Parin, 1967).

The characters of the cephalic lateralis system have not gone unmentioned in apogonid taxonomy. Lachner (1953) described *Gymnapogon japonicus* Regan, 1905 as resembling gobiids in general body shape and in having papillae arranged in a definite pattern over the head and body. He included illustrations and descriptions of papillae patterns in other species of *Gymnapogon.* Mention of the presence of papillae and pores leading to subsurface channels has been made for many of the species and genera of the Pseudaminae (Lachner, 1953; Smith, 1961; Randall et al., 1985; Gon, 1986; Randall and Ida, 1993; Baldwin and Johnson, 1999; Randall, 2001), and the Apogoninae (Lachner, 1953; Randall et at., 1990a; Randall and Hayashi, 1990; Hayashi, 1991; Allen, 1995; Allen and Morrison, 1996; Gon and Allen, 1998; Randall, 2001; Gon and Randall, 2003).

Although several authors have noted the existence of cephalic canals, pores, and papillae, few attempts have been made to describe or compare patterns among apogonid species or supra-specific taxa. For the most part, published descriptions are brief, stating little more than that such structures exist. The potential taxonomic utility of the character set appears to have been nearly overlooked. A few authors have suggested that information useful in elucidating interfamilial relationships may lie in these characters, as few families within the Perciformes possess cephalic sensory papillae associated with the lateralis system (Johnson, 1993; Baldwin and Johnson, 1999). Even though parallels have been drawn between the cephalic lateralis systems of apogonids and gobiids, and the characters have proven themselves to be highly useful in goby taxonomy, there have been few investigations into their utility in apogonid taxonomy and systematics.

Hayashi (1991) published one of the few papers that examined the cephalic lateralis of a cardinalfish species. In this paper, he illustrated and briefly described the cephalic lateralis of *Cercamia eremia* (Allen, 1987). When Randall and Smith (1988) published their description of the genus *Cercamia* they suggested that this new genus was most closely related to *Rhabdamia* or *Pseudamiops*. Hayashi (1991) investigated this hypothesis by comparing the osteology of *Cercamia eremia* with the osteological data collected by Fraser (1972) for the latter two taxa. Hayashi (1991) complemented the osteological comparisons with comparisons of characters of the acoustico-lateralis system. He compared the sensory papillae patterns on the head and body of *Cercamia eremia* with the type species of each pseudamine genus (excluding *Paxton*, as the genus was not yet described) and the cephalic canal system of *C. eremia* and *Rhabdamia* (*Verulux*) *cypselura* Weber, 1909. He concluded that *C. eremia* had significantly fewer sensory papillae on its head and body than did the pseudamine species, and that the cephalic canal system was only moderately developed in comparison to the highly branched system of *R. cypselura.* Although the comparisons are interesting they are phenetic in nature and provide little insight into the nature of the evolutionary relationships among these taxa.

Thus, although the cephalic lateralis has been used for taxonomic purposes in some groups of fishes, it has been used only minimally in the Apogonidae. Furthermore, the cephalic lateralis system has not even been adequately described in most species of the Apogonidae. This dissertation, then, aims to describe the cephalic lateralis of the Apogonidae in detail, investigating its value in basic taxonomy, as well as, its utility in a phylogenetic analysis of the group, that will attempt to shed light on the evolutionary relationships of the generic and subgeneric taxa within the group.

CHAPTER 2. DESCRIPTIONS AND ILLUSTRATIONS OF THE CEPHALIC LATERALIS OF CARDINALFISHES

The taxonomic and systematic utility of cephalic lateralis characters, particularly the patterns of the sensory papillae, has been known and used, at least for gobiids, since Sanzo (1911) published his paper touting the importance of the sensory papillae patterns in goby systematics. Within the past two decades gobioid systematists have used cheek papillae patterns to investigate a variety of systematic questions ranging in scope from species identification to the construction of hypotheses of evolutionary relationships.

Although the characters of the cephalic lateralis system have not gone unmentioned in apogonid taxonomy, there have been few attempts made, to describe or compare patterns among apogonid species or supra-specific taxa. For the most part, published descriptions are brief, stating little more than that such structures exist. The potential taxonomic utility of the character set appears to have been nearly overlooked. Even though parallels have been drawn between the cephalic lateralis systems of apogonids and gobiids, and the characters have proven themselves to be highly useful in goby taxonomy, there have been few investigations into their utility in apogonid taxonomy and systematics. Furthermore, the cephalic lateralis system has not even been adequately described in most species of the Apogonidae.

This chapter presents detailed descriptions of the cephalic lateralis of the type species of each apogonid genus and subgenus and comments on the variability of this system within the supra-specific taxon to which the species belongs. This data has been collected for the purpose of not only increasing the general body of knowledge about apogonids, but also with the specific intent of developing a data set capable of producing a reliable hypothesis of the evolutionary relationships among the genera and subgenera of the family Apogonidae.

Description and Illustration of the Cranial Lateralis Systems

Institution Abbreviations

The following acronyms designate institutions and collections cited: BPBM, Bernice Pauahi Bishop Museum, Honolulu; CAS, California Academy of Sciences, San Francisco; G, uncatalogued specimens collected by David W. Greenfield (specimens are to be incorporated into the CAS collection and will receive CAS collection numbers); NJSA, New Jersey State Aquarium, Camden; SU, Stanford Collection at the California Academy of Sciences, San Francisco; USNM, National Museum of Natural History, Washington, D.C; and WAM, Western Australian Museum, Perth.

Methods

Measurements were made using dial calipers and are expressed in millimeters. Measurements were taken to the nearest 0.1 mm. Lengths given for specimens are standard lengths (SL), the straight-line distance from the anterior-most point of the snout to the base of the caudal fin.

Specimens of the type species, but not the type specimens themselves, of each subgenus and genus were studied and the pore and papillae patterns were described and drawn. It was not possible to obtain specimens of *Rhabdamia* (*Rhabdamia*) *clupeiformis* Weber, 1909, the type species of the *Rhabdamia* (*Rhabdamia*) subgenus; specimens of *Rhabdamia* (*Rhabdamia*) *gracilis* (Bleeker, 1856[c]) and *Rhabdamia* (*Rhabdamia*) *spilota* Allen & Kuiter, 1994 were examined instead. The completeness of the superficial neuromast pattern was dependent upon the condition of the specimen; therefore, the illustrations are composites of all type specimens observed. Additional species in each genus and subgenus were examined to assess the degree of intra-generic and intra-subgeneric variability in the pore and papillae patterns.

Illustrations were facilitated by use of a dissecting microscope with a camera lucida attachment. The *Holapogon maximus* (Boulenger, 1888) and *Coranthus polyacanthus* (Vaillant, 1877) specimens were too large to illustrate with the camera lucida attachment. Instead, digital photographs of the specimens were taken and traced. Scale bars in all illustrations, with the exceptions of *H. maximus* and *C. polyacanthus*, represent 1 mm. Scale bars in the illustrations of *H. maximus* and *C. polyacanthus* represent 3 mm.

Visualization of papillae patterns was enhanced by temporarily staining the specimens (with the exception of the paratype specimen of *Paxton concilians* Baldwin & Johnson, 1999) with Cyanine Blue (Acid Blue 113) following Saruwatari et al. (1997). The pores and stained papillae patterns were observed with the aid of a dissecting microscope. Blowing air onto the specimens further enhanced visualization. The air functioned to inflate the canals and temporarily erect the papillae. The pores and stained papillae patterns were observed with the aid of a dissecting microscope.

Presentation of Data

Canal divisions and terminology follow accepted nomenclature: supraorbital, infraorbital, supratemporal, and preoperculomandibular canals (Figure 1) (Takagi, 1998; Bond, 1996). All descriptions begin with the anterior-most portion of each canal system. For descriptive purposes, each canal system is arbitrarily subdivided into multiple segments. These divisions are made for the sake of clarity, as the portions are most generally confluent.

Description of the supraorbital canal begins with the terminal pore located on the snout and proceeds posteriorly to the supratemporal canal (Figure 1A, B). The supraorbital canal is described in three segments: the nasal, interorbital, and postorbital portions (Figure 2B). The nasal portion extends from the tip of the snout to the anterior margin of the orbit. The interorbital portion refers to the area between the eyes. The postorbital portion refers to the area between the posterior margin of the orbit and the supratemporal canal.

For those canals traversing the dorsal and ventral surfaces of the head, such as the supraorbital and mandibular canals, the margins are referred to as medial and lateral. The supratemporal canal is an exception to this convention (Figure 1B). Margins of the supratemporal canal are referred to as anterior and posterior.

Description of the infraorbital canal begins with the terminal pore located just posterior to the nostrils and proceeds posteriorly through the suborbital and postorbital space to the canal's anastomosis with the supraorbital canal (Figure 1A). The margins of the infraorbital canal are referred to as either proximal or distal in reference to their proximity to the orbit. The infraorbital canal is described in three confluent sections: the lachrymal, suborbital, and postorbital portions (Figure 2A). The lachrymal portion extends from the anterior nostril to the anterior margin of the orbit. The suborbital portion continues posteriorly below the orbit to the end of the maxilla. The postorbital portion extends dorsally from the terminus of the maxilla along the posterior margin of the orbit.

The preoperculomandibular canal is described in two portions: the mandibular portion and the preopercular portion. Description of the mandibular portion begins with the pores at the tip of the mandible, or dentary pores, and terminates with the pore located at the base of the preopercle (Figure 1C). The base of the preopercle represents the terminal point of the mandibular portion when a terminal pore is absent. Description of the preoperculomandibular canal continues with the preopercular portion. Descriptions present the ventral portion first followed by the vertical portion (Figure 1A). The margins of the preopercular portion of the canal are referred to as either proximal or distal in reference to their proximity to the orbit.

Perforations in the roof of the canals are referred to as pores. The shape and relative size of the pores are described when possible. Pores are represented in illustrations as circles, ovals or slits. In contrast to pores, sensory papillae are represented by triangular hatch marks.

All branches from stems of the main canals are designated as secondary canals. Some of these extensions terminate in defined pores, whereas others are open-ended but do not end in a pore with a defined, observable margin. This distinction is noted. Canals in soft tissues or in scales are termed superficial canals.

Descriptions are presented by subfamily, with those of the apogonine taxa being presented prior to those of the pseudamine taxa. Descriptions within each subfamily are arranged in alphabetical order by genus, and within genus alphabetically by subgenus. Each account consists of a detailed description of the cephalic lateralis of the type species of the genus/subgenus and comments on the variability of this system within the generic/subgeneric taxon to which the species belongs. If the morphology for a given canal portion does not vary among the species, and is therefore consistent with the type species, no comparative comments are made for that canal portion in the remarks section. Materials examined are listed under their respective taxonomic heading. The data for each lot of material include the catalog number, total number of specimens, and size range in mm standard length.

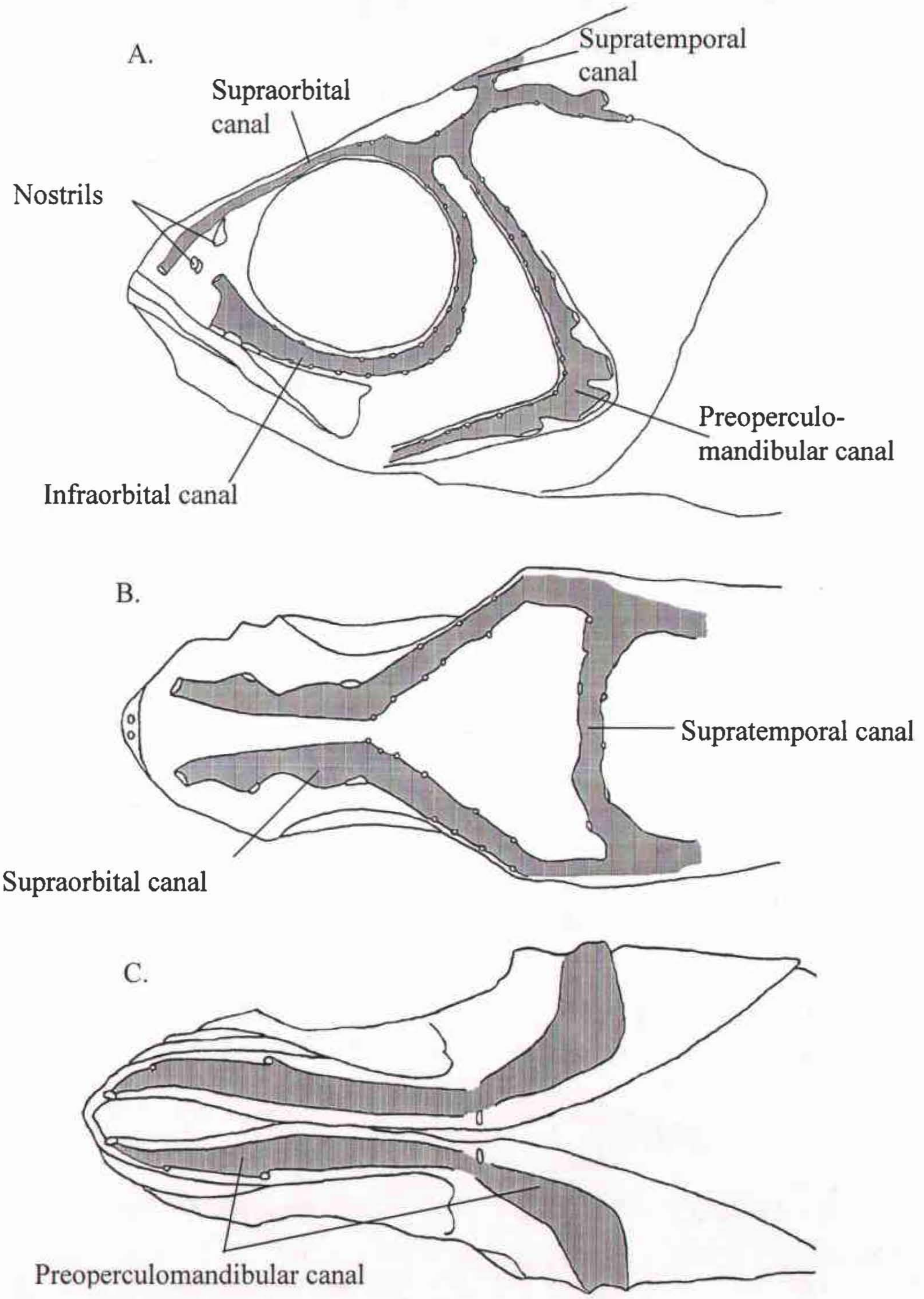


Figure 1. General structure of the canal system in the apogonid fishes. A. Lateral view, B. Dorsal view, C. Ventral view

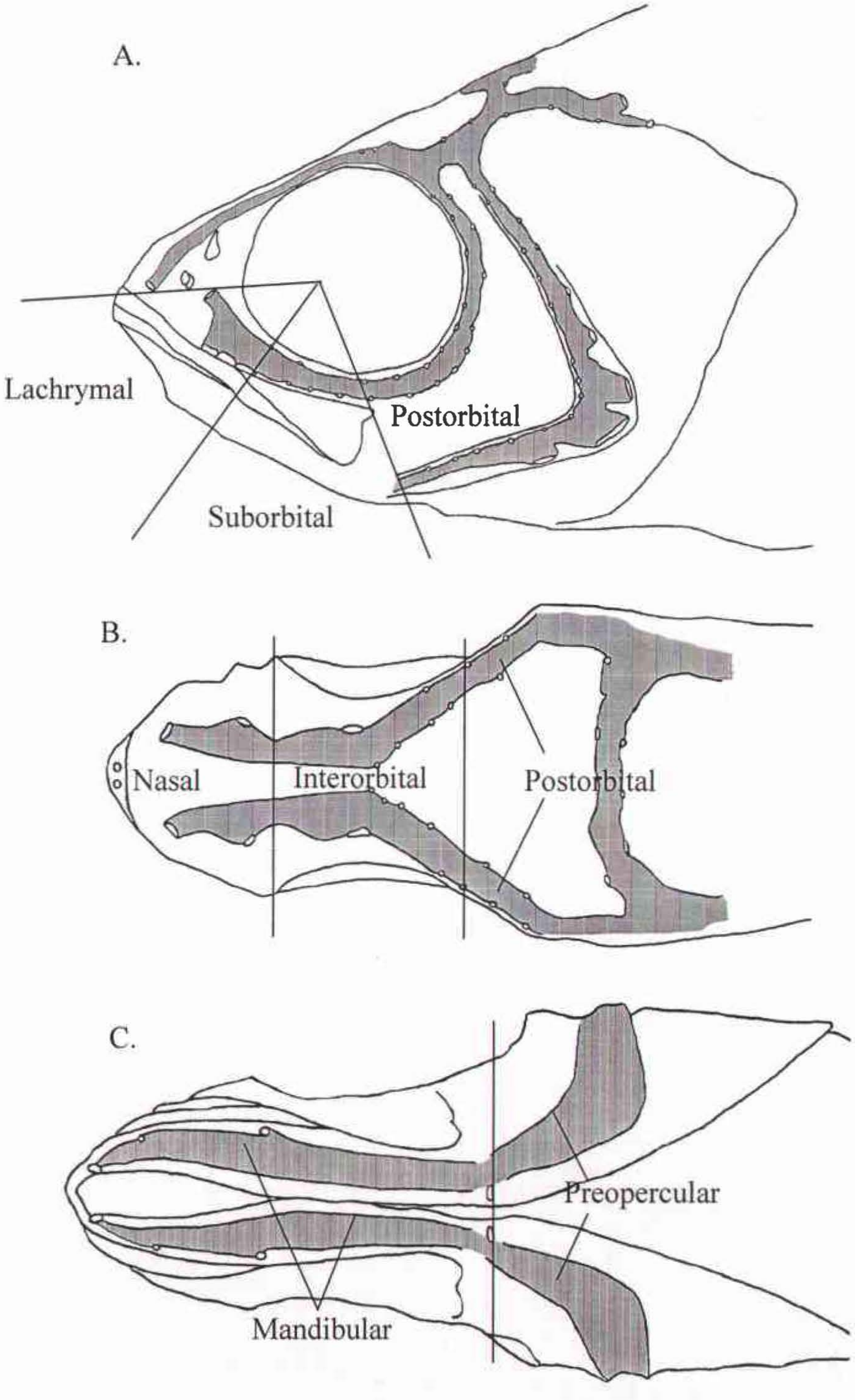


Figure 2. Illustration of arbitrary canal divisions. A. Lateral view, B. Dorsal view, C. Ventral view

Subfamily Apogoninae

Apogon (*Apogon*) Lacepède, 1801

Material Examined

Type species: *Apogon ruber* Lacepède, 1801 [= *Apogon imberbis* (Linnaeus, 1758), according to Fraser & Robins (1970)], by monotypy; SU 24039; 2, 73.6—76.8 mm

Apogon crassiceps Garman, 1903; G99-6; 2, 30.6—32.4 mm

Apogon doryssa (Jordan & Seale, 1906); G99-1; 1, 30.7 mm

Apogon erythrinus Snyder, 1904; G94-6; 9, 33.0—37.4 mm

Supraorbital Canal

Nasal Portion

- Extends to tip of snout (Figure 3A)
- Terminates anteriorly in a slit-like pore
    - Skin covering pore formed into a cleft extending midway to anterior nostril
- Lateral margin perforated by a relatively large, oval-shaped pore just medial to posterior nostril
- Portion of canal anterior of posterior nostril perforated by relatively few pores
    - Pores are concentrated toward canal margins

Interorbital Portion

- Margins and median of canal perforated by many small pores
- Lateral margin near longitudinal midpoint of interorbital space formed into a projection that extendsposteriolaterally toward orbit and terminates in a pore

Postorbital Portion

- Canal formed into a few, relatively broad secondary extensions that project posteriorly along median of postorbital space
    - Margins and medians of extensions densely perforated by small pores
    - Extensions do not end in a single distinct pore
- Expanse of canal along dorsoposterior margin of orbit perforated by numerous small pores

Sensory Papillae Pattern

- Minute papillae on lips and dorsal surface of snout between terminal pores
- Median of canal anterior of posterior nostril densely covered by sensory papillae (Figure 3B)
- Longitudinal band of sensory papillae extends posteriorly from anterior interorbital space to just anterior of postorbital secondary canal development
    - Initially row is two to three papillae wide, width tapers to one papilla near row's end
- Second, more lateral, longitudinal row of papillae overlaps the first longitudinal row in mid-interorbital space anteriorly and extends posteriorly along dorsal margin of orbit to edge of preopercle
- Anterior portions of secondary postorbital canal projections intersected by multiple transverse rows of papillae
- General crosshatch pattern of papillae in preorbital, interorbital, and postorbital space formed from intersection of longitudinal rows by numerous short transverse rows

Supratemporal Canal (Figure 3B)

- Anterior margin and median perforated by numerous small pores
- Posterior margin formed into numerous open-ended, posteriorly projecting, secondary extensions
    - Margins of extensions perforated by numerous pores

Sensory Papillae Pattern

- Two longitudinal rows of papillae extend posteriorly from lateral portions of supratemporal canal along portion of canal posterior of anastomosis of infraorbital, supratemporal, and preoperculomandibular canals toward edge of opercle
- Several short, transverse rows extend dorsally from longitudinal row

Infraorbital Canal (Figure 3A)

Lachrymal Portion

- Terminates anteriorly in a large, slit-like pore just posterior of midpoint of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two, long, slit-like pores

Suborbital Portion

- Margins and median perforated by many small pores

Postorbital Portion

- Proximal margin and median perforated by numerous small pores
- Distal margin formed into numerous open-ended, secondary projections that extend onto cheek
    - Margins of projections perforated by numerous small pores

Sensory Papillae Pattern

- Internarial space with rows of sensory papillae, several of which extend beyond posterior nostril to orbit
- Several longitudinal rows form a band that extends posteriorly along ventral suborbital portion from anterior of the first slit-like lachrymal pore to just posterior of terminus of maxilla
- Longitudinal row, superior to suborbital band, extends posteriorly from ventral-most point of orbit
- Numerous transverse rows extend ventrally from orbit to meet suborbital band

Preoperculomandibular Canal

Mandibular Portion (Figure 3C)

- Terminates anteriorly in a pair of small round pores that perforate the dentary
- Canals just posterior of apex of dentary perforated by a moderately-sized pair of oval-shaped mental pores
- Medial and lateral margins perforated by numerous small pores
- Lateral margin formed into two short, posteriorly projecting extensions that terminate in pores near first quarter and midpoint of maxilla
- Lateral margin adjacent to terminus of maxilla formed into few short projections that terminate in pores
- Mandibular portion does not terminate in a large pore

Preopercular Portion (Figure 3A)

- Median of ventral flange perforated by numerous small pores
- Proximal margin of vertical flange perforated by numerous, small pores

- Distal margin formed into open-ended projections that terminate along edge of preopercle
    - Margins, near base of projections, perforated by numerous small pores
- Dorsal-most portion of distal margin formed into open-ended secondary projections that extend beyond margin of preopercle onto opercle
    - Margins of projections perforated by numerous pores

Sensory Papillae Pattern

- Sensory papillae densely concentrated on anterior portion of basihyal, forming a chevron pattern posteriorly
- Minute sensory papillae medial to anterior half of canal
- Mandibular median densely covered by short semi-longitudinal rows of sensory papillae
- Anterior portion of ventral preopercular flange with crosshatch pattern of sensory papillae
- Median of vertical preopercular flange with row of papillae
- Transverse row of papillae on opercle just posterior of edge of preopercle

Remarks

The cephalic lateralis systems of the fishes in the genus *Apogon* vary considerably; so much so, that some of the variations have been helpful in diagnosing phenetic groups within *Apogon sensu stricto*. The supratemporal canal extends to the tip of the snout in all species of *Apogon*; however, the morphology of the flap of skin covering this pore varies. In *Apogon imberbis* and *A. crassiceps* the lateral edge of the covering forms a cleft that extends mid-way to the anterior nostril. In *A. crassiceps* and

A. doryssa the lateral edge of the covering is not free from the surrounding skin. Greenfield (2001) used the morphological variation of this pore, in addition to the number of scales between the lateral line and the first section of the dorsal fin, to describe two phenetic groups: the *A. erythrinus* and *A. crassiceps* complexes (see Chapter 1).

Other variations exist in the supratemporal canal morphology of this subgenus. *A. imberbis*, *A. crassiceps, and A. doryssa* are characterized by the presence of a single pore perforating the lateral margin adjacent to the posterior nostril. In contrast, the lateral margin adjacent to the posterior nostril in *A. erythrinus* is formed into numerous short, projections that extend toward the orbit and terminate in pores. A single pore perforates the lateral margin near the interorbital midpoint in *A. imberbis*, *A. crassiceps*, and *A. doryssa* as well. As opposed to a single pore, this portion of the canal in *A. erythrinus* is perforated by numerous small pores that are located at the ends of short projections that extend posteriodorsally toward the orbit.

Four equidistant pores perforate the medial margin of the mandibular canal of *A. doryssa.* Pores perforate the lateral margin opposite the first three of these pores. The fourth pore is singular and large, occupying the position of terminal pore. The perforation pattern of the mandibular canal portion is similar in the other three species examined. In each case, the lateral margin is perforated by two single, moderately-sized pores, the first being located one quarter of the way along the length of the canal and the second located halfway along the length of the canal. A few small pores perforate the lateral margin adjacent to the terminus of the maxilla. The pores perforating the lateral margin in *A. imberbis* are located at the end of short projections. In both *A. crassiceps* and *A. erythrinus* the canal itself is wider in comparison to *A. imberbis*, thereby eliminating the need for projections to extend the pores toward the dentary. Thus, in these species the lateral pores appear to be back-turned but are not located at the tips of projections. A small pore perforates the medial margin in the terminal position in *A. crassiceps*, *A. erythrinus*, and *A. imberbis*.

The variation in the sensory papillae patterns is slight among the species, generally consisting of a crosshatch pattern across the dorsolateral surfaces of the head and dense papillae on the median of the mandibular canal.

A.

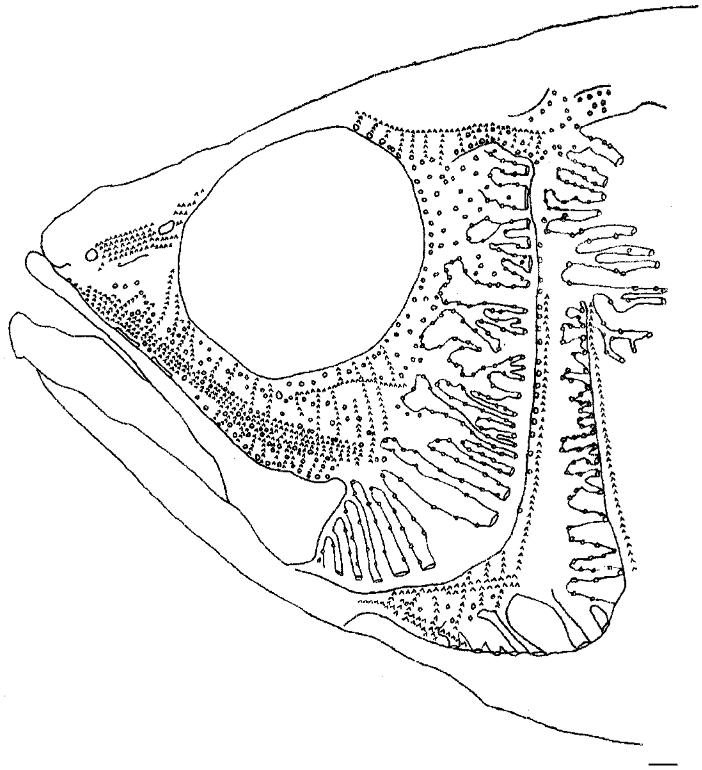


Figure 3. Cephalic lateralis of *Apogon* (*Apogon*) *imberbis* A . Lateral view

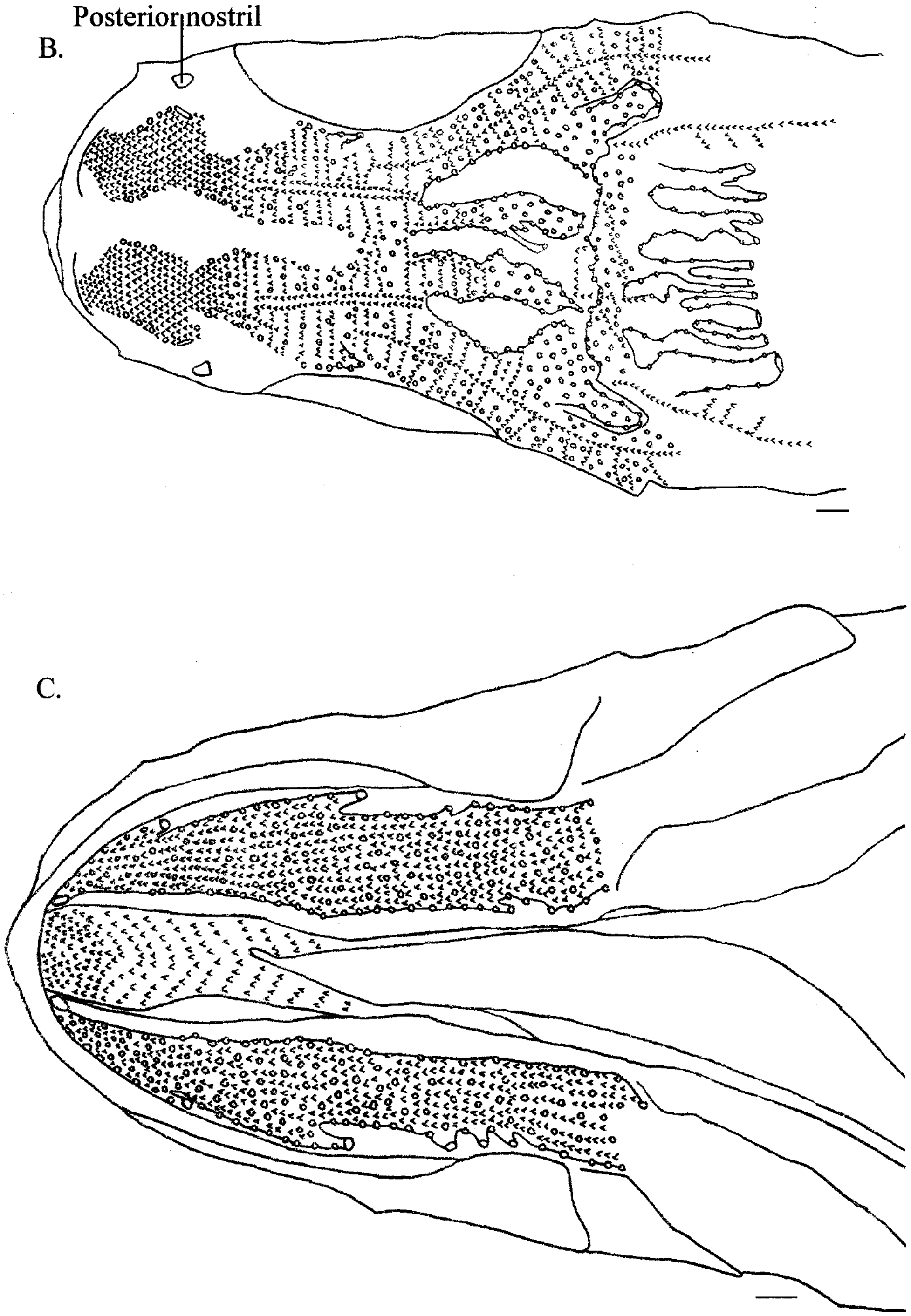


Figure 3 (continued). Cephalic lateralis of *Apogon* (*Apogon*) *imberbis* B. Dorsal view, C. Ventral view

Apogon (*Brephamia*) Jordan in Jordan & Jordan, 1922

Material Examined

Type species: *Amia parvula* Smith & Radcliffe in Radcliffe, 1912, by original designation (also monotypic); BPBM 32081; 1, 27.1 mm

Supraorbital Canal

Nasal Portion

- Does not extend to tip of snout (Figure 4A)
- Terminates anteriorly in a slit-like pore that parallels the premaxilla
- Lateral margin perforated by a relatively large pore just anterior of and medial to posterior nostril (Figure 4B)

Interorbital Portion

- Margins perforated by few small pores
- Lateral margin perforated by a large pore near longitudinal midpoint of interorbital space

Postorbital Portion

- Canal formed into a few secondary extensions that project posteriorly along median of postorbital space
    - Margins and median of extensions perforated by small pores
    - Each extension terminates in a single, distinct pore-opening
- Proximal margin, along dorsoposterior margin of orbit, perforated by a few moderately-sized pores

Supratemporal Canal (Figure 4B)

- Anterior margin of canal perforated by numerous small pores
- Anterior margin formed into one moderately-long, anteriorly projecting, secondary extension
    - Margins of extension perforated by a few pores
- Posterior margin of canal formed into a few, short, open-ended, posteriorly projecting secondary extensions
    - Margins of extensions perforated by a few small pores

Infraorbital Canal (Figure 4A)

Lachrymal Portion

- Terminates anteriorly in a relatively large pore just posterior of anterior nostril
- Distal margin, along ventral edge of lachrymal, perforated by two long, slit-like pores

Suborbital Portion

- Proximal margin perforated by numerous small pores
- Distal margin of posterior portion perforated by a few small and moderately-sized pores along edge of maxilla

Postorbital Portion

- Proximal margin perforated by many small pores
- Distal margin formed into several open-ended secondary projections that extend posteriorly onto cheek

Preoperculomandibular Canal

Mandibular Portion (Figure 4C)

- Terminates anteriorly in a pair of small round pores that perforate the dentary (Figure 4B)
- Canals just posterior of apex of dentary perforated by a relatively large pair of mental pores
- Medial and lateral margins perforated by several small pores
    - Largest lateral pores located one-quarter and one-half way along the length of the canal
- Lateral margin not formed into projections
- Terminates in a moderately-sized pair of round pores adjacent to origin of preopercle

Preopercular Portion (Figure 4A)

- Proximal margin perforated by numerous moderately-sized pores
- Distal margin formed into several broad extensions that terminate in large pores along edge of preopercle
- Dorsal-most portion of distal margin formed into an open-ended projection that extends posteriorly beyond margin of preopercle onto opercle

Sensory Papillae Pattern

- Row of small papillae along median of mandibular canal
    - Extends posteriorly onto ventral flange of preopercle
- Sensory papillae on anterior portion of basihyal

Remarks

Apogon (*Brephamia*) is a monotypic subgenus. *Brephamia* possesses a relatively simple cephalic lateralis system with little secondary canal development. The supraorbital canal does not extend to the tip of the snout and is characterized by the presence of a large nasal pore and a large interorbital pore. The distal margins of the infraorbital and medial margins of the supraorbital canals are developed into only a few, narrow projections. The development of the anterior margin of the supratemporal canal into a projection is rare among apogonids. This character is also possessed by species of the genus *Siphamia*. The anterior margin of the supratemporal canal of *Siphamia* is developed into multiple projections, whereas, in *Brephamia* the margin is developed into a single median projection.

A.

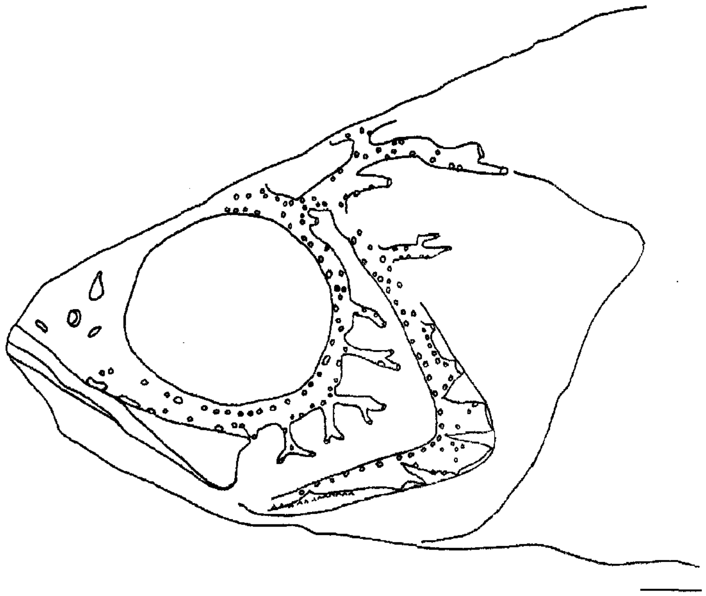


Figure 4. Cephalic lateralis of *Apogon* (*Brephamia*) *parvulus*. A. Lateral view

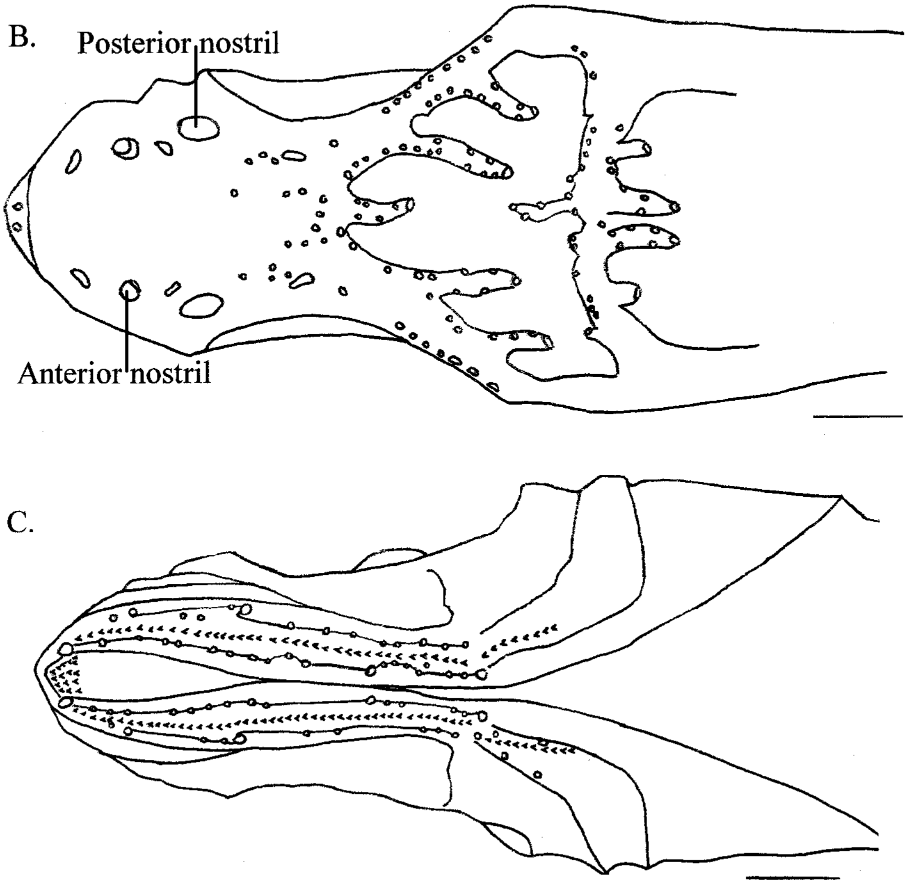


Figure 4 (continued). Cephalic lateralis of *Apogon* (*Brephamia*) *parvulus*. B. Dorsal view, C. Ventral view

Apogon (*Jaydia*) Smith, 1961

Material Examined

Type species: *Apogon ellioti* Day, 1875 [= *Apogon truncatus* Bleeker, 1854[b], according to Gon (1996)], by original designation; CAS 29412; 3, 74.8—80.8 mm.

Apogon poecilopterus Cuvier in Cuvier & Valenciennes, 1828; BPBM 29962; 2, 70.0—74.1 mm

Supraorbital Canal

<u>Nasal Portion</u>

- Extends almost to tip of snout (Figure 5A)
- Terminates anteriorly in a slit-like pore
    - Lateral edge of pore up-turned toward anterior nostril
    - Lateral edge of pore just anterior and medial of anterior nostril
- Lateral margin perforated by a moderately-sized lunate pore just medial to posterior nostril (Figure 5B)
- Margins and median perforated by many small pores
    - Pores concentrated toward canal margins

<u>Interorbital Portion</u>

- Margins and median perforated by many small pores
- Lateral margin perforated by a moderately-sized, oval-shaped pore in anterior interorbital space

Postorbital Portion

- Canal formed into a few secondary extensions that project posteriorly along median of postorbital space
    - Margins of extensions densely perforated by small pores
    - Each extension terminates in a single, distinct pore-opening
    - Extensions do not terminate in a distinct pore
- Expanse of canal between dorsoposterior margin of orbit and secondary extensions perforated by numerous small pores

Supratemporal Canal (Figure 5B)

- Anterior margin perforated by numerous small pores
- Posterior margin formed into numerous open-ended, posteriorly projecting extensions
    - Margins of extensions perforated by few small pores

Infraorbital Canal (Figure 5A)

Lachrymal Portion

- Terminates anteriorly in a moderately-sized, slit-like pore located just posterior of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two long, slit-like pores
- Median superior to lachrymal pores perforated by numerous small pores

Suborbital Portion

- Margins and median perforated by many small pores
- Distal margin of posterior portion forming projections that terminate in pores along maxilla

Postorbital Portion

- Proximal margin perforated by numerous small pores
- Distal margin forming numerous open-ended, projections that extend posteriorly onto cheek
  - Margins of projections perforated by numerous small pores

Preoperculomandibular Canal

Mandibular Portion (Figure 5C)

- Terminates anteriorly in a pair of pores that perforate the dentary
- Canals just posterior of apex of dentary perforated by a moderately-sized pair of oval-shaped mental pores
- Medial and lateral margins perforated by numerous small pores
- Lateral margin not formed into extensions
- Mandibular portion terminates in a large pore adjacent to origin of preopercle

Preopercular Portion (Figure5A)

- Proximal margin perforated by numerous small pores
- Distal margin forming projections that terminate in pores along ventral and vertical edges of preopercle
  - Margins of projections perforated by numerous small pores
- Dorsal-most portion of distal margin forming numerous open-ended projections that extend beyond margin of preopercle onto opercle
  - Margins of projections perforated by numerous small pores

Sensory Papillae Pattern

- Sensory papillae covering median of mandibular canal in short semi-longitudinal rows
- Sensory papillae densely concentrated on anterior portion of basihyal, forming a chevron pattern posteriorly
- Transverse row of papillae on opercle just posterior of margin of preopercle

Remarks

The supraorbital canal terminates just short of the tip of the snout in species of *Jaydia*, and is characterized by the presence of two large pores perforating the lateral margin, the first near the posterior nostril and the second in the mid-interorbital space.

Numerous small pores perforate the anterior margin of the supratemporal canal. A few small pores perforate the canal median in *Apogon poecilopterus*, but not in *A. truncatus*. The posterior margin in all *Jaydia* species is formed into a number of highly perforated, posteriorly projecting extensions. The extensions of *A. poecilopterus* are comparatively longer and narrower than are those of *A. truncatus*.

The general pore and canal configuration of this section is consistent across the species. A few sensory papillae are present in the internarial space of *A. poecilopterus*. Numerous small pores perforate the margins of the preoperculomandibular canal in *Jaydia* species. The medians of both the mandibular and preopercular sections are more densely perforated in *A. poecilopterus* than in *A. truncatus*. Sensory papillae are present on the basihyal and canal medians in these species.

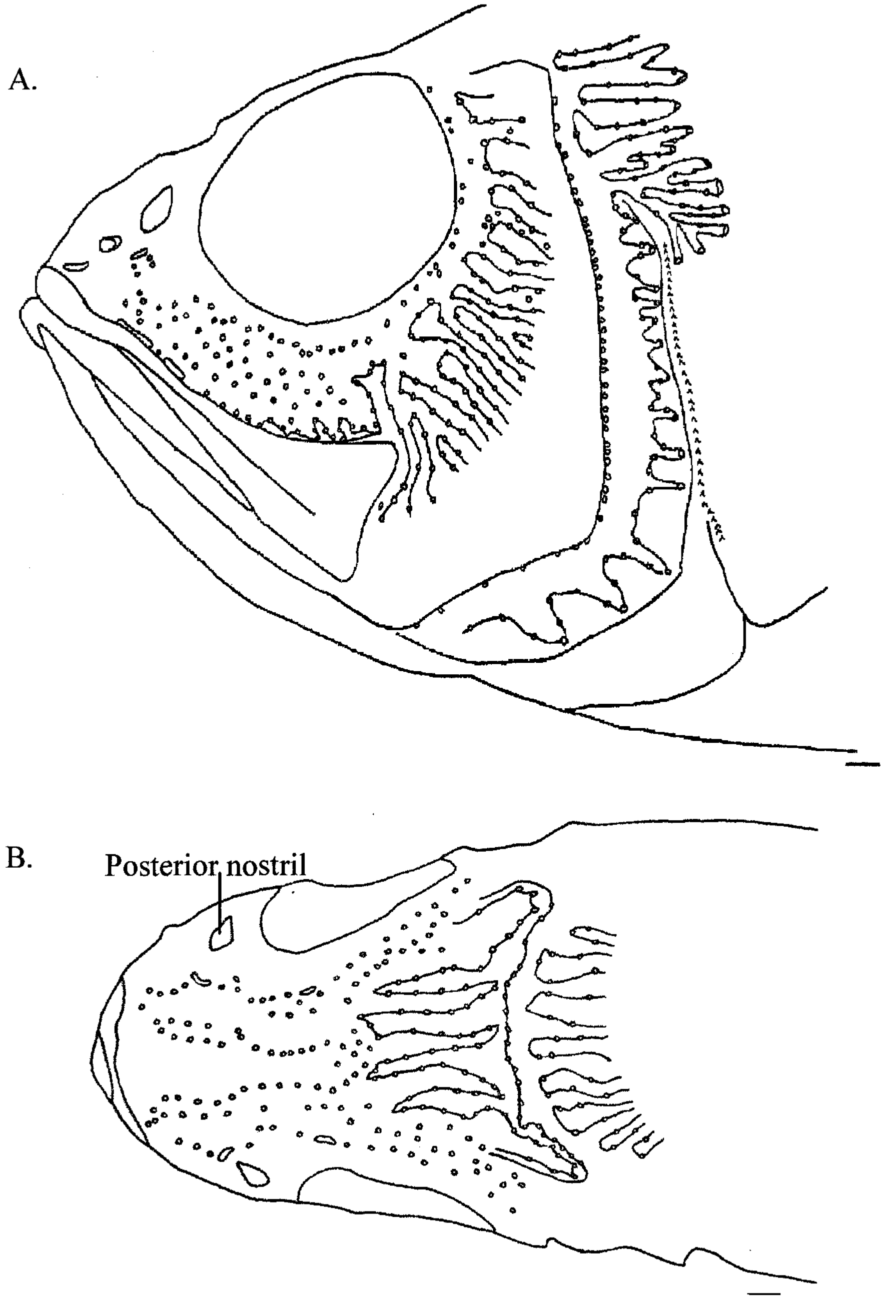


Figure 5. Cephalic lateralis system of *Apogon* (*Jaydia*) *truncatus*. A. Lateral view, B. Dorsal view

C.

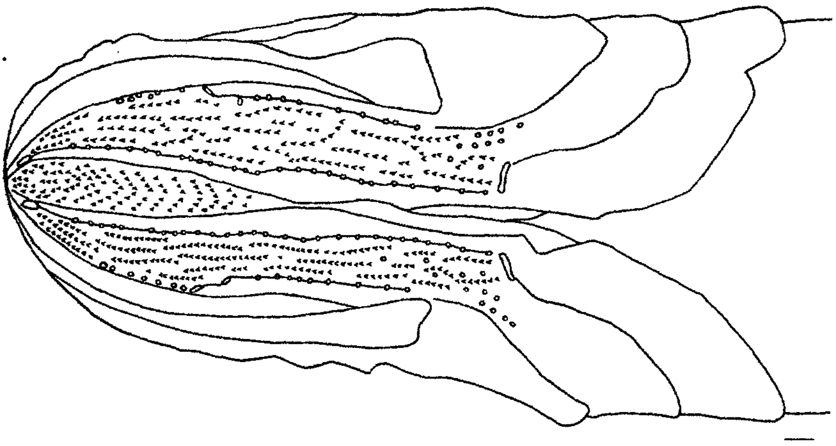


Figure 5 (continued). Cephalic lateralis system of *Apogon* (*Jaydia*) *truncatus*. C. Ventral view.

Apogon (*Lepidamia*) Gill, 1863

Material Examined

Type species: *Apogon kalosoma* Bleeker, 1852[a], by original designation (also monotypic); BPBM 27660; 5, 42.6—68.8 mm

Apogon multitaeniatus Cuvier in Cuvier & Valenciennes, 1828; BPBM 36361; 6, 60.0—99.8 mm

Apogon natalensis Gilchrist & Thompson, 1908; BPBM 21770; 1, 80.0 mm

Supraorbital Canal

Nasal Portion

- Extends to tip of snout (Figure 6A)
- Terminates anteriorly in a slit-like pore that parallels the premaxilla
    - Pore quite wide, extends from just anterior of the anterior nostril to the midline of head

- Lateral margin perforated by a large slit-like pore just dorsal of internarial space (Figure 6B)

Interorbital Portion

- Medial margin, from anterior nostril to longitudinal midpoint of interorbital space, perforated by numerous small pores
- Lateral margin perforated by comparatively fewer pores
    - Pores located at ends of short extensions, particularly along expanse of canal from just anterior of posterior nostril to anterior interorbital space
- Median of interorbital space perforated by a few small pores

Postorbital Portion

- Lateral margin along dorsoposterior margin of orbit perforated by numerous pores
- Canal formed into a number of narrow, open-ended secondary extensions that project posteriorly along median of postorbital space
    - Margins of extensions perforated by numerous small pores

Sensory Papillae Pattern

- Short, longitudinal rows of sensory papillae cover canal from terminal pore through anterior interorbital space
- Transverse rows of papillae radiate dorsally from dorsoposterior margin of orbit

Supratemporal Canal (Figure 6B)

- Anterior margin and median perforated by numerous small pores
- Posterior margin formed into numerous open-ended, secondary projections
    - Margins of projections perforated by numerous small pores

Sensory Papillae Pattern

- Two longitudinal rows of sensory papillae intersect canal near midline of body

Infraorbital Canal (Figure 6A)

Lachrymal Portion

- Terminates anteriorly in a relatively large, slit-like pore just posterior of midpoint of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two long, slit-like pores

Suborbital Portion

- Proximal margin perforated by numerous pores
- Median perforated by few pores
- Distal margin along posterior half of maxilla perforated by several moderately-sized pores

Postorbital Portion

- Proximal margin perforated by numerous pores
- Distal margin formed into numerous open-ended projections that extend posteriorly onto cheek
    - Margins of projections perforated by numerous pores

Sensory Papillae Pattern

- Internarial space densely covered by sensory papillae
    - Papillae extend beyond posterior nostril toward orbit
- Sensory papillae densely cover suborbital canal median, not in clear rows

Preoperculomandibular Canal

Mandibular Portion (Figure 6C)

- Terminates anteriorly in a pair of oval-shaped pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a moderately-sized pair of oval-shaped mental pores
- Medial and lateral margins perforated by numerous pores
- Lateral margin formed into a short, posteriorly projecting extension that terminates in a pore near longitudinal midpoint of maxilla
- Medial and lateral margins formed into open-ended, projections near terminus of maxilla
- Median between terminus of maxilla and terminal pore perforated by several small pores
- Canal terminates posteriorly in a narrow, oval-shaped pore adjacent to origin of preopercle

Preopercular Portion (Figure 6B)

- Proximal margin perforated by numerous small pores
- Distal margin formed into short, open-ended projections that extend toward edge of preopercle
    - Margins of extensions perforated by small pores
- Dorsal-most portion of distal margin formed into open-ended projections that extend posteriorly beyond margin of preopercle onto opercle
    - Margins of projections perforated by several pores

Sensory Papillae Pattern

- Semi-longitudinal rows of papillae cover median portion of mandibular canal
- Sensory papillae form an irregular chevron pattern on basihyal
- Minute papillae cover lips
- Anterior half of lower jaw with minute papillae medial to canal
- Short transverse rows of papillae along proximal margin of ventral preopercular flange
- Rows of papillae on median of vertical preopercular flange
- Transverse row of papillae on opercle just posterior of preopercle

Remarks

The supraorbital canal extends to the tip of the snout in species of *Lepidamia.* A large ovate pore perforates the lateral margin anterior of the posterior nostril. There is no large interorbital pore. Instead, the lateral margin of the anterior interorbital space is formed into a number of projections that extend toward the orbit and terminate in pores. Posteriorly, the distal margin is formed into a number of highly perforated projections that extend posteriorly to nearly meet the supratemporal canal. Although this general canal structure is consistent within *Lepidamia*, the perforation density varies among the species of this subgenus. In *Apogon kalosoma* and *Apogon natalensis* the canal medians are not perforated but are densely covered with sensory papillae. In contrast, the entire canal system, including the skin outside of the canal (to the extent that the entire head is covered with pores), of *A. multitaeniatus* is highly perforated by very small pores and the presence of sensory papillae is greatly reduced.

The supratemporal canal is highly perforated in all species. Numerous small pores perforate the anterior margin and median. The posterior margin in all species is formed into a number of highly perforated, posteriorly projecting extensions.

The general pore and canal configuration of the infraorbital canal is consistent among the species. The canal medians of both *A. kalosoma* and *A. natalensis* are densely covered with sensory papillae. The lips and snout of *A. natalensis* are also covered with minute papillae. In comparison to *A. kalosoma* and *A. natalensis*, the canal median of *A. multitaeniatus* is more densely perforated. In this species the area of the infraorbital canal, as with the supraorbital canal, is highly perforated by small, round pores, so much so that the perforation extends beyond the margins of the canal to cover the entire lateral surface of the head.

In species of *Lepidamia* the lateral margin of the mandibular portion is formed into a number of projections that extend laterally from the canal and terminate in pores. These projections originate from specific areas: the first quarter of the canal is bounded posteriorly by a short projection, as is the second quarter; the third quarter is bounded posteriorly by at least two projections extending from the lateral margin of the canal. The median and medial margin of the mandibular section and the median and proximal margin of the preopercular section are densely perforated. Sensory papillae are present on the basihyal and canal medians in both *A. kalosoma* and *A. natalensis*, whereas, sensory papillae are present only on the basihyal in *A. multitaeniatus*. Minute papillae cover the surface of the skin medial to the mandibular canal in *A. natalensis*.

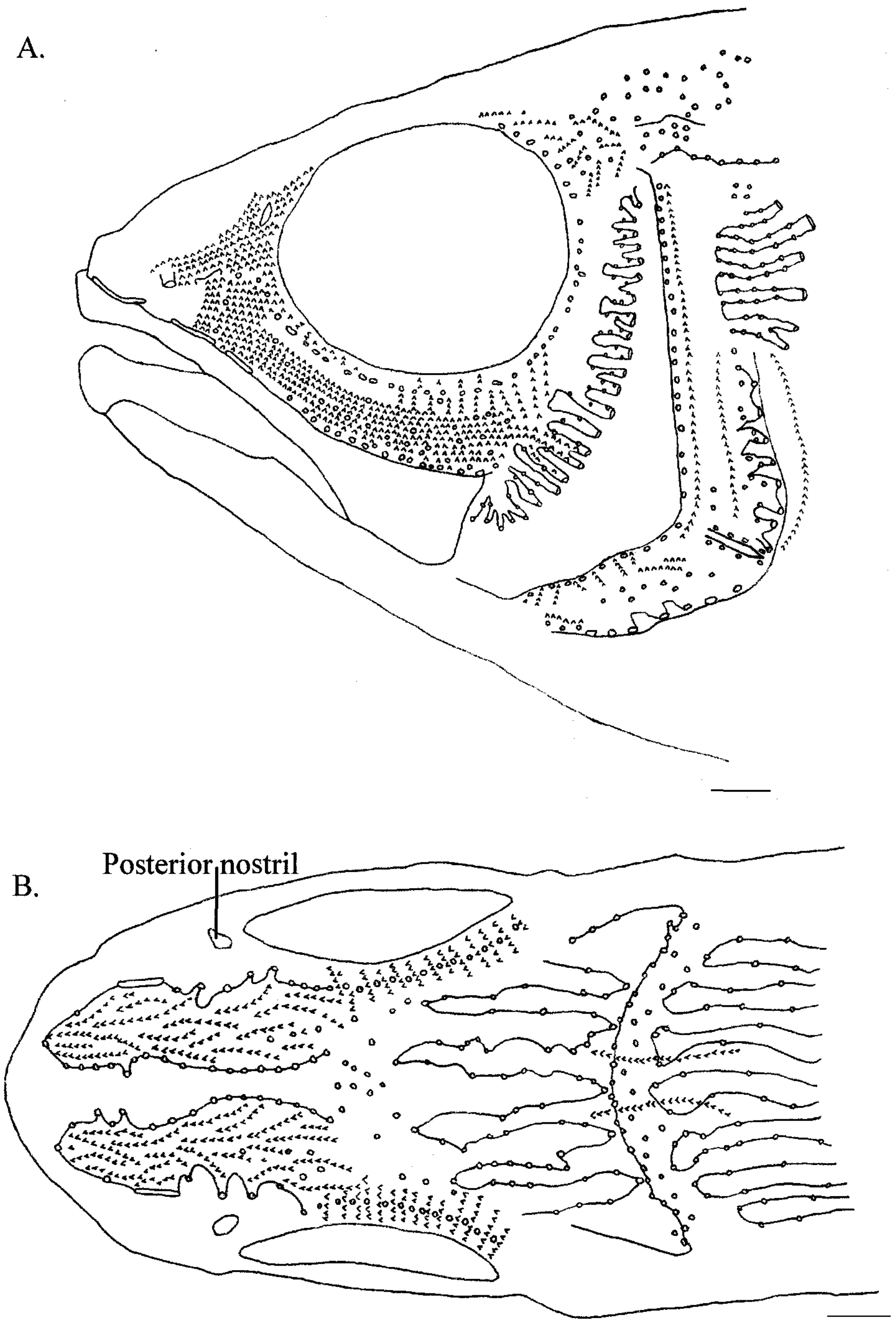


Figure 6. Cephalic lateralis of *Apogon* (*Lepidamia*) *kalosoma*. A. Lateral view, B. Dorsal view

C.

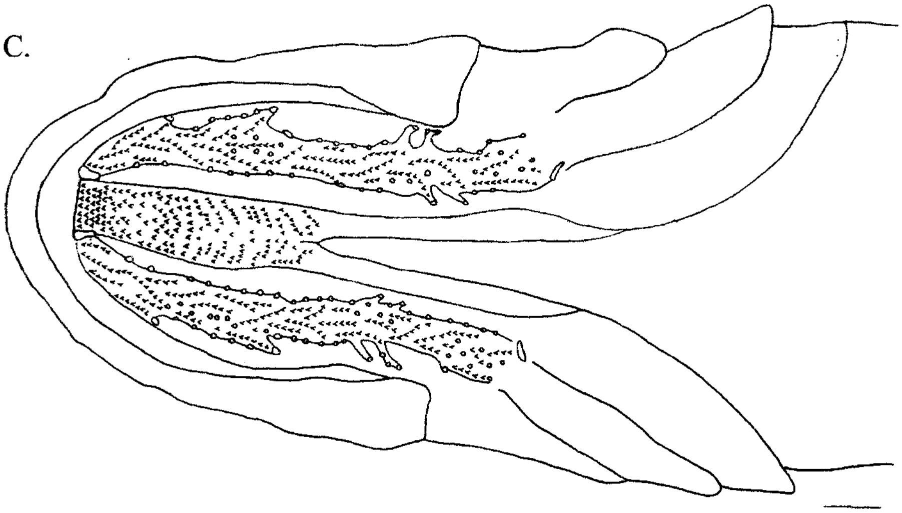


Figure 6 (continued). Cephalic lateralis of *Apogon* (*Lepidamia*) *kalosoma*. C. Ventral view

Apogon (*Ostorhinchus*) Lacepède, 1802

Material Examined

Type species: *Ostorhinchus fleurieu* Lacepède, 1802, by monotypy; SU 27353; 3, 65.3—73.3 mm

Apogon apogonoides (Bleeker, 1856[a]); BPBM 31910; 2, 45.3—50.9 mm

Apogon bandanensis Bleeker, 1854[c]; BPBM 17768; 2, 23.4—41.5 mm

Apogon maculiferus Garrett, 1864; BPBM 24106; 2, 71.2—80.9 mm

Apogon quadrifasciatus Cuvier in Cuvier & Valenciennes, 1828; BPBM 27553; 2, 45.0—53.8 mm

Apogon timorensis Bleeker, 1854[d]; BPBM 30390; 2, 33.4—34.1 mm

Supraorbital Canal

Nasal Portion

- Extends to tip of snout (Figure 7A)
- Terminates anteriorly in a slit-like pore that parallels the premaxilla
- Lateral margin formed into two extensions, each terminates in a pore, with one on either side of the posterior nostril (Figure 7B)

Interorbital Portion

- Medial margin, from anterior nostril to longitudinal midpoint of interorbital space, perforated by numerous small pores
- Lateral margin perforated by a large, oval-shaped pore in anterior interorbital space
- Median of interorbital space perforated by a few small pores

Postorbital Portion

- Lateral margin along dorsoposterior margin of orbit perforated by numerous pores
- Canal formed into a number of narrow, open-ended secondary extensions that project posteriorly along median of postorbital space
    - Margins of extensions perforated by numerous small pores

Sensory Papillae Pattern

- Short, semi-longitudinal rows of sensory papillae covering canal from terminal pore through anterior interorbital space
- Semi-transverse rows of papillae radiate from dorsoposterior margin of orbit
- Longitudinal row of sensory papillae extends along dorsoposterior margin of orbit from large interorbital pore to posterior of the supratemporal canal

- Crosshatch pattern of papillae along dorsoposterior margin of orbit formed from intersection of the longitudinal row with rows radiating from orbit

Supratemporal Canal (Figure 7B)

- Anterior margin and median perforated by numerous small pores
- Posterior margin formed into numerous open-ended, secondary projections
    - Margins of projections perforated by numerous small pores

Infraorbital Canal (Figure 7A)

<u>Lachrymal Portion</u>

- Terminates anteriorly in a relatively large, oval-shaped pore just posterior of midpoint of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two, long slit-like pores

<u>Suborbital Portion</u>

- Proximal margin perforated by numerous pores
- Median perforated by few pores
- Distal margin along posterior half of maxilla perforated by several moderately-sized pores

<u>Postorbital Portion</u>

- Proximal margin perforated by few pores
- Distal margin formed into numerous open-ended projections that extend posteriorly onto cheek
    - Margins of projections perforated by numerous pores

<u>Sensory Papillae Pattern</u>

- Internarial space densely covered by sensory papillae

- Band of papillae, formed from a few longitudinal rows, extends posteriorly along ventral half of suborbital canal, from the second lachrymal pore to just posterior of terminus of maxilla
- Few longitudinal rows of sensory papillae extend from posterior margin of orbit across secondary postorbital projections

Preoperculomandibular Canal

Mandibular Portion (Figure 7C)

- Terminates anteriorly in a pair of oval-shaped pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a relatively large pair of subtriangular mental pores
- Medial margin perforated by few pores
- Lateral margin formed into two short, posteriorly projecting extensions that terminate in pores one-quarter and one-half way along the length of the canal portion
- Lateral margin formed into projections that terminate in pores near the end of the maxilla
- Canal terminates posteriorly in a narrow, oval-shaped pore adjacent to origin of preopercle

Preopercular Portion (Figure 7A)

- Proximal margin perforated by numerous small pores
- Distal margin formed into short, open-ended projections that extend toward edge of preopercle
    - Margins of extensions perforated by small pores

- Dorsal-most portion of distal margin formed into open -ended projections that extend posteriorly beyond margin of preopercle onto opercle
    - Margins of projections perforated by several pores

Sensory Papillae Pattern

- Semi-longitudinal rows of papillae covering median of mandibular canal
- Sensory papillae forming a chevron pattern on basihyal
- Few longitudinal rows of papillae along proximal margin of ventral preopercular flange
- Transverse row of papillae on opercle just posterior of preopercle

Remarks

The supraorbital canal extends to the tip of the snout in species of *Ostorhinchus*. A moderately-sized pore perforates the lateral margin of the canal in the vicinity of the posterior nostril. This pore may be just in front of, medial to, or just posterior of the posterior nostril, depending on the species. The lateral margin, between the posterior nostril and the anterior margin of the orbit, is formed into one or two projections that extend posteriorly toward the orbit and terminate in pores. The interorbital portion of the canal is expanded such that the pores perforating the lateral margins lie along the rim of the orbits. A large pore, large in comparison to other pores in the interorbital area, perforates the lateral margin of the interorbital canal near the midpoint of the eye. The position and relative size of this pore distinguishes it from other pores in the interorbital area, but it is not as large as the interorbital pores possessed by some species in other apogonid taxa. Posteriorly, the distal margin is formed into a number of highly perforated secondary projections that extend posteriorly to nearly meet the supratemporal canal. Sensory papillae are present in short, semi-longitudinal rows on the nasal and anterior interorbital areas of *Ostorhinchus* species, forming a crosshatch pattern along the dorsoposterior margin of the orbit.

The morphology of the supratemporal canal is similar in all species. Numerous small pores perforate the anterior margin and median. The posterior margin is formed into a number of highly perforated, posteriorly projecting secondary extensions.

Internarial papillae are present in all species examined, extending posteriorly to the orbit in *Apogon maculiferus.* The general pore and canal configuration of the infraorbital canal is consistent among the species. A band of sensory papillae is present on the suborbital portion of the canal, extending posteriorly beyond the maxilla in *A. maculiferus* and *A. quadrifasciatus.*

In species of *Ostorhinchus* the lateral margin of the mandibular portion is formed into a number of projections that extend laterally from the canal and terminate in pores. These projections originate from specific areas: the first quarter of the canal is bounded posteriorly by a short projection, as is the second quarter; the third quarter is bounded posteriorly by at least two projections extending from the lateral margin of the canal. The medians of the mandibular portion are moderately perforated in *A. bandanensis* and *A. timorensis*, and densely perforated in *A. maculiferus* and *A. quadrifasciatus.* Sensory papillae are present on the mandibular canal medians, and extend posteriorly to the ventral preopercular flange in all species. The presence of papillae on the vertical preopercular flange varies among species. Minute papillae cover the jaws in *A. timorensis.* The distal margin of the preopercular portion is formed into short, projections that terminate in pores in all species. The perforation density of the margins of these projections varies among species.

A.

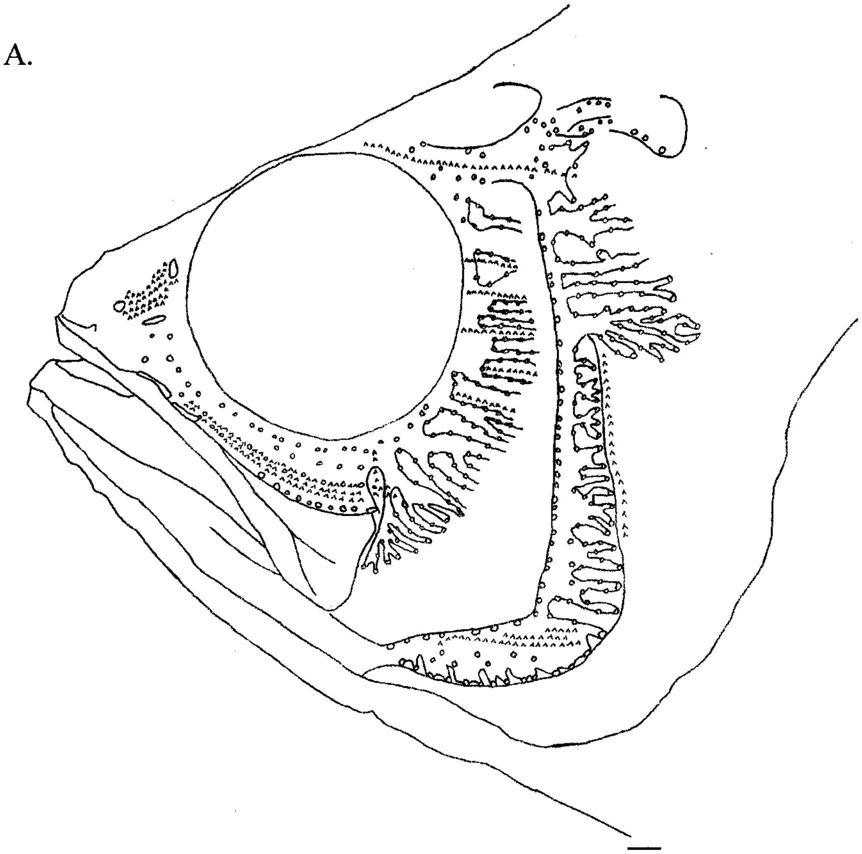


Figure 7. Cephalic lateralis of *Apogon* (*Ostorhinchus*) *fleurieu*. A. Lateral view

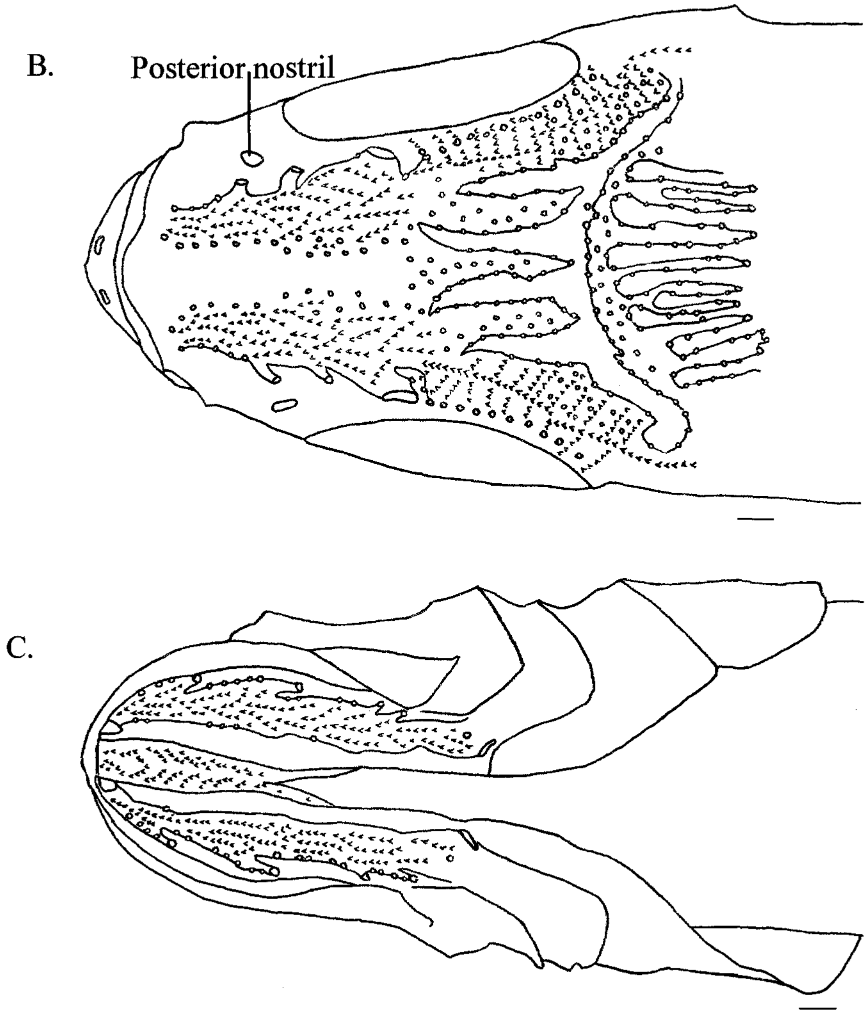


Figure 7 (continued). Cephalic lateralis of *Apogon* (*Ostorhinchus*) *fleurieu*. B. Dorsal view, C. Ventral view

Apogon (*Paroncheilus*) Smith, 1964

Material Examined

Type species: *Paracheilus stauchi* Smith, 1964 [= *Apogon affinis* (Poey, 1875) according to Maugé & Mayer (1990)], by original designation (also monotypic); USNM 213464; 5; 60.3—79.1 mm

Supraorbital Canal

Nasal Portion

- Extends almost to tip of snout (Figure 8A)
- Terminates anteriorly in a slit-like pore that parallels the premaxilla
    - Lateral edge of pore up-turned toward anterior nostril
- Expanse of supraorbital canal perforated by numerous small pores
    - Pores concentrated toward margins, few perforating canal median
- Medial margin between nostrils formed into a few projections that terminate in pores
- Lateral margin adjacent to posterior nostril perforated by a moderately-sized pore

Interorbital Portion

- Lateral margin perforated by a relatively large pore in anterior interorbital space
- Lateral margin along dorsoposterior edge of orbit perforated by several small pores

Postorbital Portion

- Canal formed into a number of open-ended, secondary extensions that project posteriorly toward supratemporal canal
    - Margins and medians of projections densely perforated by numerous small pores

Sensory Papillae Pattern

- Longitudinal row of papillae extending from terminal pore to posterior of supratemporal canal
- Disjunct longitudinal row of papillae from nasal pore to posterior of supratemporal canal
    - Extends along medians of medial-most postorbital projections
- Numerous transverse rows cross median of canal and secondary projections and form crosshatch pattern

Supratemporal Canal (Figure 8B)

- Anterior margin of canal perforated by numerous small pores
- Posterior margin of canal formed into numerous, open-ended, posteriorly projecting extensions
    - Margins of extensions perforated by numerous small pores

Infraorbital Canal (Figure 8A)

Lachrymal Portion

- Terminates anteriorly in a relatively large, oval-shaped pore just posterior of midpoint of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two long, slit-like pores
- Median superior to lachrymal pores perforated by few small pores

Suborbital Portion

- Proximal margin perforated by numerous pores
- Median perforated by few pores

- Distal margin formed into several projections that extend toward maxilla and terminate in pores

<u>Postorbital Portion</u>

- Proximal margin and median perforated by numerous pores
- Distal margin formed into numerous open-ended, branching projections that extend posteriorly onto cheek
    - Margins of projections perforated by few pores

<u>Sensory Papillae Pattern</u>

- Internarial space with rows of papillae
    - Not extending beyond posterior nostril
- Two longitudinal rows, forming a narrow band, extend posteriorly from anterior of the first lachrymal pore to the end of the maxilla
- Numerous rows radiate from ventral margin of orbit
    - Extend ventrally to meet longitudinal band

Preoperculomandibular Canal

<u>Mandibular Portion</u> (Figure 8C)

- Terminates anteriorly in a pair of small round pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a moderately-sized pair of oval-shaped mental pores
- Medial and lateral margins, along entire length of canal portion, formed into numerous short, projections that terminate in pores
- Portion terminates in a large oval-shaped pore adjacent to origin of preopercle

Preopercular Portion (Figure 8A)

- Distal margin formed into open-ended, branching projections that terminate along edge of preopercle
    - Margins of projections perforated by few small pores
- Dorsal-most portion of distal margin formed into open-ended projections that extend posteriorly beyond margin of preopercle onto opercle
    - Margins of projections perforated by several pores

Sensory Papillae Pattern

- Sensory papillae forming a chevron pattern on basihyal
- Two longitudinal rows of along median of mandibular canal
- Ventral preopercular flange with crosshatch pattern of papillae (Figure 8A)
- Median of vertical flange with row of papillae

Remarks

Apogon (*Paroncheilus*) is a monotypic subgenus, characterized by a cephalic lateralis system that is highly branched, densely perforated, and covered by a crosshatch pattern of papillae. Large nasal and interorbital pores perforate the lateral margin of the supraorbital canal. The development of the medial margin, of the nasal portion of the supraorbital canal, into projections terminating in pores is unique to *Paroncheilus.* The postorbital secondary projections are highly perforated, with transverse rows of papillae crossing their medians, and are long, extending nearly to the supratemporal canal. Both margins of the mandibular canal of *Apogon affinis* are formed into short projections along their entire length.

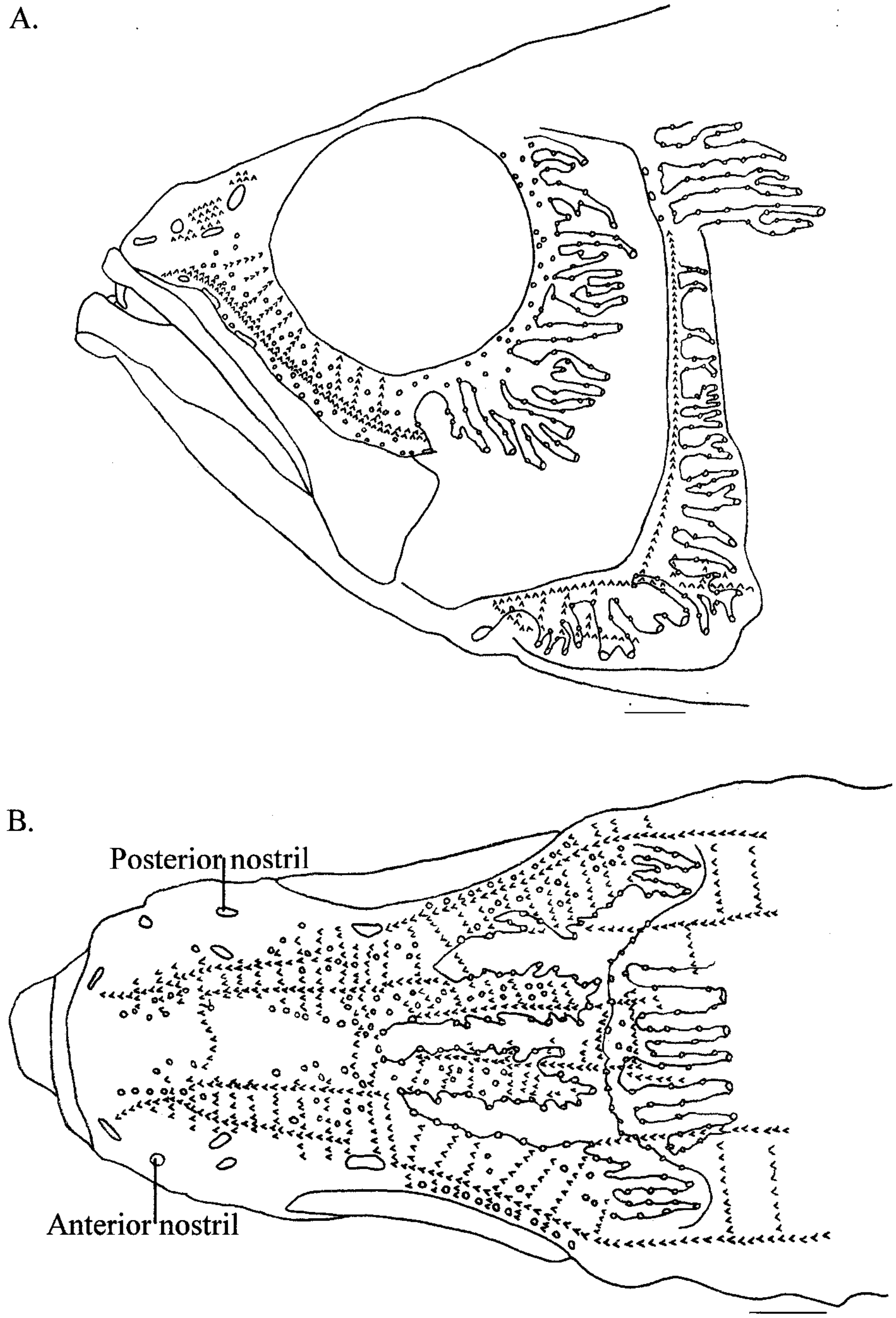


Figure 8. Cephalic lateralis of *Apogon* (*Paroncheilus*) *affinis*. A. Lateral view, B. Dorsal view

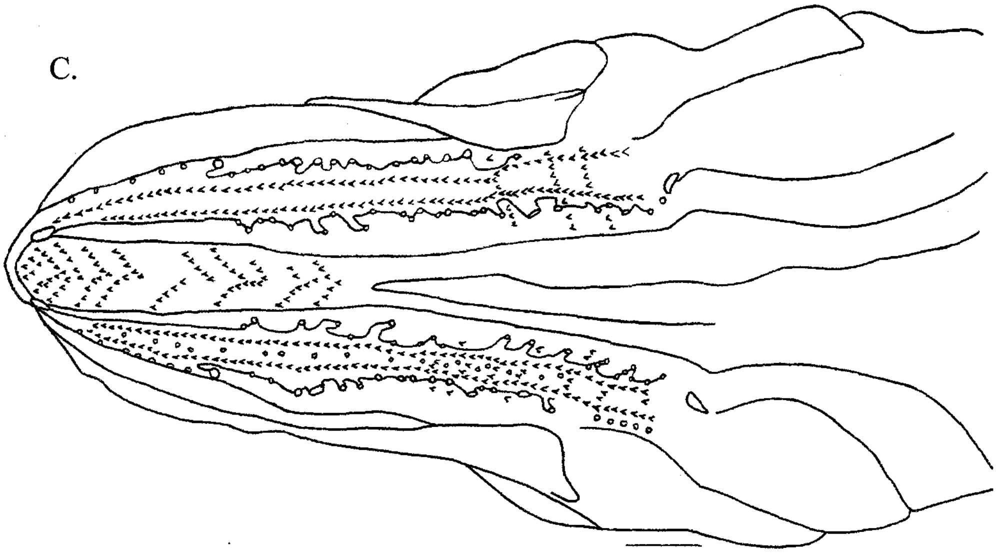


Figure 8 (continued). Cephalic lateralis of *Apogon* (*Paroncheilus*) *affinis*. C. Ventral view

Apogon (*Pristiapogon*) Klunzinger, 1870

Material Examined

Type species: *Apogon fraenatus* Valenciennes, 1832, by monotypy; BPBM 23389; 3, 33.6—36.6 mm

Apogon kallopterus Bleeker, 1856[a]; BPBM 38182; 2, 32.3—45.9 mm

Apogon taeniopterus Bennett, 1836; BPBM 33973; 1, 109.0 mm.

Supraorbital Canal

<u>Nasal Portion</u>

- Extends to tip of snout (Figure 9A)
- Terminates anteriorly in a slit-like pore that parallels the premaxilla
- Expanse of supraorbital canal perforated by numerous small pores
  - Pores concentrated toward margins, few perforating canal median

- Lateral margin, anterior of posterior nostril, perforated by a few moderately-sized pores
    - Pore closest to posterior nostril only slightly larger than other pores in series

Interorbital Portion

- Lateral margin perforated by a large pore in anterior interorbital space

Postorbital Portion

- Lateral margin perforated by numerous moderately-sized pores along dorsoposterior margin of orbit
- Canal formed into a number of open-ended, secondary extensions that project posteriorly over midline of body
    - Margins of projections perforated by numerous small pores

Sensory Papillae Pattern

- Dorsal surface of snout with minute sensory papillae (Figure 9B)
- Small sensory papillae covering canal from terminal supraorbital pore through interorbital space
    - Pattern along first third of supraorbital canal not distinct
- Transverse rows of papillae posterior of posterior nostril
- Longitudinal row of sensory papillae extends posteriorly from posterior nostril along dorsal margin of orbit to supratemporal canal
- Transverse rows of papillae radiate from dorsoposterior margin of orbit

Supratemporal Canal (Figure 9B)

- Anterior margin of canal perforated by numerous small pores
- Posterior margin of canal formed into numerous, open-ended, posteriorly projecting extensions
    - Margins of extensions perforated by numerous small pores

Infraorbital Canal

Lachrymal Portion (Figure 9A)

- Terminates anteriorly in a large, slit-like pore just posterior of the midpoint of the internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two long, slit-like pores

Suborbital Portion

- Canal margins perforated by several small and moderately-sized pores

Postorbital Portion

- Proximal margin perforated by several moderately-sized pores
- Distal margin formed into numerous open-ended projections that extend posteriorly onto cheek
    - Margins of projections perforated by few pores

Sensory Papillae Pattern

- Internarial space and region anterior of orbit densely covered by sensory papillae
- Longitudinal band of papillae extends along median of suborbital canal to end maxilla
- Numerous transverse rows of papillae radiate from ventral rim of orbit
    - Extends ventrally to meet suborbital longitudinal band

Preoperculomandibular Canal

Mandibular Portion (Figure 9C)

- Terminates anteriorly in a pair of small round pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a large pair of mental pores
- Medial margin perforated by numerous small pores
- Lateral margin perforated by numerous pores
    - Pore perforating margin one-quarter and one half way along the length of the canal enlarged
    - Canal bulges slightly in these regions
- Pores perforating margins near terminus of maxilla located on ends of short projections
- Terminates in a large slit-like pore just medial to origin of preopercle

Preopercular Portion (Figure 9A)

- Proximal margin perforated by numerous moderately-sized pores
- Median perforated by a few small pores
- Distal margin formed into several relatively broad, open-ended projections that extend toward edge of preopercle

Sensory Papillae Pattern

- Minute papillae covering area between dentary pores, area medial to anterior portion of canal, and surface of both jaws
- Sensory papillae in rows on anterior portion of basihyal, becoming chevron-shaped posteriorly
- Small papillae covering median of mandibular canal

  - Two longitudinal rows continue posteriorly onto ventral preopercular flange (Figure 9A, C)
- Ventral portion of preopercular flange with crosshatch pattern of sensory papillae (Figure 9C)

Remarks

The supraorbital canal extends to the tip of the snout in *Pristiapogon* species. A few moderately-sized pores perforate the lateral margin of the canal anterior of the posterior nostril. The large pore adjacent to the posterior nostril in many apogonids is absent; the pore closest to the posterior nostril is only slightly larger than the other pores in the series. A large pore perforates the lateral margin in the anterior interorbital space of *Apogon fraenatus.* In *Apogon kallopterus* and *Apogon taeniopterus* this pore is absent; the lateral margin is instead formed into a number of extensions that terminate in pores along the dorsal margin of the orbit. Posteriorly, the distal margin is formed into several highly perforated projections that extend posteriorly to nearly meet the supratemporal canal. Sensory papillae are present on the nasal and interorbital areas, forming a crosshatch pattern along the dorsoposterior margin of the orbit. Minute papillae are present on the jaws, snout, and mental area in these species.

Numerous small pores perforate the anterior margin of the supratemporal canal in *A. fraenatus* and *A. kallopterus*. The anterior margin of *A. taeniopterus* is formed into a central, anteriorly projecting, open-ended extension (similar to *Apogon* (*Brephamia*) and *Siphamia* species). A short, longitudinal row of papillae flanks each side of the extension. Numerous small pores perforate the remainder of the anterior margin in *A.*

taeniopterus. The posterior margin of the supratemporal canal in *Pristiapogon* species is formed into a number of highly perforated, posteriorly projecting extensions.

Internarial papillae were present in all species examined, extending posteriorly to the orbit in *A. fraenatus* and *A. taeniopterus*. Minute papillae are present anterior of the anterior nostril in *A. taeniopterus*. The general pore and canal configuration of the infraorbital canal is consistent among the species. A band of sensory papillae extends longitudinally along the suborbital portion of the canal in these species. Several transverse rows of sensory papillae radiate from the ventral margin of the orbit to meet this longitudinal band in all species. These transverse rows are more numerous in *A. taeniopterus*.

In species of *Pristiapogon* the projections formed from the lateral margin of the mandibular portion are developed to a variable degree. In *A. taeniopterus* the projections are well developed, as they are in *Ostorhinchus*. In both *A. fraenatus* and *A. kallopterus*, the lateral margin is not developed into projections, but rather, forms bulges where these projections would be. The locations of the projections and/or bulges are similar to those of the species of *Ostorhinchus*, however, in *Ostorhinchus*, the first quarter of the canal is bounded posteriorly by a short projection, as is the second quarter; and the third quarter is bounded posteriorly by at least two lateral projections. Sensory papillae are present on the mandibular canal medians, extending posteriorly onto the ventral preopercular flange, in all species. The presence of papillae on the vertical preopercular flange varies among the species. Sensory papillae are present on the opercle in *A. taeniopterus*. Minute papillae cover the jaws in*A. kallopterus* and *A. taeniopterus*. The distal margin of the preopercular portion is formed into projections that terminate in pores in all species.

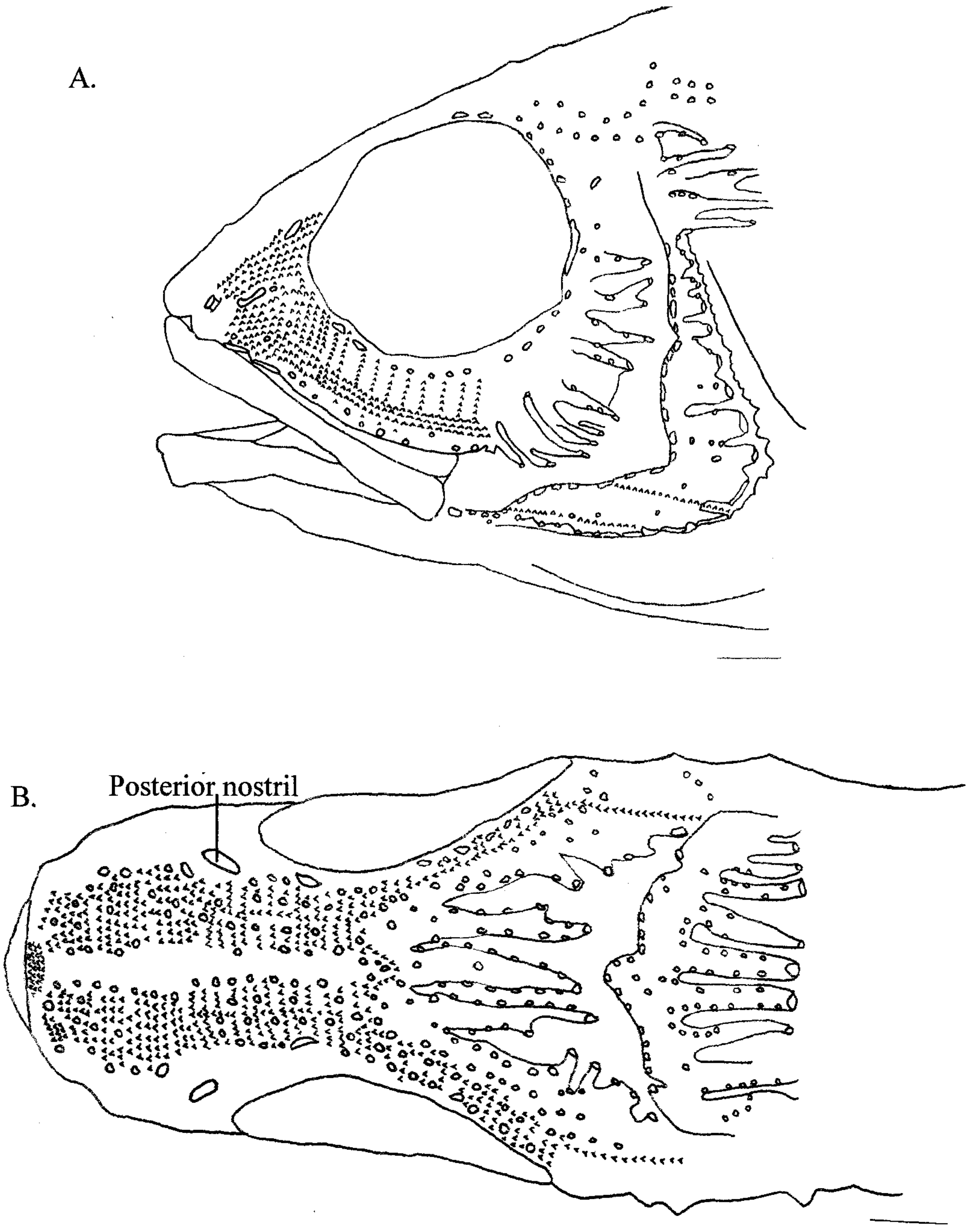


Figure 9. Cephalic lateralis of *Apogon* (*Pristiapogon*) *fraenatus*. A. Lateral view, B. Dorsal view

C.

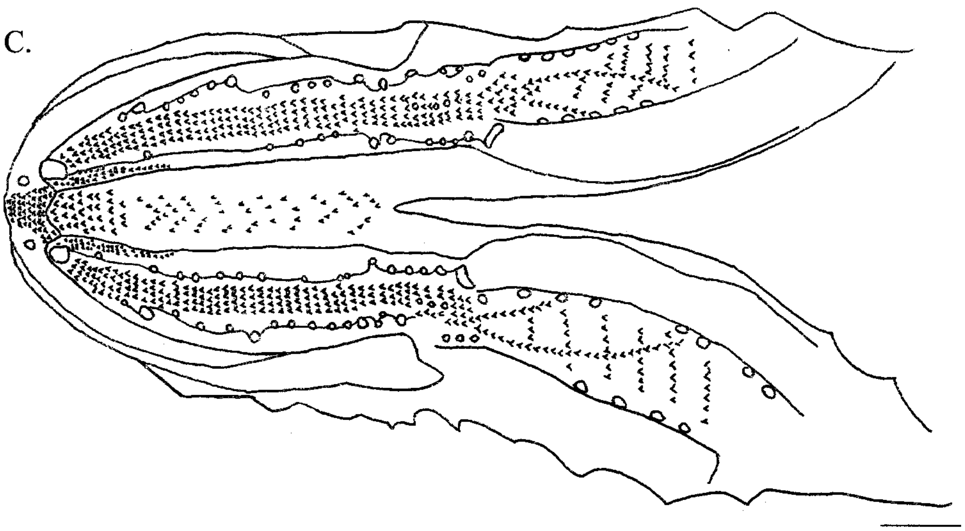


Figure 9 (continued). Cephalic lateralis of *Apogon* (*Pristiapogon*) *fraenatus*. C. Ventral view

Apogon (*Pristicon*) Fraser, 1972

Material Examined

Type species: *Apogon trimaculatus* Cuvier in Cuvier & Valenciennes, 1828, by original designation; BPBM 7480; 1, 63.1 mm

Supraorbital Canal

Nasal Portion

- Extends almost to tip of snout (Figure 10A)
- Terminates anteriorly in a slit-like pore that parallels the premaxilla
- Lateral margin, just anterior of and medial to posterior nostril, perforated by a large, oval-shaped pore (Figure 10B)
- Lateral margin, adjacent to posterior nostril, formed into a projection that terminates in a pore

Interorbital Portion

- Margins and median, from terminal pore through interorbital space, perforated by many small pores
- Lateral margin just anterior of longitudinal midpoint of orbit formed into a projection that terminates in a pore and extends posteriorly along orbit
- Median of interorbital space perforated by numerous small pores

Postorbital Portion

- Canal formed into several secondary extensions that project posteriorly along median of body from postorbital area toward supratemporal canal
  - Margins of extensions perforated by numerous small
- Expanse between dorsoposterior margin of orbit and extensions perforated by numerous small pores

Sensory Papillae Pattern

- Longitudinal row of papillae extends posteriorly from supraorbital terminal pore to supratemporal canal
- Nasal portion of supraorbital canal covered by semi-transverse rows of papillae
- Papillae in preorbital and interorbital space in many short transverse rows
- Rows of papillae radiating dorsally from orbit toward secondary extensions of supraorbital canal
- Crosshatch pattern of papillae formed from intersection of longitudinal row by the numerous transverse rows

Supratemporal Canal (Figure 10B)

- Anterior margin perforated by numerous small pores
- Posterior margin formed into numerous open-ended, posteriorly projecting secondary extensions
    - Margins of extensions perforated by few pores

Sensory Papillae Pattern

- Longitudinal row of papillae extends posteriorly from supraorbital canal beyond supratemporal canal
    - Several transverse rows extend ventrally from longitudinal row
- Two, longitudinal rows of papillae, located near midline of body, project posteriorly along extensions

Infraorbital Canal (Figure 10A)

Lachrymal Portion

- Terminates anteriorly in a large, slit-like pore located just posterior of midpoint of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two long, slit-like pores
- Median of canal superior to lachrymal pores perforated by numerous small pores

Suborbital Portion

- Margins and median perforated by many small pores

Postorbital Portion

- Proximal margin perforated by numerous small pores
- Median perforated by few pores

- Distal margin formed into several open-ended, projections that extend posteriorly onto cheek
    - Margins of projections perforated by numerous small pores

Sensory Papillae Pattern

- Internarial space with several rows of sensory papillae
    - Few rows extend posteriorly beyond nostril toward orbit
- Two longitudinal rows of papillae extend posteriorly along ventral portion of suborbital canal, from first lachrymal pore to just posterior of terminus of maxilla
- Crosshatch pattern formed from the intersection of the suborbital longitudinal row by numerous transverse rows

Preoperculomandibular Canal

Mandibular Portion (Figure 10C)

- Terminates anteriorly in a pair of small round pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a moderately-sized pair of mental pores
- Medial and lateral margins perforated by numerous small pores
- Lateral margin formed into a short, posteriorly projecting extension that terminates in a pore near midpoint of maxilla
- Both margins, near the terminus of the maxilla, perforated by pores located at the tips of small projections
- Portion terminates in a large, oval-shaped pore just medial to origin of preopercle

Preopercular Portion (Figure 10A)

- Margins and median of ventral preopercular flange perforated by numerous small pores
- Proximal margin of vertical preopercular flange perforated by numerous, moderately-sized pores
- Distal margin of vertical preopercular flange formed into open-ended projections that terminate along edge of preopercle
    - Margins, near base of projections, perforated by few small pores
- Dorsal-most portion of distal margin formed into open-ended projections that extend posteriorly beyond margin of preopercle onto opercle
    - Margins of projections perforated by several pores

Sensory Papillae Pattern

- Sensory papillae densely concentrated on anterior portion of basihyal, forming a chevron pattern posteriorly
- Several longitudinal rows of sensory papillae covering mandibular median
- Ventral preopercular flange with crosshatch pattern of sensory papillae (Figure 10A, C)
- Median of vertical preopercular flange with row of papillae
- Transverse row of papillae on opercle just posterior of margin of preopercle

Remarks

Pristicon is a monotypic subgenus. The pore and papillae patterns of *Apogon trimaculatus* are similar to those of the *Pristiapogon* species but with a few notable exceptions. A large pore perforates the lateral margin of the supraorbital canal just dorsal of the internarial space in *A. trimaculatus*. This pore is absent in *Pristiapogon*. In *A. trimaculatus*, the lateral margin medial to the posterior nostril forms a short projection that terminates in a pore. This same morphology is repeated again in the anterior interorbital space. A large nasal and a large interorbital pore replace these two projections in *Pristiapogon*. In *A. trimaculatus* the lateral margin, half way along the length of the mandibular canal, is formed into a short projection that terminates in a pore. Posteriorly, the pores perforating both margins are located at the ends of short projections. In *Pristiapogon* the canal bulges in the corresponding areas but is not developed into projections.

A.

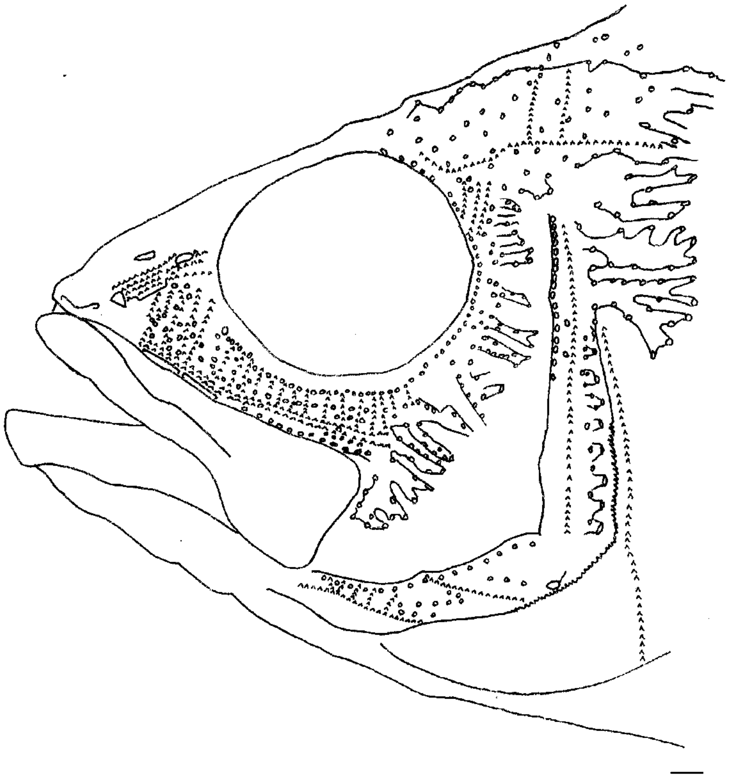


Figure 10. Cephalic lateralis system of *Apogon* (*Pristicon*) *trimaculatus*. A. Lateral view

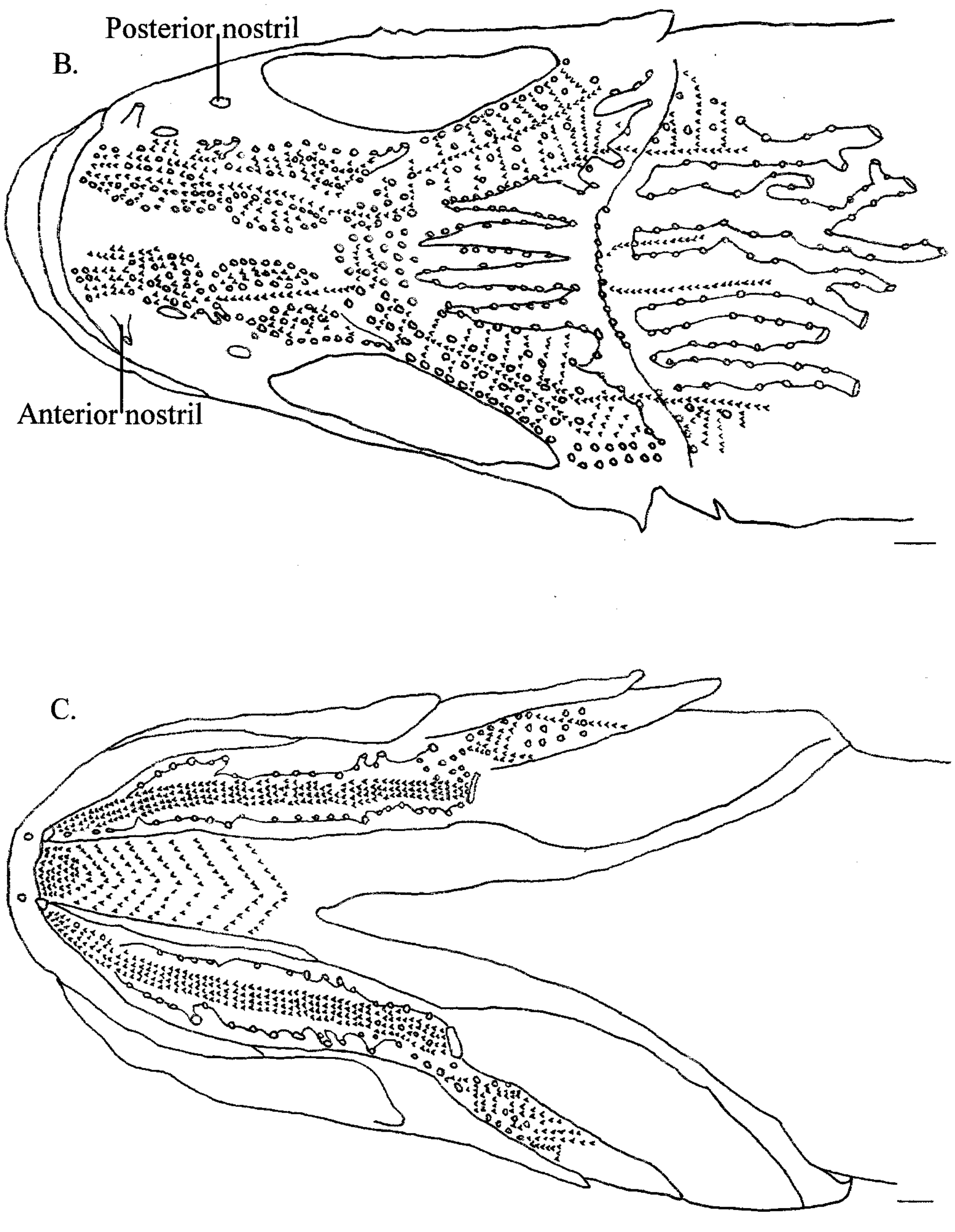


Figure 10 (continued). Cephalic lateralis system of *Apogon* (*Pristicon*) *trimaculatus*. B. Dorsal view, C. Ventral view.

Apogon (*Yarica*) Whitley, 1930

Material Examined

Type species: *Apogon yarica var. torresiensis* Castelnau, 1875, [variety elevated to species level for the purposes of the type species, no known type specimens, status of this species is uncertain], by original designation (also monotypic).

Apogon hyalosoma Bleeker, 1852[b]; BPBM 22187; 1, 94.0 mm

Supraorbital Canal

Nasal Portion

- Extends almost to tip of snout (Figure 11A)
- Terminates anteriorly in a slit-like pore that parallels the premaxilla
  - Pore located medial to anterior nostril
- Lateral margin just anterior of and medial to posterior nostril perforated by moderately-sized pore
- Medial margin, opposite nasal pore, perforated by three small pores

Interorbital Portion

- Interorbital portion of canal perforated by few small pores
- Lateral margin near longitudinal midpoint of orbit formed into two short, projections that extend posteriorly along orbit and terminate in pores

Postorbital Portion

- Lateral margin along dorsoposterior portion of orbit perforated by several small pores
- Canal formed into several secondary extensions that project posteriorly along median of body from postorbital area toward supratemporal canal
  - Margins of extensions perforated by numerous small pores

Sensory Papillae Pattern

- Snout anterior of terminal pore covered with minute sensory papillae (Figure 11A, B)
- Portion of supraorbital canal anterior of posterior nostril covered with small papillae
- Few rows of sensory papillae radiating from dorsoposterior margin of orbit

Supratemporal Canal (Figure 11B)

- Anterior margin of canal perforated by few small pores

Infraorbital canal (Figure 11A)

Lachrymal Portion

- Terminates anteriorly in a large oval-shaped pore located just posterior of the midpoint of the internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two long, slit-like pores

Suborbital Portion

- Proximal margin perforated by few small pores

Postorbital Portion

- Proximal margin perforated by several small pores
- Distal margin formed into a few open-ended projections that extend posteriorly onto cheek
    - Margins of projections sparsely perforated by small pores

Sensory Papillae Pattern

- Internarial space covered with minute sensory papillae

Preoperculomandibular Canal

Mandibular Portion (Figure 11C)

- Terminates anteriorly in a pair of small round pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a large pair of oval-shaped mental pores
- Medial and lateral margins perforated by a few small pores
- Lateral margin formed into extensions that terminate in pores one-quarter and one-half way along the length of the maxilla
- Lateral margins, near the widest part of the maxilla, formed into two short projections that terminate in pores
- Terminates in a relatively large, slit-like pore just medial to origin of preopercle

Preopercular Portion (Figure 11A)

- Distal margin of ventral preopercular flange perforated by a few small pores (Figure 11C)
- Proximal margin of vertical preopercular flange perforated by numerous small pores
- Distal margin formed into a number of open-ended extensions that terminate in pores along posterior edge of the preopercle

Sensory Papillae Pattern

- Minute papillae densely concentrated on anterior portion of basihyal, forming a chevron pattern posteriorly
- Median of mandibular canal covered with minute sensory papillae
    - Pattern difficult to discern
- Small sensory papillae form longitudinal rows on ventral preopercular flange

Remarks

Yarica is a monotypic subgenus. Medial to the posterior nostril, the lateral margin is perforated by a relatively large pore. The lateral margin in the mid-interorbital space is formed into a few short, projections that terminate in pores. These projections are in contrast to the large interorbital pore that is common in a number of other apogonids. The interorbital space of *Apogon hyalosoma* is illustrated without sensory papillae. This portion of the specimen was damaged and papillae were not visible. The presence of sensory papillae on the internarial space, nasal portion of the supraorbital canal, along the dorsoposterior margins of the orbits, and also the dense covering of papillae on the mandibular portion suggest that if the specimen were not damaged, papillae would have been seen in the interorbital area.

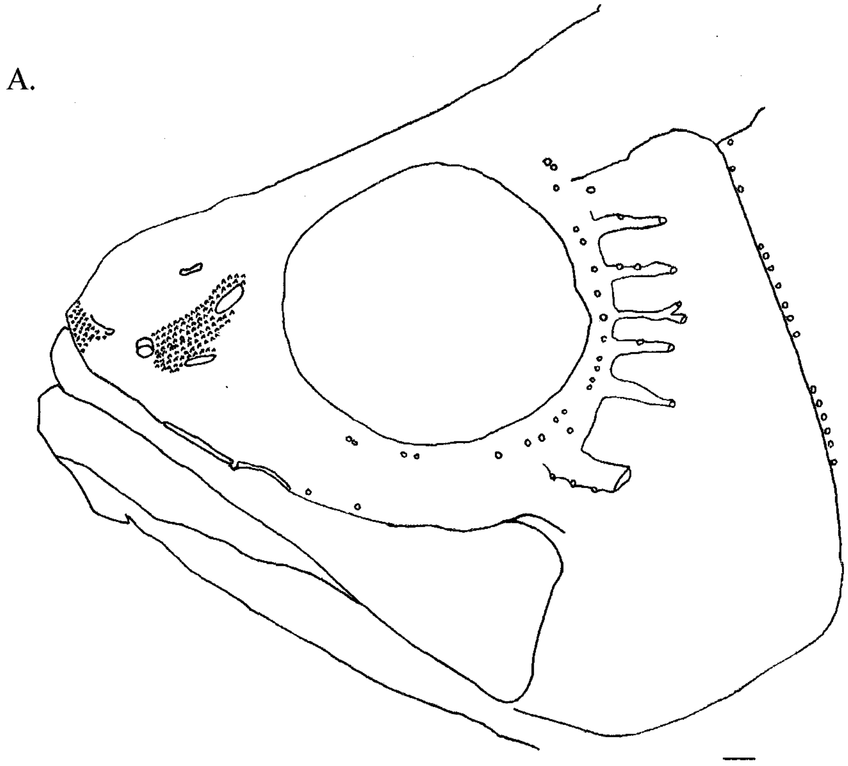


Figure 11. Cephalic lateralis of *Apogon* (*Yarica*) *hyalosoma*. A. Lateral view

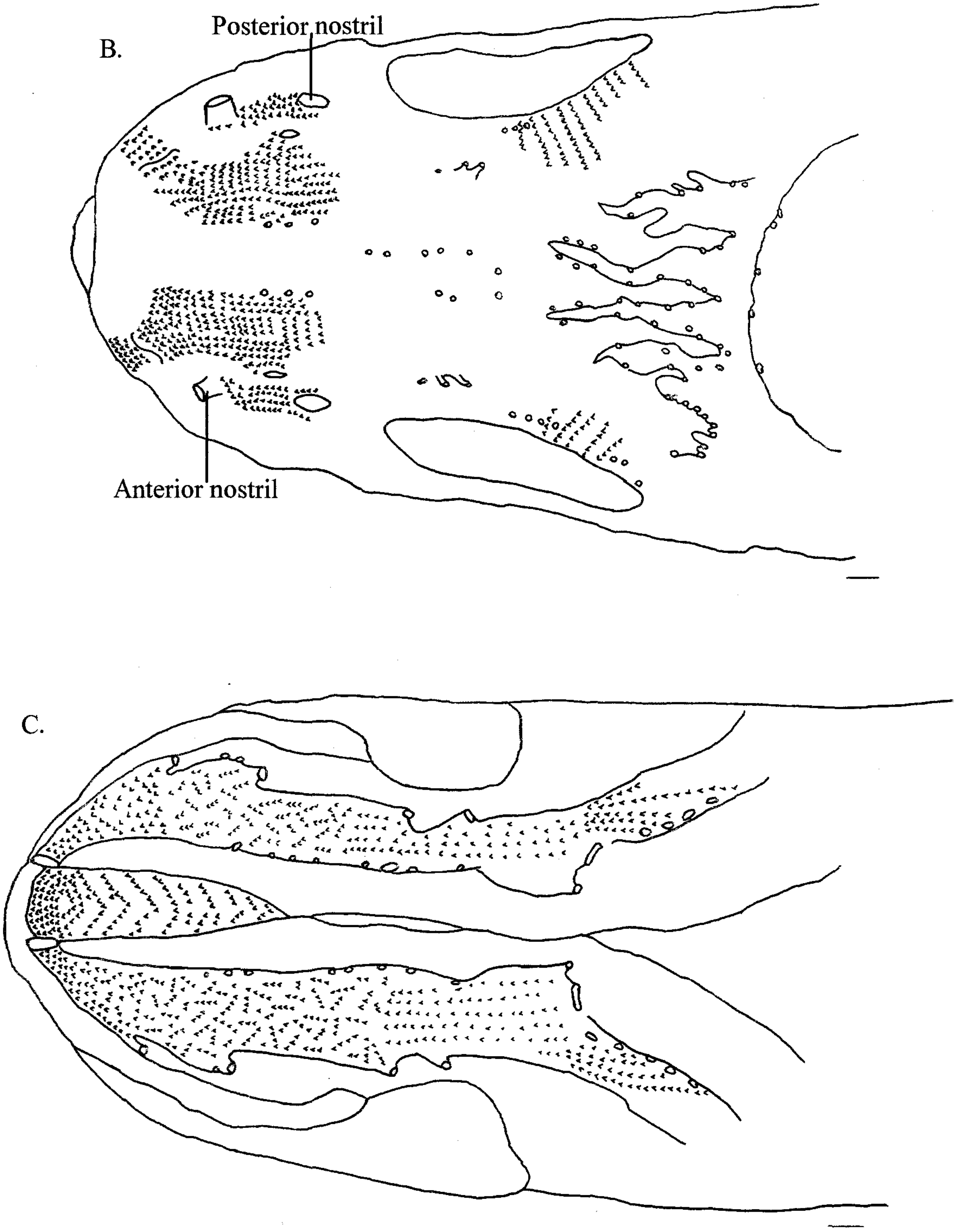


Figure 11 (continued). Cephalic lateralis of *Apogon* (*Yarica*) *hyalosoma*. B. Dorsal view, C. Ventral view

Apogon (*Zapogon*) Fraser, 1972

Material Examined

Type species: *Apogon evermanni* Jordan & Snyder, 1904, by original designation; BPBM 31911; 2, 37.4—75.3 mm; BPBM 9326; 1, 93.4 mm

Supraorbital Canal

<u>Nasal Portion</u>

- Extends to tip of snout (Figure 12A)
- Terminates anteriorly in a wide slit-like pore
    - Lateral edge of pore just medial to and anterior of anterior nostril
- Lateral margin, just anterior of and medial to posterior nostril, perforated by a large, pore (Figure 12B)

<u>Interorbital Portion</u>

- Lateral margin in anterior interorbital space perforated by a large pore
- Posterior interorbital space perforated by three round pores
    - Pores form an equilateral triangle

<u>Postorbital Portion</u>

- Canal formed into two open-ended secondary projections postorbitally
    - Each projection extends dorsally toward midline of body

<u>Sensory Papillae Pattern</u>

- Minute papillae covering pre-nasal area of snout
- Crosshatch pattern of sensory papillae covering expanse of canal from terminal pore through postorbital space

- Transverse rows extend from lateral margin to lateral margin, across median portion of head in mid-interorbital space

Supratemporal Canal (Figure 12B)

- Anterior margin of canal not perforated
- Posterior margin perforated by few moderately sized pores
    - Not formed into secondary projections

Sensory Papillae Pattern

- Crosshatch pattern of papillae across supratemporal canal

Infraorbital Canal (Figure 12A)

Lachrymal Portion

- Terminates anteriorly in a large, oval-shaped pore located just posterior of midpoint of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two long, slit-like pores

Suborbital Portion

- Distal margin of posterior half formed into a few short projections that terminate in pores
    - Margins of projections not perforated
    - Projections do not extend to maxilla, giving the appearance of a perforated suborbital canal median

Postorbital Portion

- Distal margin formed into a few open-ended projections that extend posteriorly
    - Margins of projections not perforated

Sensory Papillae Pattern

- Area between anterior nostril and terminal pore with transverse rows of papillae
- Internarial space with rows of sensory papillae, few rows extend beyond posterior nostril to orbit
- Three longitudinal row of papillae extend along suborbital canal from anterior of first lachrymal pore to terminus of maxilla
- Transverse rows of papillae radiate ventrally from orbit
    - Form suborbital crosshatch pattern by intersection with longitudinal rows
- Crosshatch pattern of sensory papillae covering postorbital portion of infraorbital canal, extends posteriorly onto cheek

Preoperculomandibular Canal

Mandibular Portion (Figure 12C)

- Terminates anteriorly in a pair of moderately-sized round pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a large pair of subtriangular mental pores
- Lateral margin perforated by three moderately-sized pores located one-quarter, two-quarters, and three-quarters along the length of the canal portion
    - Pores not located at ends of extensions
- Posterior two lateral pores are paired by pores perforating the opposing medial margin
- Mandibular portion of canal terminates in a large, slit-like pore adjacent to origin of preopercle

Preopercular Portion (Figure 12A)

- Distal margin formed into projections that terminate in pores along posterior margin of preopercle
- Dorsal-most portion of distal margin formed into a few open-ended projections that extend posteriorly beyond preopercle onto opercle

Sensory Papillae Pattern

- Minute papillae on both jaws
- Basihyal with chevron pattern of papillae
- Mandibular median with semi-longitudinal rows
- Ventral preopercular flange with crosshatch pattern of papillae (12A, C)
- Vertical preopercular flange with two columns of sensory papillae

Remarks

Zapogon is a monotypic subgenus. *Apogon evermanni* is unique in that its canal system is not highly perforated. The structure of the canal system was visualized not by following the outlines formed from perforations, but by inflation of the canals. The pores are relatively few and large in comparison to other species of apogonids, particularly those species currently considered to be members of the large genus *Apogon*. The canals of *A. evermanni* are simple in structure, with little secondary development. The entire surfaces of all canals are densely covered by sensory papillae, to the extent that transverse rows cross the head and longitudinal rows continue posteriorly from the supratemporal canal toward the trunk canal.

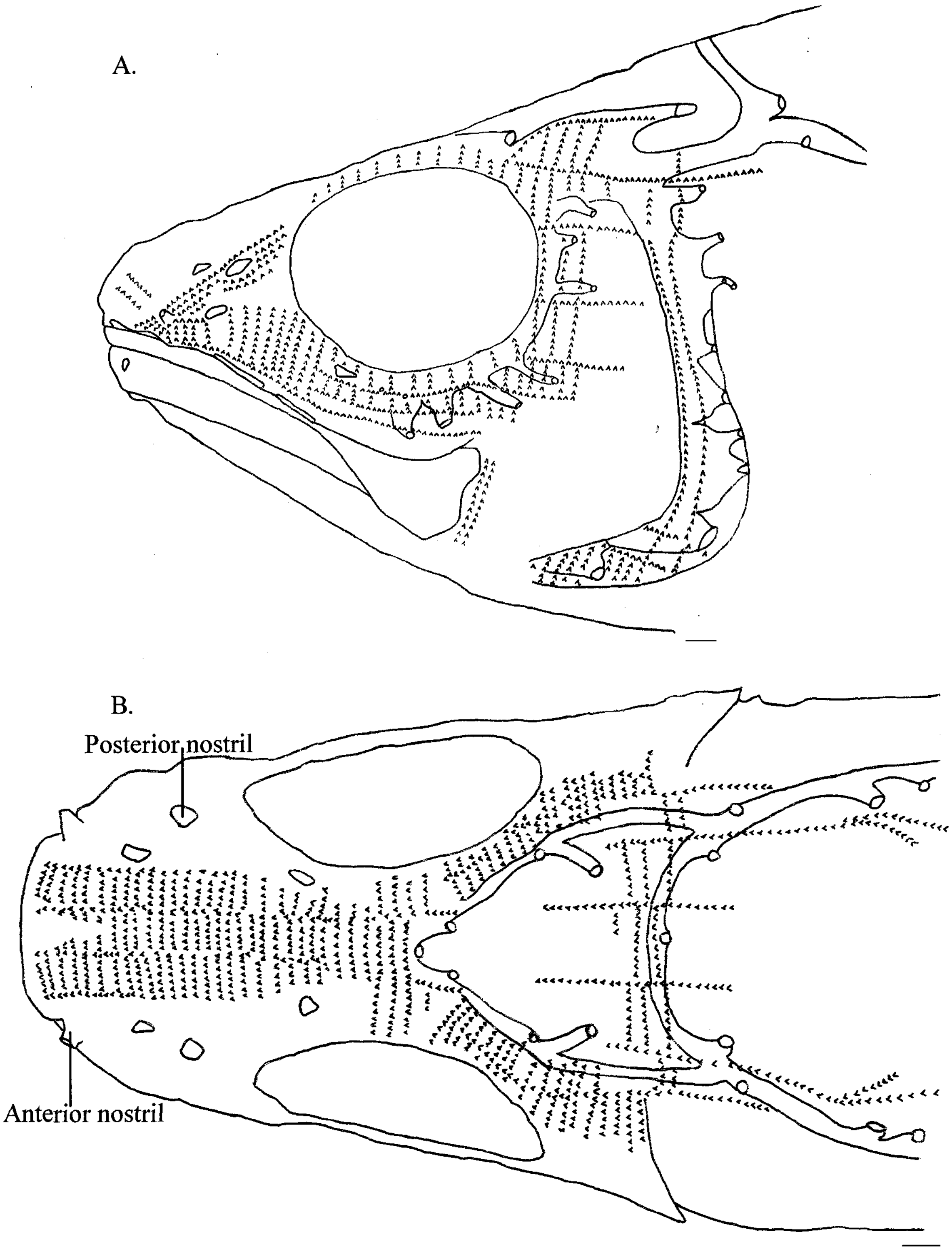


Figure 11. Cephalic lateralis of *Apogon* (*Yarica*) *hyalosoma*. A. Lateral view, B. Dorsal view

C.

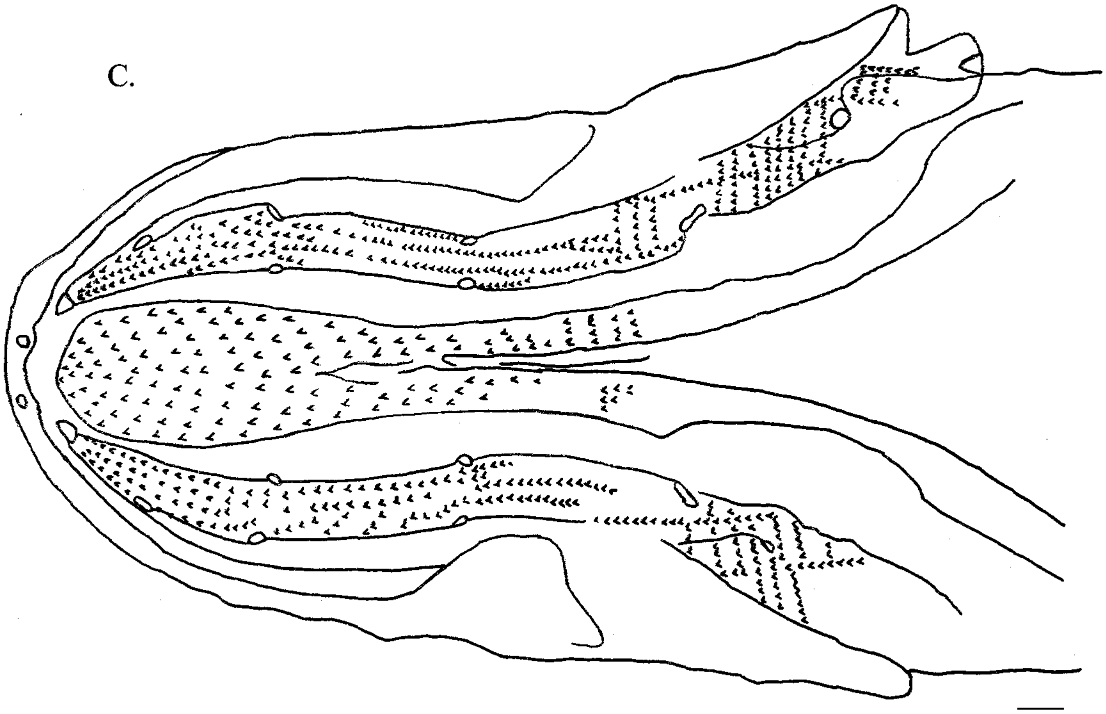


Figure 12 (continued). Cephalic lateralis of *Apogon* (*Zapogon*) *evermanni*. C. Ventral view

***Apogon* (*Zoramia*) Jordan, 1917[b]**

Material Examined

Type species: *Apogon graeffii* Günther, 1873 [= *Apogon leptacanthus* Bleeker, 1856d according to Fraser & Lachner (1985)], by original designation (also monotypic); BPBM 6958; 18, 21.3—34.9 mm

Apogon fragilis Smith, 1961; BPBM 9699; 4, 28.1—32.3 mm

Apogon perlitus Fraser & Lachner, 1985; BPBM 10545; 4, 35.6—39.8 mm

Supratemporal Canal

Nasal Portion

- Does not extends to tip of snout, terminates medial to anterior nostril (Figure 13A)
- Lateral margin just medial to interorbital space perforated by large pore (Figure 13B)
- Medial margin, anterior of posterior nostril, perforated by a few small pores

Interorbital Portion

- Expanse of canal perforated by several small pores
    - Concentrated toward margins with a few along midline of canal
    - Particularly concentrated along medial margin between posterior nostril and large interorbital pore
- Lateral margin just anterior of longitudinal midpoint of interorbital space perforated by a large pore

Postorbital Portion

- Lateral margin and median along dorsoposterior margin of orbit perforated by numerous small pores
- Canal formed into several open-ended, secondary extensions that project posteriorly from postorbital space toward supratemporal canal
    - Margin of extensions perforated by many small pores

Sensory Papillae Pattern

- Longitudinal row of sensory papillae extends along midline of supraorbital canal from terminal pore to postorbital portion of canal
- Second longitudinal row of papillae extends along lateral margin from terminal pore to posterior nostril

Supratemporal Canal (Figure 13B)

- Anterior margin of canal perforated by numerous small pores
- Posterior margin of canal formed into numerous open-ended, posteriorly projecting secondary extensions
    - Margins of extensions perforated by a few pores

Infraorbital Canal (Figure 13A)

<u>Lachrymal Portion</u>

- Terminates anteriorly in a large pore located just posterior of the midpoint of the internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two long, slit-like pores
- Median superior to lachrymal pores perforated by numerous small pores

<u>Suborbital Portion</u>

- Proximal margin perforated by many small pores
- Posterior half of distal margin formed into numerous projections that terminate in pores along maxilla

<u>Postorbital Portion</u>

- Proximal margin perforated by numerous small pores
- Distal margin formed into numerous open-ended, projections that extend posteriorly onto cheek
    - Margins of projections perforated by few small pores

Preoperculomandibular Canal

Mandibular Portion (Figure 13C)

- Terminates anteriorly in a pair of moderately-sized, subtriangular pores that perforate the dentary (Figure 13B)
- Canal just posterior of apex of dentary perforated by a large pair of subtriangular mental pores
- Both margins perforated by numerous moderately-sized pores along expanse of canal
- Lateral margin perforated by a large ovoid pore about half way along length of canal
    - Pore not located at end of projection
- Mandibular portion terminates in a moderately-sized, slit-like pore just anterior of origin of preopercle

Preopercular Portion (Figure 13A)

- Both margins of ventral preopercular flange perforated by numerous small pores
- Proximal margin of vertical preopercular flange perforated by numerous small pores
- Distal margin formed into numerous open-ended extensions that terminate along margin of preopercle
- Dorsal-most portion of distal margin formed into several, open-ended projections that extend posteriorly onto opercle

Sensory Papillae Pattern

- Sensory papillae forming chevron pattern on basihyal
- Two longitudinal rows of sensory papillae along median of mandibular canal
- Few rows extend from mandibular portion onto ventral preopercular flange
- Transverse row of papillae on opercle just posterior of preopercle

Remarks

Variation in the canal structure among the species of *Zoramia* is slight. Only minor variation occurs in the perforation density. The variation is more significant, however, in the degree to which the canals are covered by papillae. *Apogon fragilis* has the fewest papillae with a single longitudinal row extending along the median of the supraorbital canal and a sparse chevron pattern on the basihyal. *Apogon perlitus* has the most dense papillae coverage. Whereas *A. fragilis* has only a single row of sensory papillae extending along the supratemporal canal, *A. leptacanthus* and *A. perlitus* have two longitudinal rows along the nasal portion, the more medial of which, extends posteriorly to the supratemporal canal. In *A. perlitus*, numerous transverse rows of papillae cross the supraorbital canal forming a crosshatch pattern via intersections with these two longitudinal rows. *Apogon perlitus* and *A. leptacanthus* also have papillae covering the internarial space. *Apogon leptacanthus* has a single longitudinal row of papillae along the median of the suborbital portion, whereas *A. perlitus* has a crosshatch pattern of papillae along the suborbital portion, formed from the intersection of this longitudinal row with numerous rows that radiate ventrally from the orbit.

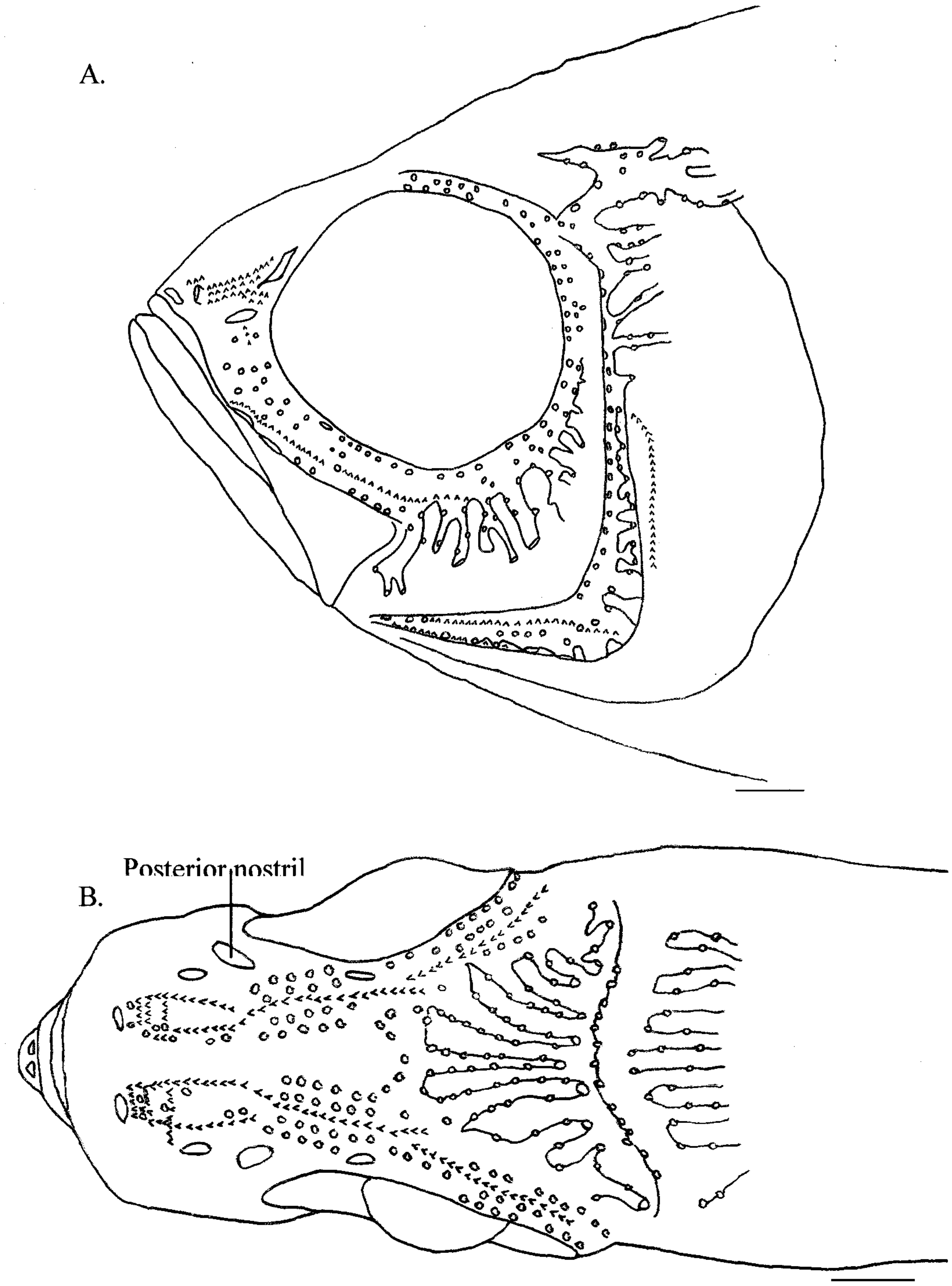


Figure 13. Cephalic lateralis of *Apogon* (*Zoramia*) *leptacanthus*. A. Lateral view, B. Dorsal view

C.

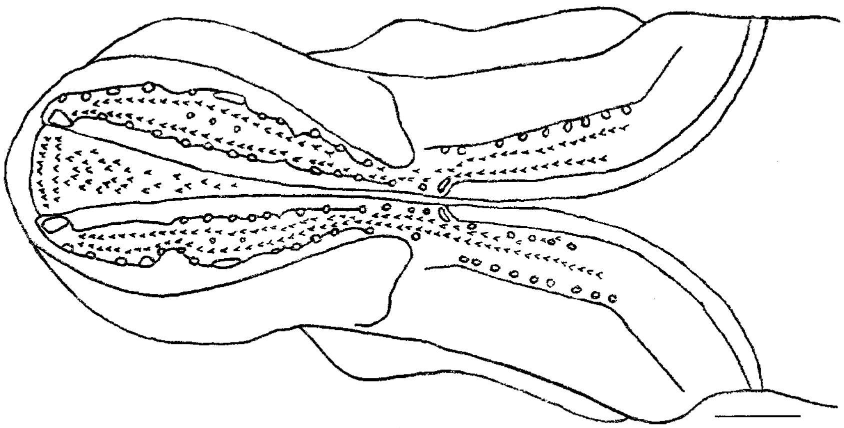


Figure 13 (continued). Cephalic lateralis of *Apogon* (*Zoramia*) *leptacanthus*. C. Ventral view

Apogonichthys Bleeker, 1854[a]

Material Examined

Type species: *Apogonichthys perdix* Bleeker, 1854[a], by monotypy; BPBM 15198; 19, 18.9—42.1 mm

Apogonichthys ocellatus (Weber, 1913); BPBM 11013; 2, 32.5—33.5 mm

Supratemporal Canal

Nasal Portion

- Extends to tip of snout (Figure 14A)
- Terminates anteriorly in a slit-like pore
  - Pore appears to be under a flap of skin positioned medial to and anterior of anterior nostril
- Lateral margin superior to internarial space perforated by a moderately-sized round pore (Figure 14B)

- Medial margin perforated by a few small pores

Interorbital Portion

- Lateral margin in anterior-most portion of interorbital space perforated by a moderately-sized round pore
- Medial margin in anterior interorbital space perforated by few small pores
- Lateral margin near longitudinal midpoint of interorbital space perforated by a large, slit-like pore

Postorbital Portion

- Lateral margin, along dorsoposterior margin of orbit, perforated by a few small pores
- Canal formed into several long and narrow, open-ended secondary projections that extend posteriorly toward supratemporal canal

Supratemporal Canal (Figure 14B)

- Anterior margin perforated by several small pores
- Posterior margin formed into several open-ended, posteriorly projecting, secondary extensions

Infraorbital Canal (Figure 14A)

Lachrymal Portion

- Terminates anteriorly in a moderately-sized lunate pore located just posterior of anterior nostril
- Distal margin, along ventral edge of lachrymal, perforated by two, slit-like pores

Suborbital Portion

- Posterior half of distal margin perforated by few small, round pores

Postorbital Portion

- Proximal margin perforated by a few moderately-sized pores
- Distal margin formed into several open-ended projections that extend posteriorly onto cheek

Preoperculomandibular Canal

Mandibular Portion (Figure 14C)

- Terminates anteriorly in a pair of small round pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a pair of slit-like mental pores
- Medial and lateral margins perforated by several moderately-sized pores
- Terminates posteriorly in a slit-like pore adjacent to origin of preopercle

Preopercular Portion (Figure 14A)

- Distal margin formed into numerous extensions that terminate in pores along edge of preopercle
- Dorsal-most portion of distal margin formed into a few extensions that extend posteriorly beyond the preopercle

Sensory Papillae Pattern

- Small sensory papillae covering anterior portion of basihyal and mandibular median

Remarks

The canal morphologies of *Apogonichthys perdix* and *Apogonichthys ocellatus* are very similar. The cephalic lateralis system of *Apogonichthys* is not highly perforated; the canals are relatively simple in structure, with little secondary development. *Apogonichthys ocellatus* appears to have a few more small pores perforating the proximal margin of the infraorbital canal and lacks the minute sensory papillae present on the ventroanterior portion of the mandible in *A. perdix*.

A.

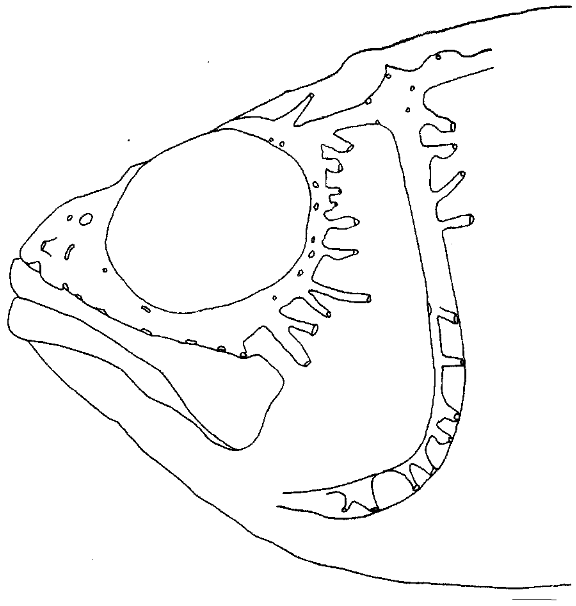


Figure 14. Cephalic lateralis of *Apogonichthys perdix*. A. Lateral view

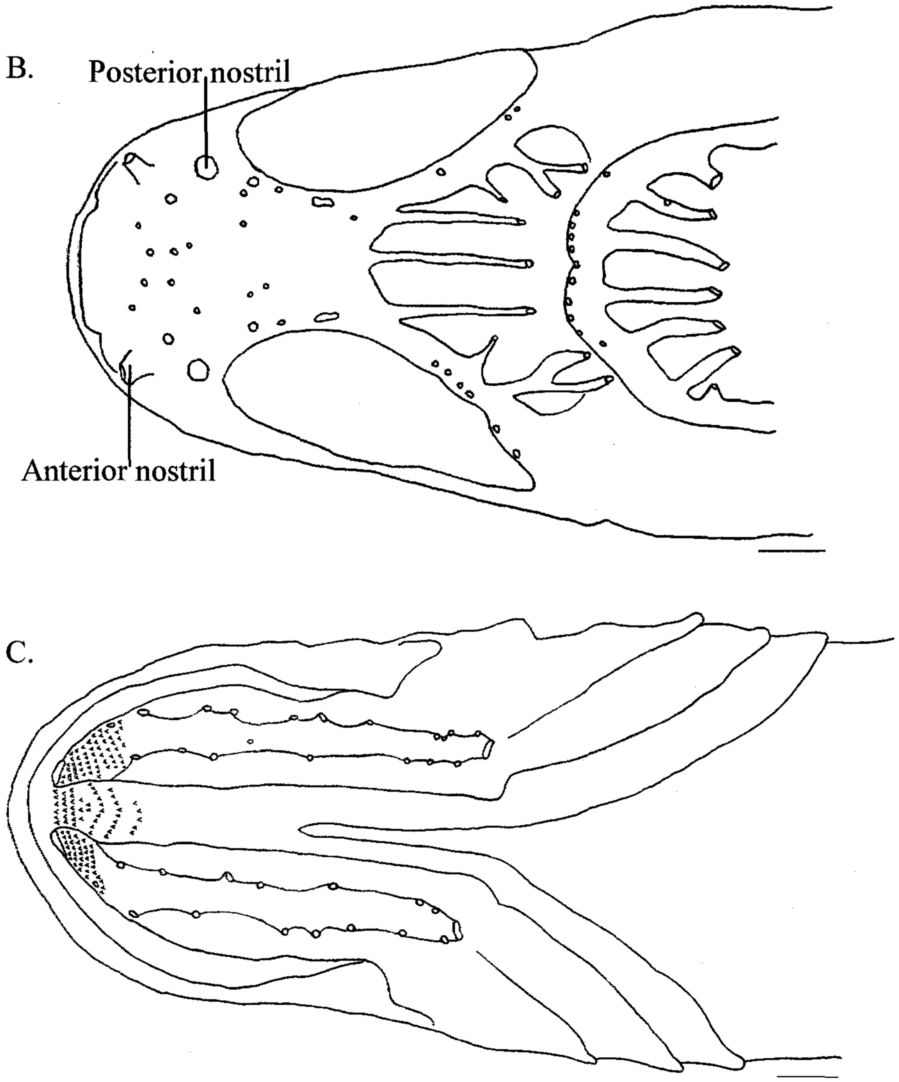


Figure 14 (continued). Cephalic lateralis of *Apogonichthys perdix*. B. Dorsal view, C. Ventral view

Archamia Gill, 1863

Material Examined

Type species: *Archamia bleekeri* (Günther,1859), by monotypy; BPBM 36865; 2, 20.7 — 29.6 mm

Archamia fucata (Cantor, 1849); BPBM 28973; 2, 47.7 —48.3 mm

Archamia leai Waite, 1916; BPBM 34248; 2, 58.1—66.0 mm

Archamia macroptera (Cuvier in Cuvier & Valenciennes, 1828); BPBM 30133; 4, 44.3—67.8 mm

Supraorbital Canal

Nasal Portion

- Extends nearly to tip of snout (Figure 15A)
- Terminates anteriorly in a slit-like pore that parallels the premaxilla
- Lateral margin dorsal of the internarial space perforated by a large, elongate pore (Figure 15B)

Interorbital Portion

- Lateral margin along dorsoanterior portion of orbit formed into a few short, projections that extend toward orbit and terminate in pores
- Lateral margin perforated by a large pore near longitudinal midpoint of orbit
- Median along dorsoposterior portion of orbit perforated by several small pores

Postorbital Portion

- Canal forming a number of open-ended, secondary projections that extend posteriorly from post-interorbital space toward supratemporal canal
    - Margins of projections perforated by numerous small pores

Sensory Papillae Pattern

- Longitudinal row of papillae extends from terminal pore to longitudinal midpoint of interorbital space

Supratemporal Canal (Figure 15B)

- Anterior margin formed into few short, anteriorly projecting secondary extensions
- Remainder of anterior margin perforated by numerous small pores
- Posterior margin formed into several open-ended, posteriorly projecting secondary extensions
    - Margins of extensions perforated by numerous small pores

Infraorbital Canal (Figure 15A)

Lachrymal Portion

- Terminates anteriorly in a large slit-like pore just posterior of midpoint of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two long, slit-like pores
- Median superior to lachrymal pores perforated by several small pores

Suborbital Portion

- Margins and median perforated by several moderately and small-sized pores

Postorbital Portion

- Proximal margin perforated by several small pores
- Distal margin formed into numerous open-ended projections that extend posteriorly onto surface of the cheek
    - Margins of extensions perforated by few small pores

Sensory Papillae Pattern

- Internarial space with few sensory papillae
- Longitudinal row of sensory papillae extends along canal median from the second lachrymal pore to the posterior edge of orbit
- Several short rows radiate from ventral margin of orbit and intersect longitudinal row to form a crosshatch pattern
- Few short, longitudinal rows of papillae superior to and posterior of terminus of maxilla

Preoperculomandibular Canal

Mandibular Portion (Figure 15C)

- Terminates anteriorly in a pair of small round pores that perforate the dentary
- Canal just posterior of dentary perforated by a relatively large pair of mental pores
- Margins perforated by several small pores
- Large pores perforated the lateral margin one-quarter and one-half way along the expanse of the mandibular canal

Preopercular Portion (Figure 15A)

- Proximal margin perforated by several small pores
- Distal margin formed into several broad, open-ended projections that extend toward edge of preopercle
- Dorsal-most portion of distal margin formed into a number of posteriorly projecting, secondary extensions that terminate in pores

Sensory Papillae Pattern

- Two longitudinal rows of sensory papillae cover mandibular canal median
- Several short longitudinal rows of papillae present on ventral portion of preopercular flange

Remarks

The cephalic lateralis patterns of the *Archamia* species range from the densely perforated and papilliated condition of *Archamia macroptera* to the more simple, less perforated pattern exhibited by *A. bleekeri.* In comparison to these two species, *A. fucata* and *A. leai* occupy positions of intermediate complexity.

In *A. fucata*, *A. leai*, and *A. macroptera* the suborbital portion of the infraorbital canal is highly perforated and covered by a crosshatch pattern of papillae. The distal margins of the postorbital, infraorbital, and preopercular canal portions are characterized by a significant degree of secondary canal development in all species. The margins of these projections are perforated in *A. fucata*, *A. leai*, and *A. macroptera.* The medians of these projections are perforated in *A. macroptera*, but they are not perforated in *A. fucata*, *A. leai.* . The supraorbital canal is also densely perforated and covered by a crosshatch pattern of papillae in *A. fucata*, *A. leai*, and *A. macroptera.* The supraorbital canal of *A. bleekeri* lacks the crosshatch pattern and is instead characterized by a longitudinal row of papillae that extends from the terminal pore to the mid-interorbital space. The posterior portion of the interorbital canal is formed into secondary projections that extend posteriorly to the supratemporal canal in all species. The medians and margins of these projections are less densely perforated in *A. bleekeri.*

In all the species studied the anterior margin of the supratemporal canal is densely perforated and formed into a few short, anteriorly projecting extensions. The posterior margin is developed into many long, narrow, densely perforated secondary projections.

The margins of the mandibular canal in *A. macroptera*, particularly the lateral margin, are formed into numerous projections that extend toward the outer boundaries of this region and terminate in pores. The mandibular median is perforated by numerous pores and is covered by papillae in an irregular pattern. The lateral margins of the mandibular canal of *A. fucata* and *A. leai* are not as highly branched; the branches that extend laterally near the terminus of the maxilla in *A. macroptera* are absent in these species. The lateral margin of the mandibular canal of *A. bleekeri* is not branched, although large pores perforate the lateral margin in the areas corresponding to the branches of the other species.

Numerous pores perforate the proximal margin of the preopercular canal in all species. The distal preopercular margin is formed into numerous long, narrow projections that extend to the edge of the preopercle. In *A. fucata*, *A. leai*, and *A. macroptera* the projections are narrow and densely perforated. The projections in *A. bleekeri* are comparatively broad and their margins are not perforated.

Another significant difference is the presence or absence of a single large pore perforating the lateral margin of the supraorbital canal in the mid-interorbital space. In each species a large pore perforates the lateral margin just anterior of the posterior nostril. The lateral margin just posterior of the posterior nostril in *A. fucata*, *A. leai*, and *A. macroptera* is developed into a few projections that terminate in pores. The lateral margin of *A. bleekeri* is not perforated until the interorbital portion of the canal. The lateral margin in the interorbital space of *A. macroptera*, *A. leai*, and *A. fucata* is developed into a number of short, projections that extend toward the rim of the orbit and terminate in pores. In contrast, the mid-interorbital space of *A. bleekeri* is characterized by the presence of a large pore perforating the lateral margin.

A.

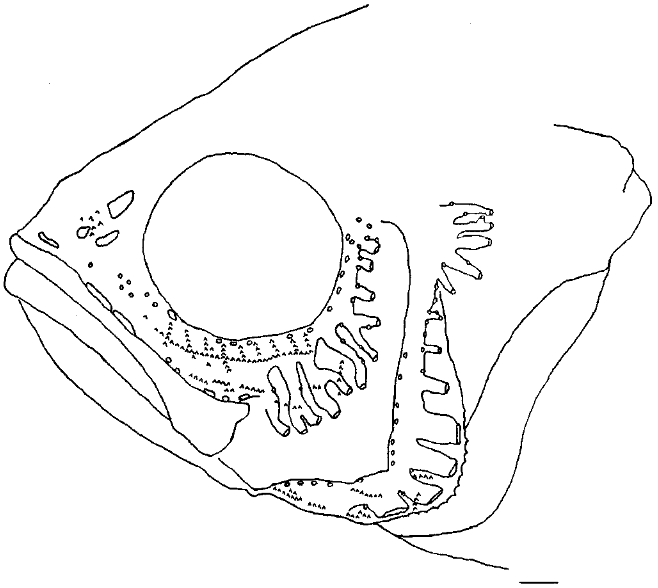


Figure 15. Cephalic lateralis of *Archamia bleekeri*. A. Lateral view

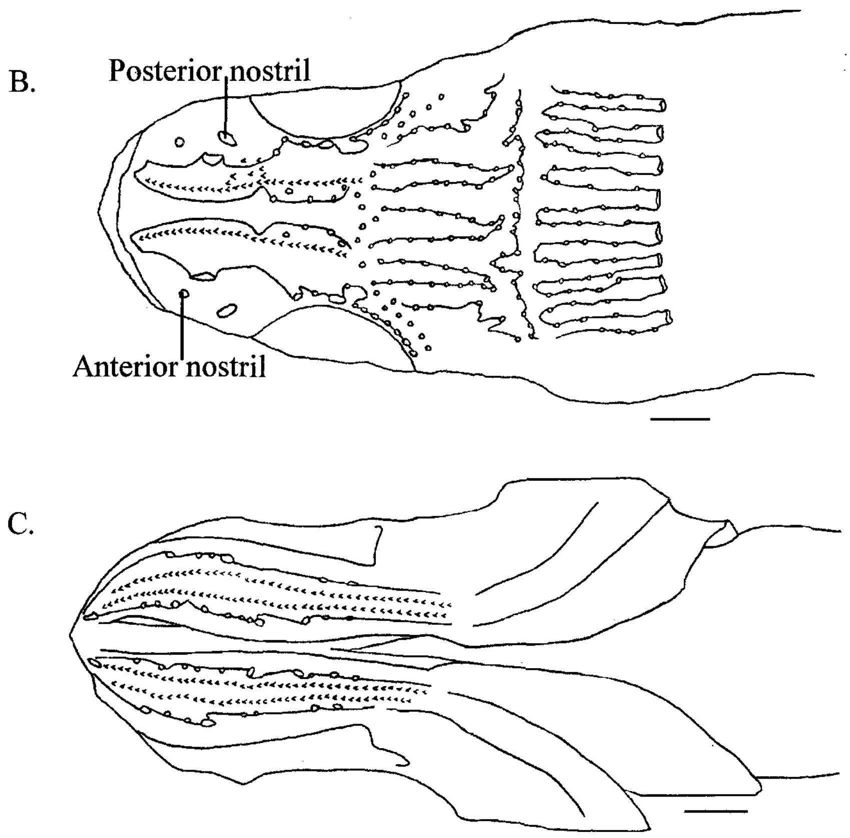


Figure 15 (continued). Cephalic lateralis of *Archamia bleekeri.* B. Dorsal view, C. Ventral view

Astrapogon **Fowler, 1907**

Material Examined

Type species: *Astrapogon stellatus* (Cope, 1867), by original designation (also monotypic); USNM 184234, 1, 148.8 mm

Supraorbital Canal

<u>Nasal Portion</u>

- Extends almost to tip of snout (Figure 16A)
- Terminates anteriorly in a slit-like pore that parallels the premaxilla

    - Lateral edge of terminal pore is directly anterior of and medial to the anterior nostril
- Margins and median of canal anterior of orbit perforated by numerous small pores
- Lateral margin perforated by a large pore just medial to posterior nostril

Interorbital Portion

- Lateral margin perforated by two, relatively-large pores near longitudinal midpoint of interorbital space
- Pores perforating lateral margin of canal from posterior nostril through interorbital space comparatively large

Postorbital Portion

- Canal formed into a few secondary projections that extend posteriorly along median of postorbital space toward supratemporal canal
    - Margins of extensions perforated by numerous small pores

Sensory Papillae Pattern

- Portion of canal anterior of posterior nostril densely covered by sensory papillae
- Longitudinal row of sensory papillae extends from terminal pore through interorbital space terminating at ends of postorbital projections
- Second, more lateral longitudinal row of sensory papillae extends posteriorly from terminal pore through interorbital space continuing along dorsoposterior margin of orbit

Supratemporal Canal (Figure 16B)

- Anterior margin perforated by several small pores
- Posterior margin formed into several long, open-ended, posteriorly projecting secondary extensions
    - Margins of extensions perforated by numerous small pores
- Skin from canal to origin of dorsal fin densely perforated by small pores
    - Pores not confined to any sort of canal and/or canal-extension

Infraorbital Canal

Lachrymal Portion

- Terminates anteriorly in a large, oval-shaped pore just posterior of the midpoint of the internarial space
- Internarial space with rows of sensory papillae
    - Papillae not extending posteriorly to orbit
- Two long, slit-like pores perforating distal margin of canal along ventral edge of lachrymal

Suborbital Portion

- Proximal margin perforated by several moderately-sized pores
- Few pores perforating distal margin of canal along posterior half of maxilla

Postorbital Portion

- Proximal margin perforated by several moderately-sized pores
- Distal margin formed into numerous open-ended projections that extend onto cheek
    - Margins of extensions perforated by numerous small pores

Sensory Papillae Pattern

- Two longitudinal rows of sensory papillae extend posteriorly from first lachrymal pore to posterior of terminus of maxilla
- Crosshatch pattern of papillae on cheek posterior of orbit

Preoperculomandibular Canal

Mandibular Portion

- Terminates anteriorly in a pair of small round pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a pair of mental pores
- Medial and lateral margins perforated by a few moderately-sized pores
- Lateral margin formed into bulges one-quarter and two-quarters along its length
  - Moderately-sized pores perforating margin in this area
- Mandibular portion terminates in a large pore adjacent to origin of preopercle

Preopercular Portion

- Proximal margin perforated by many small pores
- Distal margin formed into numerous open-ended projections that extend toward edge of preopercle
  - Margins of projections perforated by numerous small pores

Sensory Papillae Pattern

- Sensory papillae in short, semi-longitudinal rows on canal median
- Minute sensory papillae forming chevron pattern on basihyal
- Ventral flange with a crosshatch pattern of sensory papillae
- Vertical flange with two rows of sensory papillae
- Transverse row of papillae on opercle just posterior of margin of preopercle

Remarks

The pores and papillae are uniquely dense along the supraorbital canal in *Astrapogon stellatus*; it appears that some type of sensory structure, whether pores or papillae, cover the entire surface of the canal. The pores are not confined within canal margins; rather, the skin appears densely perforated throughout the dorsal surface of the head.

A.

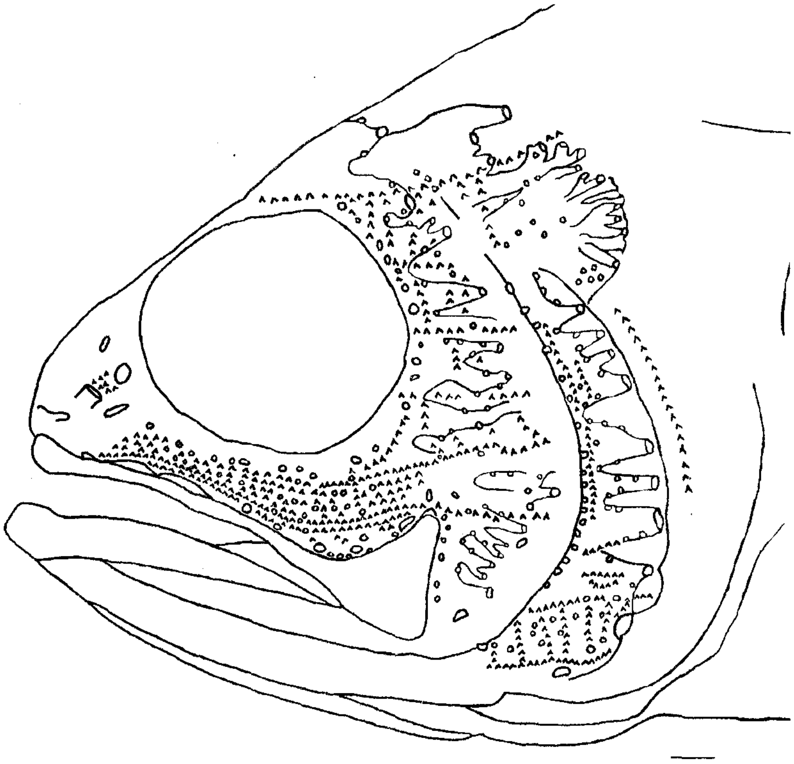


Figure 16. Cephalic lateralis of *Astrapogon stellatus*. A. Lateral view

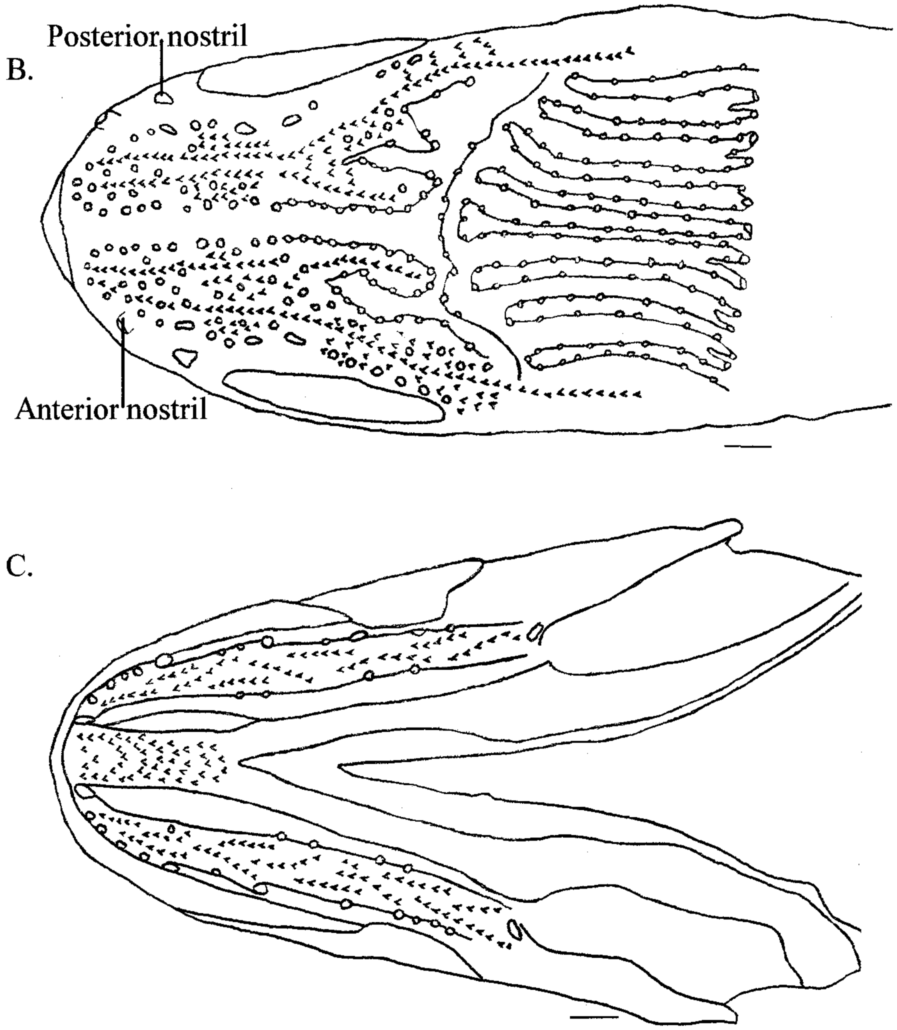


Figure 16 (continued). Cephalic lateralis of *Astrapogon stellatus*. B. Dorsal view, C. Ventral view

Cercamia Randall & Smith, 1988

Material Examined

Type species: *Cercamia cladara* Randall & Smith, 1988, by original designation; BPBM 37409; 3, 21.8—36.9 mm

Cercamia eremia (Allen, 1987); BPBM 22312; 5, 29.0—36.5 mm

Supraorbital Canal

Nasal Portion

- Does not extend to tip of snout (Figure 17A)
- Terminates anteriorly in an oval-shaped pore
- Lateral margin between terminal pore and posterior nostril perforated by several small pores (Figure 17B)
- Lateral margin just anterior of posterior nostril perforated by a moderately-sized round pore

Interorbital Portion

- Medial margin perforated by a few small pores in anterior interorbital space
- Lateral margin along dorsal rim of orbit perforated by several small pores

Postorbital Portion

- Medial margin formed into a few open-ended, secondary projections that extend posteriorly and medially toward midline of body
    - Margins of extensions perforated by few pores

Sensory Papillae Pattern

- Short longitudinal rows of papillae medial to terminal pore
- Longitudinal row of papillae extends from terminal pore to longitudinal midpoint of interorbital space
- Canal from anterior nostril through postorbital space crossed by multiple transverse rows of sensory papillae
    - Few rows in mid interorbital space completely traverse the dorsal surface

Supratemporal Canal (Figure 17B)

- Anterior and posterior margins perforated by numerous small pores
- Posterior margin of canal formed into one, median, open-ended, posteriorly projecting secondary extension

Infraorbital Canal (Figure 17A)

Lachrymal Portion

- Terminates anteriorly in a moderately-sized pore located just posterior of the midpoint of the internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two moderately-sized, slit-like pores
- Median superior to lachrymal pores perforated by a few small pores

Suborbital Portion

- Canal quite narrow
- Both margins perforated by numerous small, round pores

Postorbital Portion

- Both margins perforated by many small, round pores
- Distal margin formed into a few open-ended projections that extend posteriorly
    - Margins of projections perforated by several small pores

Sensory Papillae Pattern

- Internarial space with a few rows of papillae
- One row of papillae extends ventrally from posterior nostril to premaxilla

Preoperculomandibular Canal

Mandibular Portion (Figure 17C)

- Terminates anteriorly in a pair of small oval-shaped pores that perforate the dentary (Figure 17A)
- Canal just posterior of apex of dentary perforated by a relatively large pair of subtriangular mental pores
- Lateral and medial margins perforated by numerous moderately-sized pores
- Medial margin one-third of the way along the canal length perforated by a relatively large round pore
- No terminal mandibular pore

Preopercular Portion (Figure 17A)

- Proximal margin perforated by several moderately-sized pores
- Distal margin formed into a few short, open-ended extensions that project toward edge of preopercle
- Distal margin not developed into extensions perforated by several small pores

- Dorsal-most portion of distal margin formed into two open-ended projections that extend posteriorly to opercle
    - Margins of projections perforated by several small pores

Sensory Papillae Pattern

- Semi-transverse rows of papillae beginning in the second third of mandibular canal becoming longitudinal posteriorly
- Sensory papillae on basihyal
    - Formed into longitudinal rows anteriorly, chevron pattern posteriorly

Remarks

Cercamia cladara and *Cercamia eremia* have similar pore and papillae patterns. The lateral margin of the supraorbital canal, near the longitudinal midpoint of the interorbital space, is formed into a single short projection that terminates in a moderately-sized pore along the margin of the orbit in *C. eremia*. The margins are otherwise not perforated prior to the development of the secondary postorbital extensions. In *C. cladara*, a few small pores perforate the proximal interorbital margin, whereas the lateral margin is not perforated. The two lachrymal pores in *Cercamia* species are located at the termini of broad projections. In most other apogonids, the canal is expanded such that the distal margin of the infraorbital canal is at the ventral edge of the lachrymal.

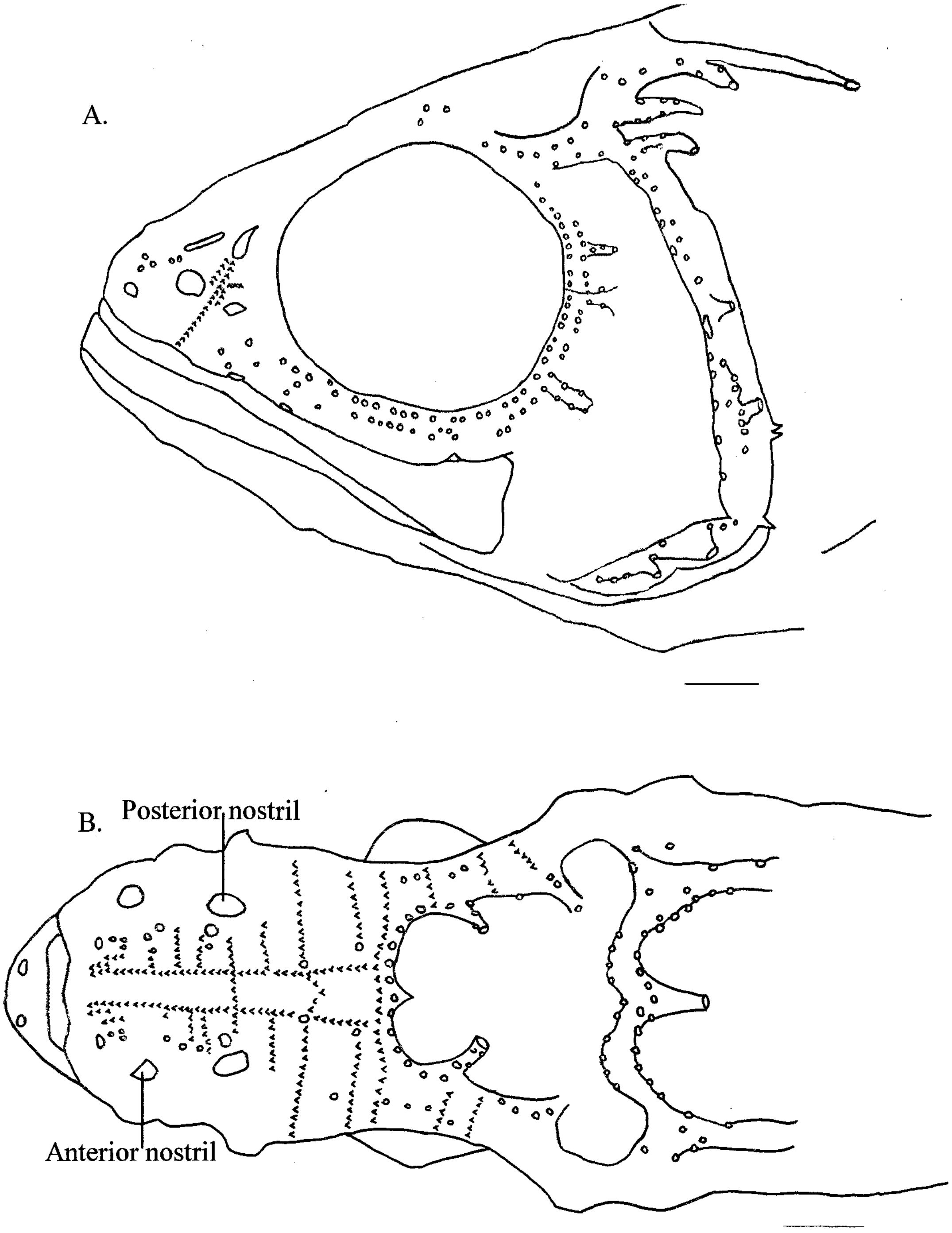


Figure 17. Cephalic lateralis of *Cercamia cladara.* A. Lateral view, B. Dorsal view

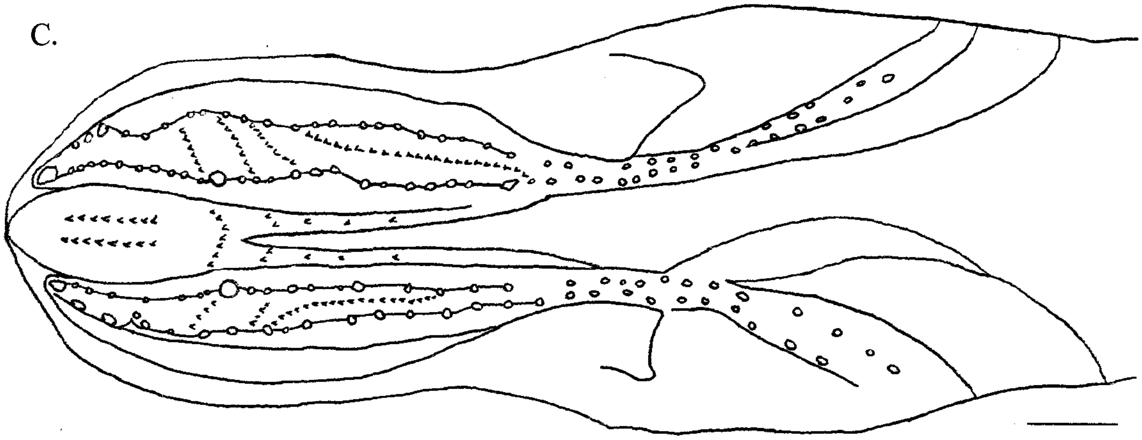


Figure 17 (continued). Cephalic lateralis of *Cercamia cladara.* C. Ventral view

Cheilodipterus Lacepède, 1801

Material Examined

Type species: *Cheilodipterus lineatus* Lacepède, 1801 [= *Cheilodipterus macrodon* (Lacepède, 1802) according to Fricke (1999)], by subsequent designation of Jordan (1917a); BPBM 32931; 2, 66.4—77.4 mm

Cheilodipterus novemstriatus (Rüppell, 1838); BPBM 30446; 1, 47.6 mm

Cheilodipterus quinquelineatus (Cuvier in Cuvier & Valenciennes, 1828); BPBM 20726; 1, 70.0 mm

Cheilodipterus singapurensis (Bleeker, 1859); BPBM 31355; 4, 47.5—92.0 mm

Supraorbital Canal

<u>Nasal Portion</u>

- Extends nearly to tip of snout (Figure 18A)
- Terminates anteriorly in a slit-like pore that parallels the premaxilla
- Medial margin perforated by many small pores from terminal pore to posterior nostril (Figure 18B)

- Lateral margin along same expanse perforated by relatively fewer pores
- Lateral margin adjacent to posterior nostril formed into two extensions that terminate in pores

Interorbital Portion

- Lateral margin formed into a number of short, projections that terminate in pores along dorsal margin of orbit

Postorbital Portion

- Canal formed into a number of open-ended, secondary projections that extend posteriorly from postorbital space toward supratemporal canal
    - Margins of projections perforated by small pores

Sensory Papillae Pattern

- Longitudinal row of sensory papillae extends from dorsoposterior margin of orbit to posterior of supratemporal canal projections

Supratemporal Canal (Figure 18B)

- Anterior margin and median perforated by numerous small pores
- Posterior margin formed into numerous open-ended, posteriorly projecting secondary extensions
    - Margins of extensions perforated by small pores

Infraorbital Canal (Figure 18A)

Lachrymal Portion

- Terminates anteriorly in a large pore located posterior of the anterior nostril
- Two, long, slit-like pores perforating distal margin of canal along ventral edge of lachrymal

- Median superior to lachrymal pores perforated by a few small pores

Suborbital Portion

- Proximal and distal margins perforated by several small, round pores

Postorbital Portion

- Proximal margin perforated by many small, round pores
- Distal margin formed into many, narrow open-ended projections that extend posteriorly onto cheek

Preoperculomandibular Canal

Mandibular Portion (Figure 18C)

- Terminates anteriorly in a pair of round pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a relatively large pair of mental pores
- Lateral margin formed into three extensions that terminate in pores
    - One at each third of the way along the expanse of canal bounded posteriorly by the terminus of the maxilla
- Medial margin of posterior half of canal formed into several extensions that terminate in pores
- No terminal mandibular pore

Preopercular Portion (Figure 18A)

- Proximal margin perforated by several small pores
- Distal margin along ventral half of vertical flange formed into a few open-ended projections that extend to edge of preopercle

- Dorsal-most portion of distal margin formed into a number of open-ended projections that extend posteriorly onto opercle

Remarks

The cephalic lateralis systems of *Cheilodipterus novemstriatus* and *C. quinquelineatus* are quite similar and yet, quite distinct from the patterns seen in *C. macrodon* and *C. singapurensis*. In *C. novemstriatus* and *C. quinquelineatus* the infraorbital canal forms a bulge near its terminus and two small pores perforate the proximal margin of the canal just superior to the terminal pore. The presence of sensory papillae is variable among the species of *Cheilodipterus*. Both *C. quinquelineatus* and *C. singapurensis* have a longitudinal row of sensory papillae extending along the median of the suborbital portion of their infraorbital canals.

The distal margin of the postorbital portion of the infraorbital canal is formed into secondary extensions in all *Cheilodipterus* species; however, the number and shape of these extensions differs among the species. In *C. macrodon* the projections are numerous and narrow. Although the postorbital projections of *C. singapurensis* are narrow and short like those of *C. macrodon* they are comparatively fewer in number. *C. quinquelineatus* and *C. novemstriatus* possess fewer postorbital projections than does *C. macrodon*, but each projection is comparatively wider and its margins are perforated by several small pores.

A large pore perforates the lateral margin adjacent to the posterior nostril in *C. novemstriatus*, *C. quinquelineatus*, and *C. singapurensis*. The lateral margin of *C. macrodon* is also perforated in this region but the pore is not significantly larger than others perforating the same expanse and, the pore is located at the end of a lateral extension from the main canal. The lateral margin of *C. macrodon* is formed into an additional projection that terminates in a pore just posterior of the posterior nostril. The lateral margin of *C. quinquelineatus* is formed into three projections that terminate in pores between the posterior nostril and the anterior margin of the orbit; this morphology continues posteriorly through the anterior interorbital canal. No such projections are found anterior of the orbit in *C. novemstriatus* and *C. singapurensis*. The lateral interorbital margins of*C. macrodon* and *C. novemstriatus* are perforated by several moderately-sized pores, a number of which are located at the ends of very short projections. In contrast the lateral interorbital margin of *C. singapurensis* is perforated by a moderately-large, singular pore. The postorbital portion of the supraorbital canal of all *Cheilodipterus* species is characterized by some degree of secondary canal development. The highest degree of secondary development, characterized by highly branching and densely perforated projections, occurs in *C. novemstriatus* and *C. quinquelineatus.* These two species also exhibit the highest degree of secondary development in the supratemporal canal. In these species not only is the posterior margin developed into projections, but the anterior margin is also developed into secondary, anteriorly projecting extensions.

Considerable variation occurs in the mandibular canal portion of *Cheilodipterus* species. Both the medial and lateral margins of the mandibular canal are formed into projections in *C. macrodon.* The medial margins of *C. quinquelineatus* and *C. novemstriatus* are more densely perforated than is that of *C. macrodon* but they are not formed into projections. The lateral margins of *C. quinquelineatus* and *C. novemstriatus* are characterized by projections that terminate in pores one-quarter, one-half, and three-quarters of the way along the length of the canal, as in *C. macrodon*. The length of these projections varies, however. In *C. novemstriatus* the projections are quite short, thereby giving the appearance of swellings, as opposed to projections, in the corresponding regions.

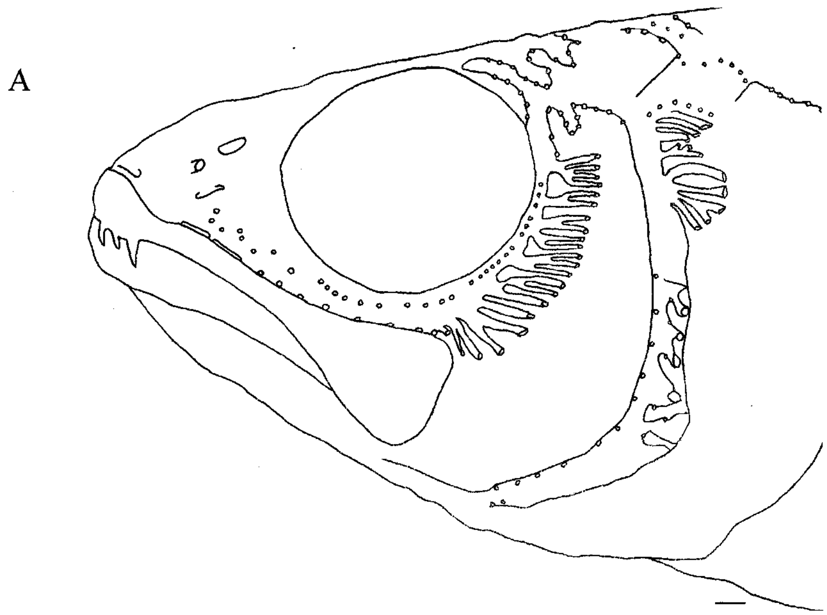


Figure 18. Cephalic lateralis of *Cheilodipterus macrodon*. A. Lateral view

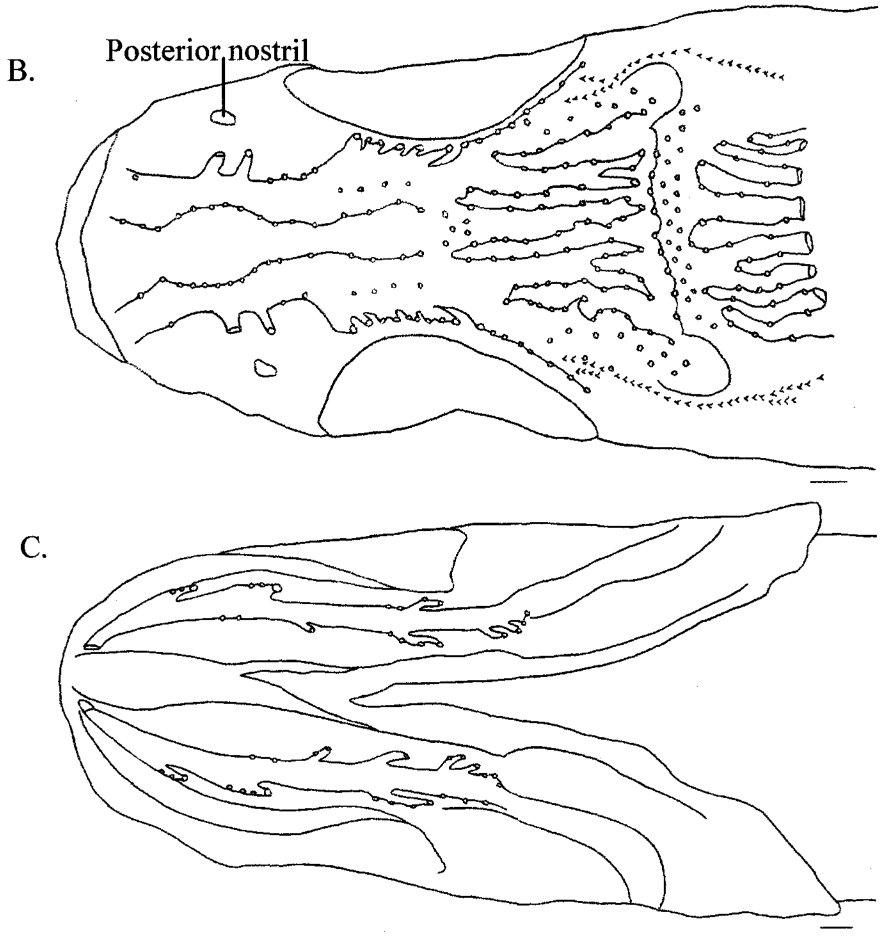


Figure 18 (continued). Cephalic lateralis of *Cheilodipterus macrodon.* B. Dorsal view, C. Ventral view

Coranthus Smith, 1961

Material Examined

Type species: *Coranthus polyacanthus* (Vaillant, 1877), by original designation (also monotypic); BPBM 26690; 1, 135.0 mm

Supraorbital Canal

Nasal Portion

- Extends nearly to tip of snout (Figures 19A, B)
- Terminates anteriorly in a slit-like pore
- Lateral and medial margins densely perforated throughout expanse (Figure 19B)
- Median perforated, but to a lesser degree
- Lateral margin formed into a projection that terminates in a pores just dorsal of internarial space

Interorbital Portion

- Lateral margin formed into short, projections that terminate in pores along dorsal margin of orbit
    - Prominently large pore perforating lateral margin absent
- Medial margin in anterior interorbital space formed into short projections that terminate in pores
- Proximal margin densely perforated along dorsoposterior margin of orbit
- Median perforated throughout expanse
    - Pores not as dense those perforating margins

Postorbital Portion

- Distal margin of canal formed into a number of secondary projections that terminate in pores and extend posteriorly toward supratemporal canal
    - Margins and medians of projections perforated by many small pores
    - Median projection confluent with supratemporal canal
- Median perforated by numerous pores but to a lesser degree than the margins

Sensory Papillae Pattern

- Papillae interspersed with pores along entire expanse of canal portion

Supratemporal Canal (Figure 19B)

- Anterior margin and median of canal perforated by numerous small pores
- Posterior margin of canal formed into numerous open-ended, posteriorly projecting secondary extensions
    - Margins of extensions perforated by many small pores

Infraorbital Canal (Figure 19A)

Lachrymal Portion

- Terminates anteriorly in a large pore located posterior of anterior nostril
- Two long, slit-like pores perforating distal margin along ventral edge of lachrymal
- Margin between terminal pore and lachrymal pores perforated by a few small pores
    - Two pores, just ventral of terminal pore, located at ends of short, anteriorly-projecting extensions
- Median superior to lachrymal pores perforated by numerous small pores

Suborbital Portion

- Proximal margin and median perforated by numerous small pores
- Distal margin formed into numerous, projections that terminate in pores and extend toward margin of maxilla
    - Margins of projections perforated by several small pores

Postorbital Portion

- Proximal margin perforated by many small pores
- Distal margin formed into many open-ended, projections that extend posteriorly onto cheek and toward preopercular ridge
    - Margins of projections perforated by numerous pores
    - Individual projections, posterior of maxilla, branch secondarily forming a finer subset of extensions

Sensory Papillae Pattern

- Internarial space with several rows of papillae
        - Few rows extending posteriorly to margin of orbit

Preoperculomandibular Canal

Mandibular Portion (Figure 19C)

- Terminates anteriorly in a pair of oval-shaped pores that perforate the dentary
- Canal just posterior of dentary perforated by a relatively large pair of mental pores
- Margins and median perforated by numerous small pores
- Lateral margin formed into four extensions that terminate in pores
    - One at each quarter of the way along the expanse of canal
    - Margins of projections perforated by small pores

- Medial margin formed into a projection that terminates in a pore midway along the length of the canal expanse
    - Margins of projections perforated by small pores
- Medial margin across from terminus of maxilla perforated by several small pores located at the ends of short projections
- Small terminal mandibular pore present adjacent to origin of preopercle.

Preopercular Portion (Figure 19A)

- Proximal margin perforated by many small pores
- Median of ventral flange perforated by numerous small pores
- Distal margin formed into numerous projections that terminate in pores along edge of preopercle
- Dorsal-most portion of the distal margin formed into projections that extend posteriorly beyond preopercle onto opercle
    - Margins of projections perforated by a few pores

Sensory Papillae Pattern

- Papillae present on anterior portion of basihyal
- Papillae interspersed among pores along mandibular canal median
- Papillae interspersed among pores on ventral preopercular flange
- Single row of papillae along vertical preopercular flange

Remarks

Coranthus is a monotypic genus. The canal system of *Coranthus polyacanthus* is highly branched. The projections that terminate in pores just ventral of the terminal infraorbital pore are a characteristic shared by *C. polyacanthus*and *Holapogon maximus.* The supraorbital canal of *C. polyacanthus* is characterized by the development of the lateral margin into extensions that terminate in pores near the posterior nostril and in the anterior interorbital space. The posterior interorbital projections are noteworthy. In many other apogonid species, these projections are posterior extensions from the posterior interorbital region. In *C. polyacanthus* the projections are more medially projected extensions from the distal margin along the dorsal rim of the orbit. There appears to be a broad medial postorbital projection that is confluent with the supratemporal canal. This region of the specimen's cephalic lateralis was resistant to inflation and thus the pattern of branching was more difficult to ascertain than in other specimens. The supratemporal canal of *C. polyacanthus* is far forward, being positioned in the posterior interorbital space, and highly arched in comparison to other apogonid species.

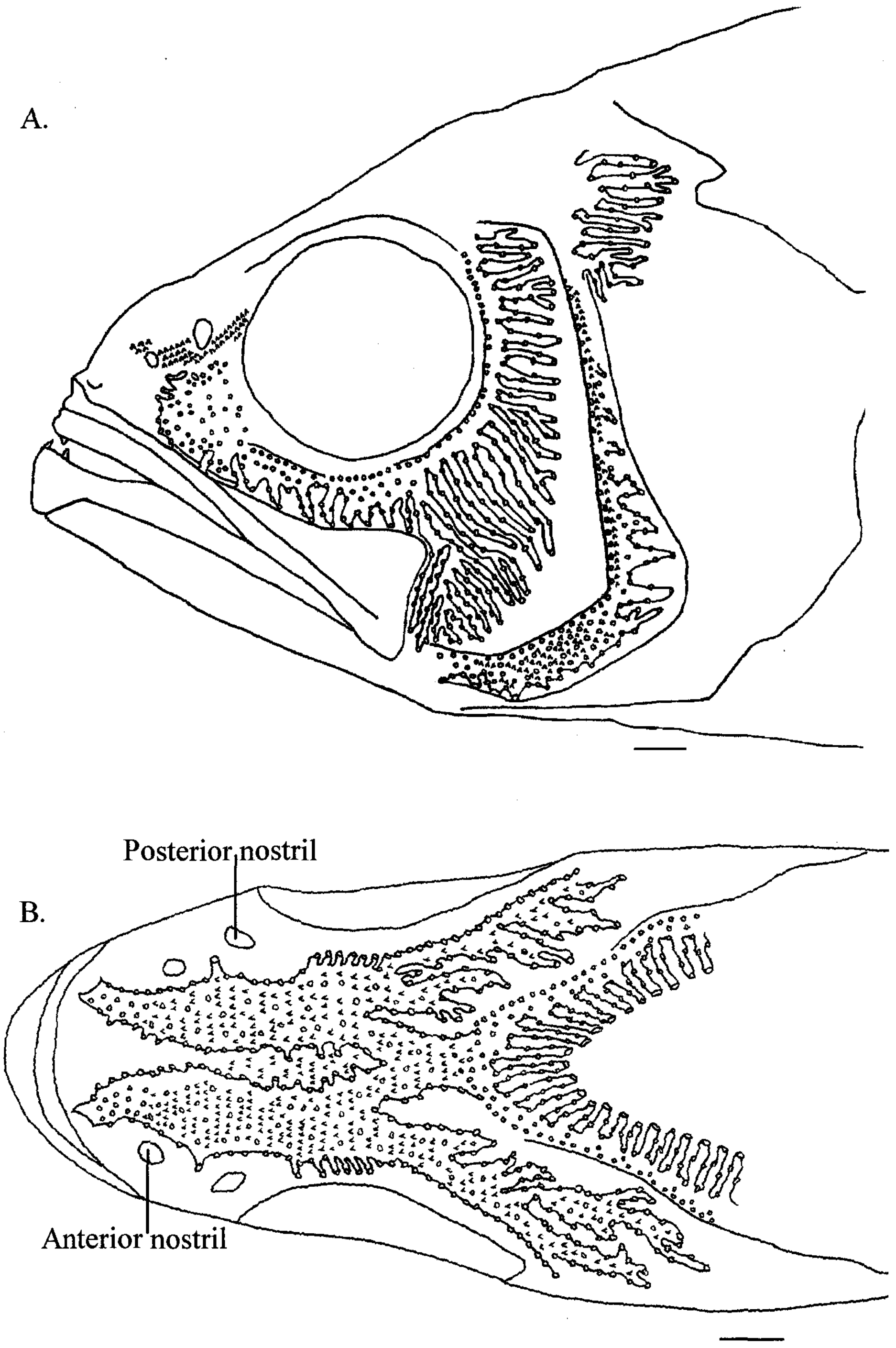


Figure 18. Cephalic lateralis of *Coranthus polyacanthus*. A. Lateral view, B. Dorsal view

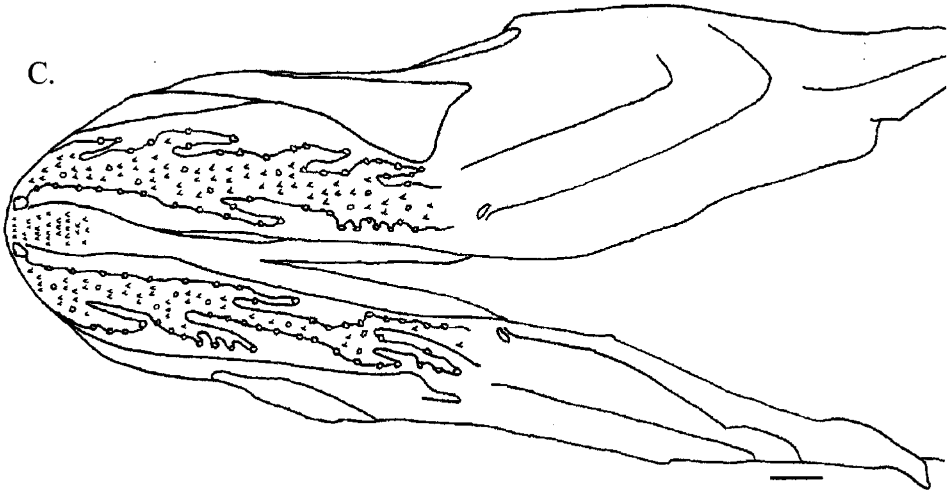


Figure 19 (continued). Cephalic lateralis of *Coranthus polyacanthus.* C. Ventral view

Foa Jordan & Evermann in Jordan & Seale, 1905

Material Examined

Type species: *Fowleria brachygrammus* Jenkins, 1903, [genus appeared first in Jordan & Seale (3 July 1905) with description of *Foa fo*, figure labeled *Foa brachygramma* (Jenkins) not *Foa fo*, genus then appeared in Jordan & Evermann (29 July 1905) with *Foa brachygramma* as type]; type by subsequent designation of Jordan & Evermann (1905); BPBM 22651; 1, 43.1 mm

Foa fo Jordan & Seale, 1905; BPBM 29990; 3, 27.4—37.0 mm

Supraorbital Canal

Nasal Portion

- Extends almost to tip of snout (Figure 20A)
- Terminates anteriorly in a slit-like pore that parallels the premaxilla
- Lateral margin just anterior of and medial to posterior nostril perforated by a large, lunate pore (Figure 20B)

- Medial margin anterior of posterior nostril perforated by several small pores

Interorbital Portion

- Margins in interorbital space perforated by numerous pores
- Lateral margin perforated by large slit-like pore near longitudinal mid-point of interorbital space
    - Pores perforating lateral margin along dorsoposterior rim of orbit larger than those perforating proximal margin or median

Postorbital Portion

- Canal formed into a number of open-ended, secondary extensions that project posteriorly along median of postorbital space
    - Margins of extensions perforated by numerous small pores

Sensory Papillae Pattern

- Longitudinal row of papillae extends along median from terminal pore to supratemporal canal
    - Branches anteriorly into two rows
        - One continuing along midline of canal to margin of snout
        - One curving obliquely toward midline of snout
- Crosshatch pattern of papillae covering entire canal surface
    - Formed from intersection of longitudinal row by numerous short transverse rows
- Medians of postorbital extensions with short transverse rows of papillae

Supratemporal Canal (Figure 20B)

- Anterior margin perforated by numerous small pores
- Posterior margin formed into numerous open-ended, posteriorly projecting secondary extensions
    - Margins of extensions perforated by numerous small pores

Infraorbital Canal (Figure 20A)

<u>Lachrymal Portion</u>

- Terminates anteriorly in a large pore located just posterior of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two long, slit-like pores

<u>Suborbital Portion</u>

- Proximal margin perforated by numerous moderately-sized pores
- Posterior half of distal margin perforated by few moderately-sized pores

<u>Postorbital Portion</u>

- Proximal margin perforated by numerous moderately-sized pores
- Distal margin formed into numerous open-ended projections that extend posteriorly onto cheek
    - Margins of extensions perforated by numerous small pores

<u>Sensory Papillae Pattern</u>

- Internarial space with several rows of papillae
    - Several rows extend posteriorly to margin of orbit
- Longitudinal row of sensory papillae extends along median from first lachrymal pore to posterior of terminus of maxilla

    - Continues posteriorly, curving ventrally, to extend to ventral edge of preopercle
- Transverse rows of papillae radiate from ventral margin of orbit
- Few longitudinal rows of papillae extend posteriorly from posterior margin of orbit

Preoperculomandibular Canal

Mandibular Portion (Figure 20C)

- Terminates anteriorly in a pair of round pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a relatively large pair of subtriangular mental pores
- Medial and lateral margins perforated by numerous moderately-sized pores
- Lateral margin perforated by comparatively large pores one-quarter and two-quarters along the length of the canal portion
- Terminates in a large, oval-shaped pore adjacent to origin of preopercle

Preopercular Portion (Figure 20B)

- Proximal margin perforated by several moderately-sized pores
- Distal margin formed into numerous open-ended extensions that terminate along posterior margin of preopercle
- Dorsal-most portion of distal margin formed into several open-ended projections that extend posteriorly beyond margin of preopercle
    - Margins of extensions perforated by few small pores

Sensory Papillae Pattern

- Basihyal with chevron pattern of papillae
- Mandibular median with several longitudinal rows of papillae

- Row of papillae extends ventrally from supraorbital canal along median of vertical preopercular flange
- Crosshatch pattern of papillae on ventral preopercular flange

Remarks

The morphology of the cephalic lateralis is consistent among the species of *Foa.* Marginal variation occurs in the patterns formed by the sensory papillae. More rows of papillae radiate from the ventral margin of the orbit in *Foa brachygramma* than in *Foa fo.* The sensory papillae present on the basihyal are denser anteriorly in *Foa fo* than they are in *Foa brachygramma.* The canal morphology of *Foa* species is quite similar to the species of *Fowleria.*

A.

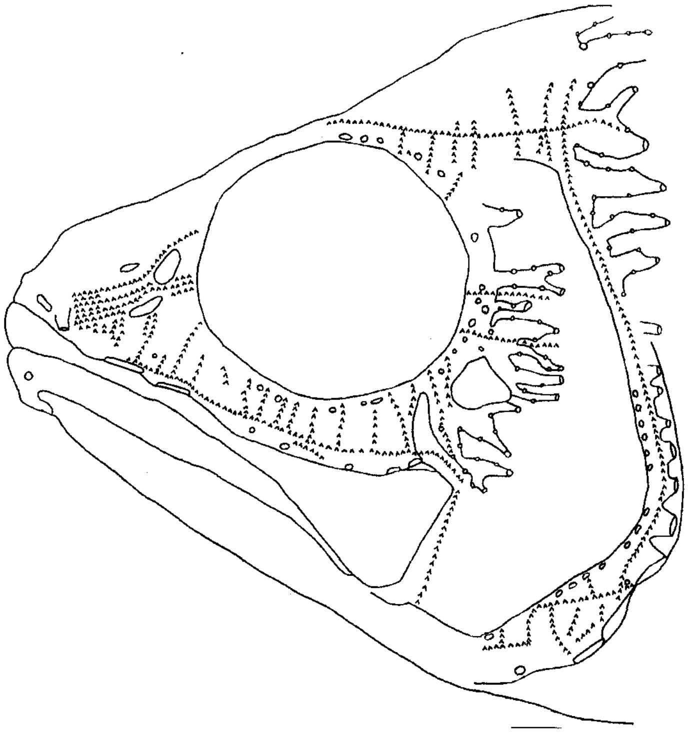


Figure 20. Cephalic lateralis of *Foa brachygramma.* A. Lateral view

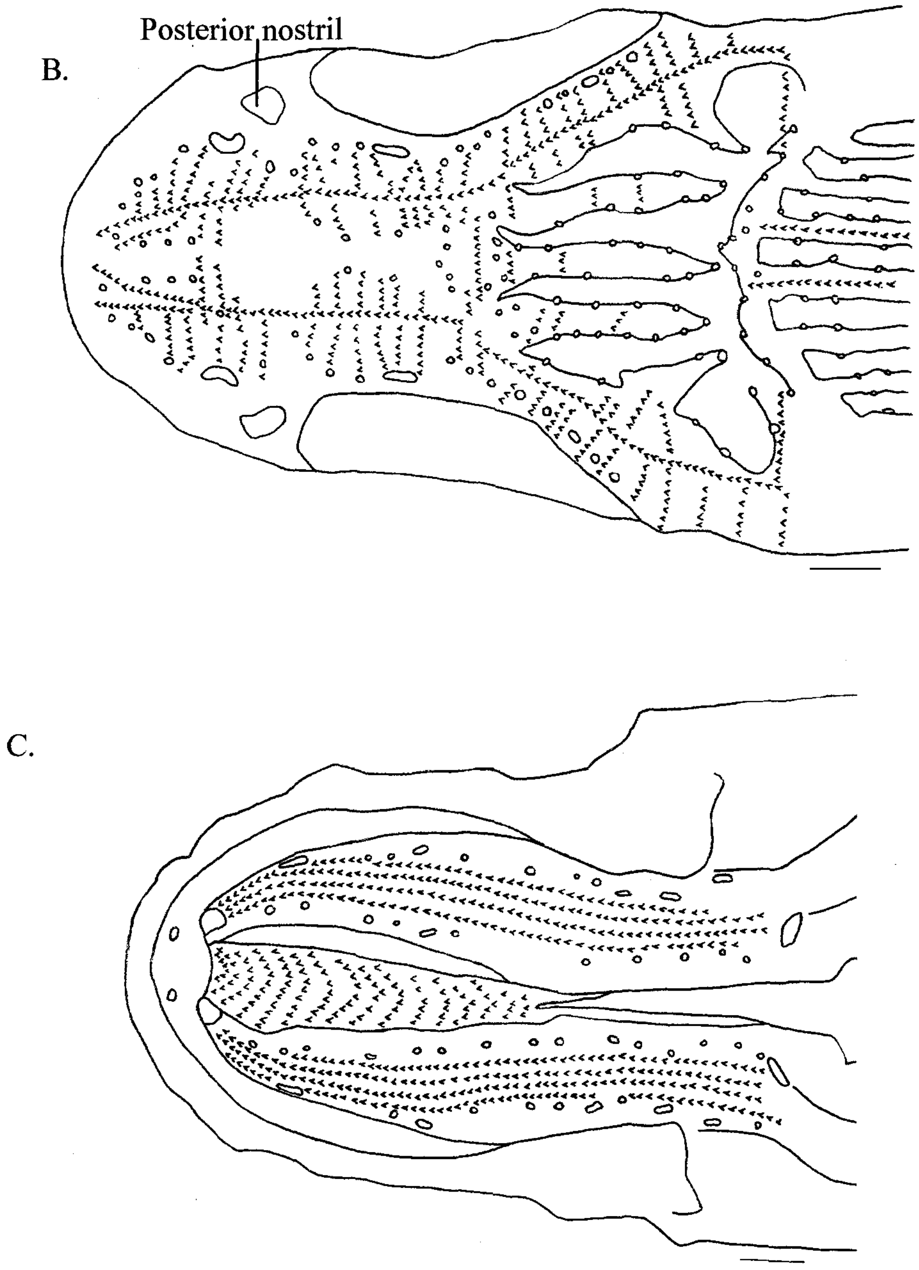


Figure 20 (continued). Cephalic lateralis of *Foa brachygramma*. B. Dorsal view, C. Ventral view

Fowleria Jordan & Evermann, 1903

Material Examined

Type species: *Apogon auritus* Valenciennes in Cuvier & Valenciennes, 1831, by original designation; BPBM 21538; 1, 64.6 mm

Fowleria isostigma (Jordan & Seale, 1906); BPBM 32083; 1, 36.0 mm

Fowleria marmorata (Alleyne & MacLeay, 1877); BPBM 32115; 2, 17.3—29.5 mm

Fowleria vaiulae (Jordan & Seale, 1906); BPBM 32376; 2, 30.8—31.3 mm

Supraorbital Canal

Nasal Portion

- Extends almost to tip of snout (Figure 21A)
- Terminates anteriorly in a moderately-sized oval-shaped pore that parallels the premaxilla
- Numerous small pores perforating canal anterior of posterior nostril
    - Concentrated along medial margin
- Lateral margin perforated by a large pore just anterior of and medial to posterior nostril (Figure 21B)

Interorbital Portion

- Medial margin perforated by numerous small pores
- Lateral margin perforated by a large slit-like pore near longitudinal midpoint of interorbital space

Postorbital Portion

- Canal formed into a number of open-ended, secondary projections that extend posteriorly along median of postorbital space
    - Margins of projections perforated by numerous small pores

Sensory Papillae Pattern

- Longitudinal row of papillae extends along median from terminal pore to supratemporal canal
    - Branches anteriorly into two rows
        - One continuing along midline of canal to margin of snout
        - One curving obliquely toward midline of snout
- Crosshatch pattern of papillae coves canal from posterior nostril to longitudinal midpoint of interorbital space
    - Formed from intersection of longitudinal row by numerous short transverse rows

Supratemporal Canal (Figure 21B)

- Anterior margin perforated by numerous small pores
- Posterior margin of canal formed into a number of open-ended, posteriorly projecting extensions
    - Margins of projections perforated by several small pores
- Sensory papillae extend from supraorbital canal curving onto and following median of supratemporal of canal
- Short longitudinal row of papillae intersects canal near midline of body

Infraorbital Canal (Figure 21A)

Lachrymal Portion

- Terminates anteriorly in a large slit-like pore just posterior of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two, long, slit-like pores
- Median of canal superior to lachrymal pore perforated by two small pores

Suborbital Portion

- Margins and median perforated by several pores

Postorbital Portion

- Proximal margin perforated by several small pores
- Distal margin formed into numerous open-ended projections that extend onto cheek
    - Margins of projections perforated by small pores

Sensory Papillae Pattern

- Internarial space with two rows of papillae
    - Ventral-most row curves between posterior nostril and terminal and extends to orbit
- Longitudinal row of sensory papillae along median from just posterior of second lachrymal pore to terminus of maxilla
    - Continues posteriorly, curving ventrally, to extend to ventral edge of preopercle
- Several transverse rows of papillae radiate from the ventral rim of the orbit
    - Forms crosshatch pattern with longitudinal row

Preoperculomandibular Canal

Mandibular Portion (Figure 21C)

- Terminates anteriorly in a pair of moderately-sized round pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a relatively large pair of subtriangular mental pores
- Medial and lateral margins perforated by numerous small and moderately-sized pores
- Lateral margin perforated by comparatively large pores one-quarter and two-quarters along the length of the canal portion
- Terminates in a large, slit-like pore adjacent to origin of preopercle

Preopercular Portion (Figure 21A)

- Proximal margin perforated by several moderately-sized pores
- Median of ventral flange perforated by numerous small pores
- Distal margin formed into a number of open-ended extensions that terminate along posterior margin of preopercle
- Dorsal-most portion of distal margin formed into a few open-ended projections that extend posteriorly beyond preopercle

Sensory Papillae Pattern

- Basihyal with chevron pattern of papillae
- Several short, semi-longitudinal rows of papillae cover mandibular canal median
- Median of vertical preopercular flange with one row of sensory papillae
- Transverse row of sensory papillae on opercle just posterior of edge of preopercle

Remarks

The general canal morphology is consistent among the *Fowleria* species. Minor variations occur in the papillae patterns. Papillae are absent from the supratemporal canal in *F. isostigma*, whereas they are present in the other species. *Fowleria marmorata* is unique among the *Fowleria* species in possessing a few rows of relatively large papillae radiating posteriorly from the posterior margin of the orbit. In *F. vaiulae* the distal margin of the postorbital portion of the infraorbital canal is not formed into open-ended projections but is highly perforated by relatively large pores. The lateral margin of the mandibular canal is similar to that of *Foa* species in that it is not formed into projections and is perforated by three regularly spaced, large pores located one-quarter, two-quarters, and three-quarters along the length of the canal portion.

A.

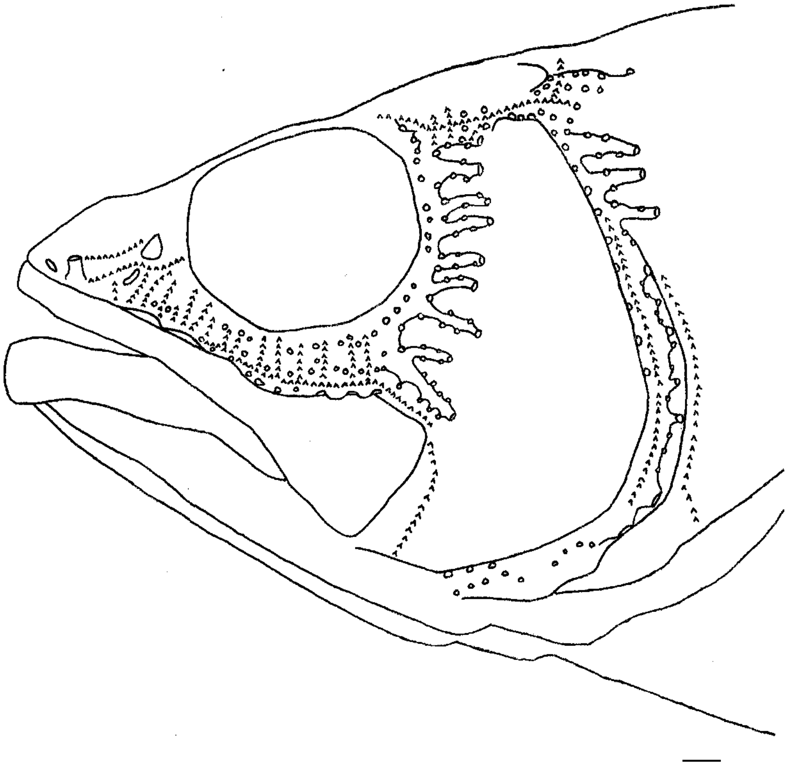


Figure 21. Cephalic lateralis of *Fowleria aurita*. A. Lateral view

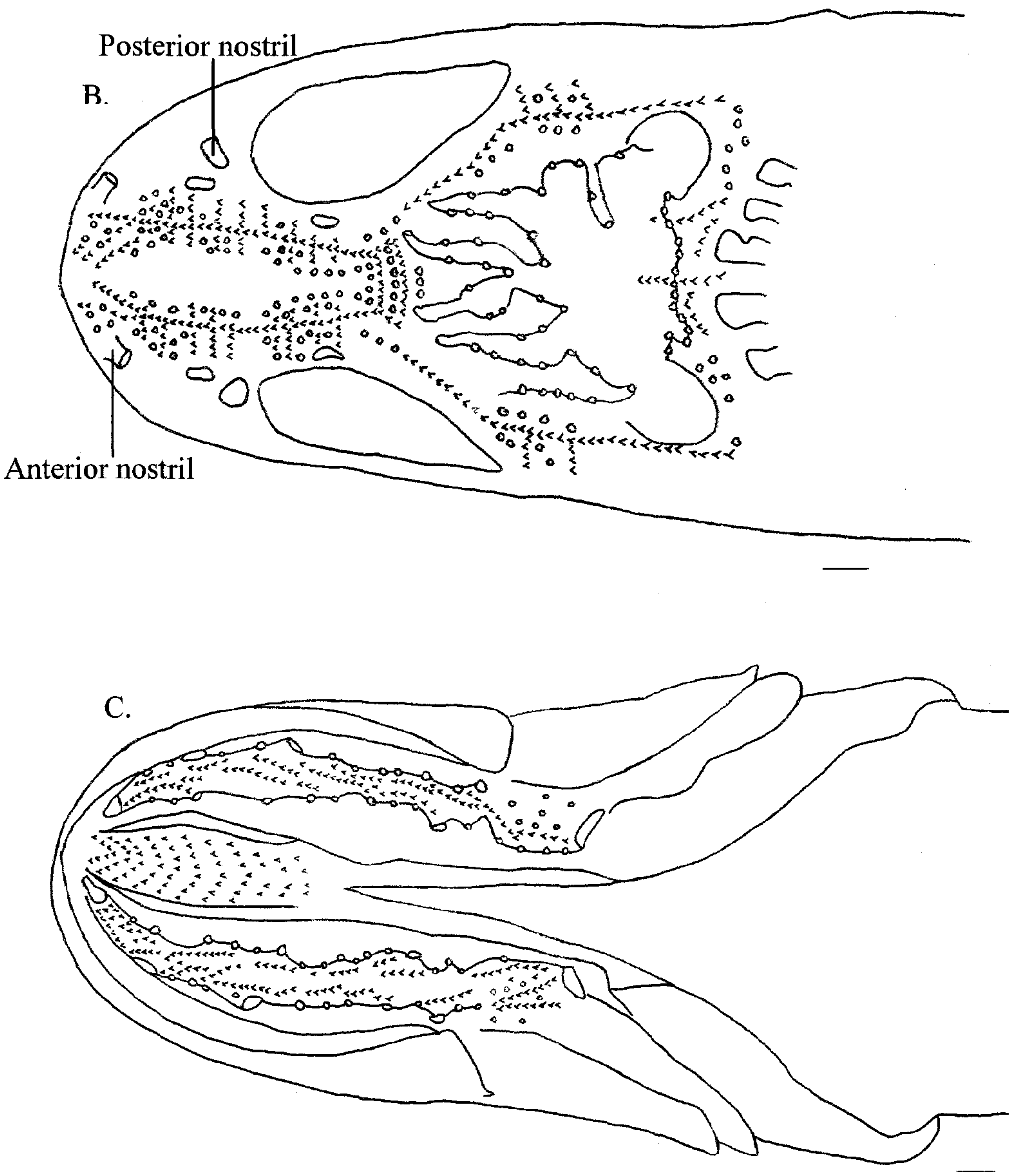


Figure 21 (continued). Cephalic lateralis of *Fowleria aurita*. B. Dorsal view, C. Ventral view

***Glossamia* Gill, 1863**

Material Examined

Type species: *Apogon aprion* Richardson, 1842, by original designation (also monotypic); USNM 217205; 11, 19.0—108.1 mm

Supraorbital Canal

Nasal Portion

- Extends almost to tip of snout (Figure 22A)
- Terminates anteriorly in a small oval-shaped pore
    - Located just anterior of and medial to anterior nostril
- Lateral margin perforated by a relatively large pore medial to posterior nostril (Figure 22B)

Interorbital Portion

- Lateral margin perforated by a large pore just anterior of longitudinal midpoint of interorbital space
- One small, medial, round pore perforating interorbital space anterior of secondary canal development

Postorbital Portion

- Canal formed into a number of open-ended, relatively short, secondary projections that extend posteriorly from postorbital space
    - Margins of projections perforated by very few pores

Sensory Papillae Pattern

- Longitudinal row of papillae extends from terminal pore to supratemporal canal
    - Slight disjunction medial to nasal pore

- Crosshatch pattern formed by intersection of this longitudinal row by numerous transverse rows
- Medians of postorbital projections with transverse rows of sensory papillae

Supratemporal Canal (Figure 22B)

- Anterior margin of canal not perforated
- Posterior margin of canal perforated by a few relatively large pores
    - Not modified into secondary extensions

<u>Sensory Papillae Pattern</u>

- Short longitudinal rows of papillae traverse canal

Infraorbital Canal (Figure 22A)

<u>Lachrymal Portion</u>

- Terminates anteriorly in a moderately-sized pore posterior of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two large slit-like pores

<u>Suborbital Portion</u>

- Median just anterior of midpoint of orbit perforated by one moderately-sized pore
- Distal margin along posterior portion of maxilla perforated by a few moderately-sized pores

<u>Postorbital Portion</u>

- Distal margin perforated by a few moderately-sized pores
    - Not developed into secondary projections

Sensory Papillae Pattern

- Rows of sensory papillae in internarial space
    - Few extend posteriorly beyond posterior nostril to margin of orbit
- Longitudinal row of papillae extends along suborbital median from second lachrymal pore to posterior of terminus of maxilla
- Numerous rows of papillae radiate from ventral rim of orbit, terminate along longitudinal row
- Irregular crosshatch pattern on cheek formed from intersection of postorbital longitudinal rows by numerous short transverse rows

Preoperculomandibular Canal

Mandibular Portion (Figure 22C)

- Terminates anteriorly in a pair of small round pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a moderately-sized pair of slit-like mental pores
- Lateral margin perforated by three moderately-sized pores at each of the first three quarters along the canal's length
    - Not formed into extensions
- Medial margin perforated by several small pores
- Terminates in a large, oval-shaped pore adjacent to ventral origin of preopercle

Preopercular Portion (Figure 22A)

- Proximal margin of canal perforated by several small pores
- Distal margin formed into a number of open-ended projections that extend toward edge of preopercle

Sensory Papillae Pattern

- Sensory papillae formed into chevron pattern on anterior of basihyal
- Two longitudinal rows of papillae extend along mandibular median
- Numerous short, transverse rows of papillae on branchiostegal membrane
- Median of ventral preopercular flange with crosshatch pattern of papillae
- Median of vertical preopercular flange with a disjunct longitudinal row of sensory papillae

Remarks

The canal system of *Glossamia* is relatively simple, with minimal secondary canal development and perforation, in comparison to other species of apogonids. Short secondary postorbital projections are present, but are simple in structure and are relatively un-perforated. The supratemporal canal is likewise weakly developed. The posterior margin is perforated, but lacks secondary development. The postorbital portion of the infraorbital canal is also notably weakly developed, with pores perforating the distal margin but without any significant secondary development. The lateral margin of the mandibular canal portion is perforated by three regularly spaced, moderately-sized pores. The positions of these pores roughly correspond to a quarterly division of the mandibular canal portion. This pattern is common in many apogonid species.

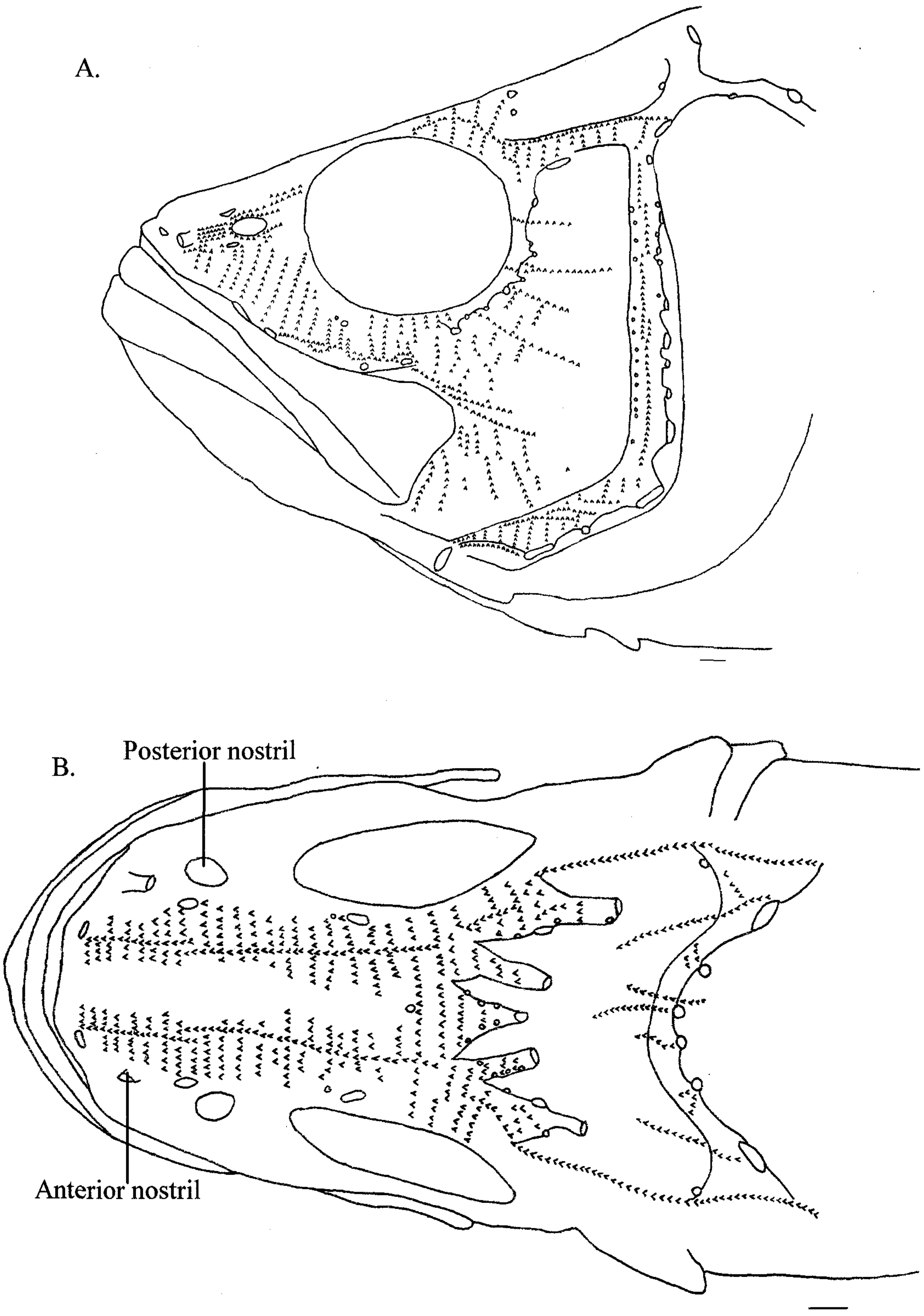


Figure 22. Cephalic lateralis of *Glossamia aprion*. A. Lateral view, B. Dorsal view

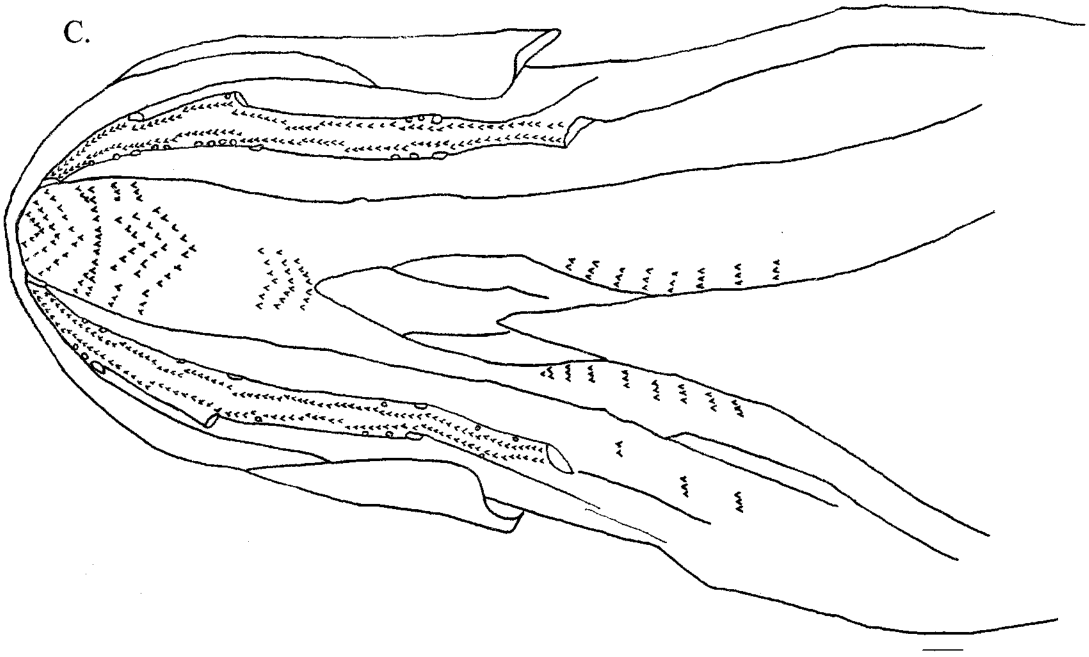


Figure 22 (continued). Cephalic lateralis of *Glossamia aprion*. C. Ventral view

Holapogon Fraser, 1973

Material Examined

Type species: *Apogon maximus* Boulenger, 1888, by original designation (also monotypic); USNM 213365; 1, 165.6 mm; CAS 87230; 2, 158.1—165.5 mm

Supraorbital Canal

Nasal Portion

- Extends nearly to tip of snout
- Terminates anteriorly in a slit-like pore that parallels the premaxilla
- Lateral margin perforated by numerous pores
    - Pores located at ends of extensions
    - Fewer anterior of posterior nostril, more numerous posterior of posterior nostril

  - Pore adjacent to posterior nostril large relative to others
- Medial margin posterior of posterior nostril formed into a few extensions that terminate in pores

Interorbital Portion

- Lateral margin formed into several short, projections that terminate in pores along dorsal rim of orbit
  - Prominently large pore perforating lateral margin absent

Postorbital Portion

- Canal formed into a number of open-ended, secondary projections that extend posteriorly from postorbital space to supratemporal canal
    - Margins and medians of projections perforated by small pores

Sensory Papillae Pattern

- Short transverse rows of papillae on canal median
- Non-continuous, short, transverse rows of papillae cross dorsal surface of head in interorbital space

Supratemporal Canal (Figure 23B)

- Anterior margin and median perforated by numerous small pores
- Posterior margin formed into numerous open-ended, posteriorly projecting secondary extensions
  - Margins of extensions perforated by few small pores

Infraorbital Canal (Figure 23A)

Lachrymal Portion

- Terminates anteriorly in a large pore located posterior of the internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two broad, slit-like pores
    - Lachrymal pores not distinct different from others along suborbital portion
- Distal margin immediately posterior of terminal pore perforated by a few small pores
    - Two pores at ends of short, anteriorly-projecting extensions

Suborbital Portion

- Proximal margin and median perforated by many small round pores
- Distal margin formed into broad, extensions that extend toward margin of maxilla and terminate in pores

Postorbital Portion

- Proximal margin and median perforated by many small, round pores
- Distal margin formed into many open-ended, projections that extend posteriorly onto cheek
    - Individual projections branch secondarily to form a finer subset of extensions

Sensory Papillae Pattern

- Few rows of papillae in internarial space

Preoperculomandibular Canal

Mandibular Portion (Figure 23C)

- Terminates anteriorly in a pair of round pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a relatively large pair of mental pores
- Lateral margin formed into extensions that terminate in pores one-quarter and two-quarters of the way along the length of the canal portion
- Lateral and medial margins of posterior half of canal formed into several extensions that terminate in pores
- Small terminal mandibular pore present adjacent to origin of preopercle.

Preopercular Portion (Figure 23A)

- Proximal margin perforated by several small pores
- Distal margin formed into several open-ended projections that extend to edge of preopercle
- Dorsal-most portion of the distal margin formed into projections that extend posteriorly beyond preopercle onto opercle
    - Margins of projections perforated by a few pores

Remarks

Holapogon is a monotypic genus. The canal system of *H. maximus* is relatively highly branched. The secondary projections of the lateral margin anterior of the posterior nostril in the supratemporal canal are unique to *Holapogon*. *Holapogon maximus* possesses a large nasal pore, but lacks the large interorbital pore common to many other apogonids. The postorbital secondary projections are highly perforated. The presence of sensory papillae is reduced in *H. maximus*, being completely absent on the infraorbital canal. Sensory papillae are present on the anterior mandibular canal but have been abraded in the specimens examined posteriorly making confirmation of their presence impossible.

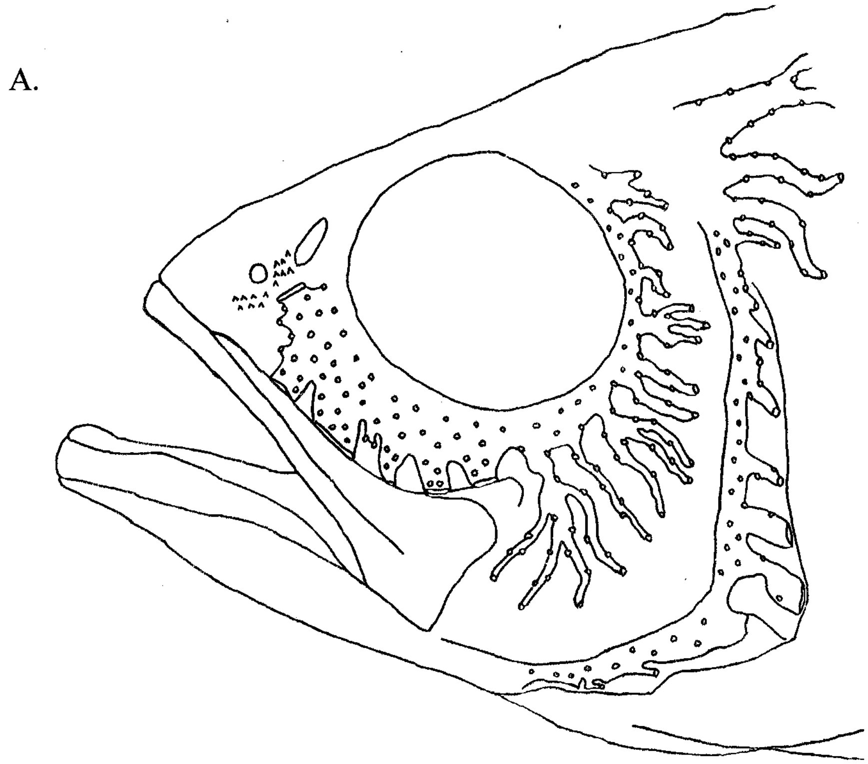


Figure 23. Cephalic lateralis of *Holapogon maximus*. A. Lateral view

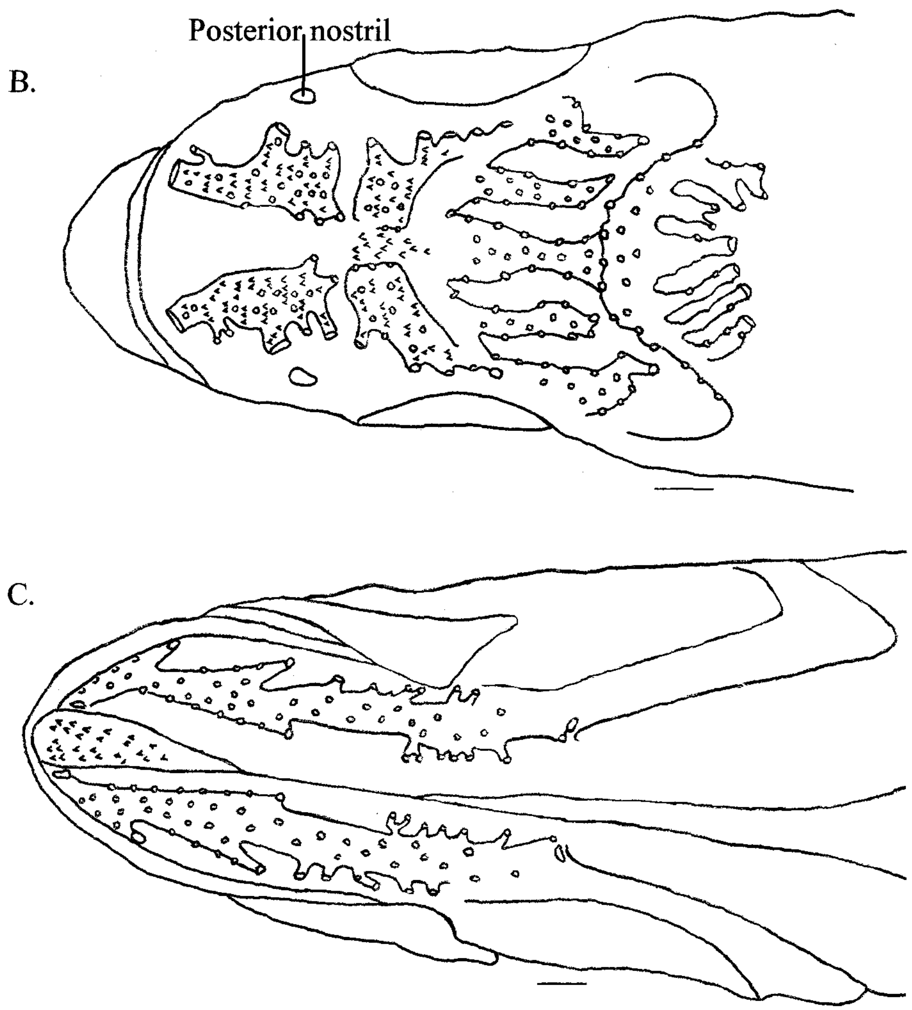


Figure 23 (continued). Cephalic lateralis of *Holapogon maximus*. B. Dorsal view, C. Ventral view

Lachneratus Fraser & Struhsaker, 1991

Material Examined

Type species: *Lachneratus phasmaticus* Fraser & Struhsaker, 1991, by original designation (also monotypic); USNM 268198; 2, 41.8—44.9 mm

Supraorbital Canal

Nasal Portion

- Extends almost to tip of snout (Figure 24A)
- Terminates in slit like pore that parallels the premaxilla
- Lateral margin just medial to and anterior of posterior nostril perforated by a large pore

Interorbital Portion

- Lateral margin near longitudinal midpoint of interorbital space perforated by a large, semi-oval pore
- Median of mid-interorbital space perforated by several small pores
- Canal formed into a few secondary projections that extend dorsally toward midline of body
    - Margins of projections not perforated

Sensory Papillae Pattern

- Few rows of papillae in internarial space
- Few short rows of sensory papillae medial to terminal pore (Figure 24B)
- Longitudinal row of sensory papillae extends posteriorly from nasal pore to anterior interorbital space

- Few transverse rows of papillae traverse dorsal surface of head from posterior nostril to supratemporal canal

Supratemporal Canal (Figure 24B)

- Anterior and posterior margins perforated by numerous small pores
- Margins not modified into secondary extensions

Infraorbital Canal (Figure 24A)

<u>Lachrymal Portion</u>

- Terminates anteriorly in a moderately-sized pore located posterior of anterior nostril
- Distal margin, along ventral edge of lachrymal, perforated by two moderately-sized, round pores

<u>Suborbital Portion</u>

- Proximal margin perforated by several small pores

<u>Postorbital Portion</u>

- Proximal margin perforated by few small pores
- Distal margin formed into a few open-ended projections

<u>Sensory Papillae Pattern</u>

- Several rows of sensory papillae radiate toward maxilla from ventral rim of orbit

Preoperculomandibular Canal

<u>Mandibular Portion</u> (Figure 24C)

- Terminates anteriorly in a pair of moderately-sized, oval-shaped pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a large pair of subtriangular mental pores

- Medial and lateral margins perforated by several small pores
- Lateral margin perforated by a large pore one-quarter of the way along the canal length
- Medial margin perforated by large pores two-quarters and three-quarters of the way along the canal length
- Two moderately-sized pores perforating both margins adjacent to origin of preopercle

Preopercular Portion (Figure 24A)

- Proximal margin perforated by a few small pores
- Distal margin formed into a few open-ended projections that extend toward posterior edge of preopercle

Sensory Papillae Pattern

- Anterior portion of basihyal with few chevron-shaped rows of sensory papillae
- Mandibular median with longitudinal row of papillae
- Few transverse rows of papillae originating from longitudinal row near midpoint of mandibular portion

Remarks

*Lachneratus*is a monotypic genus. The canal system is relatively simple, with minimal secondary canal development. A few short secondary postorbital projections are present, but are simple in structure and are un-perforated. The supratemporal canal is likewise weakly developed. Both margins are perforated, but lack secondary development. The postorbital portion of the infraorbital canal is also weakly developed, with a few pores perforating the proximal margin and with very few, short projections.

The mandibular canal is not developed into projections; the margins are perforated intermittently by small and moderately-sized pores.

A

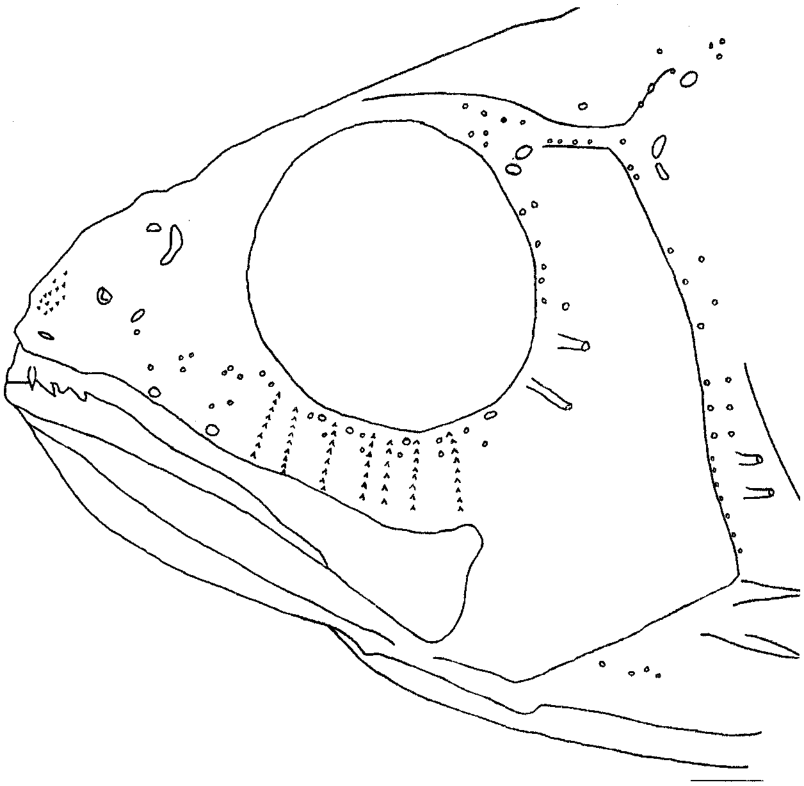


Figure 24. Cephalic lateralis of *Lachneratus phasmaticus*. A. Lateral view

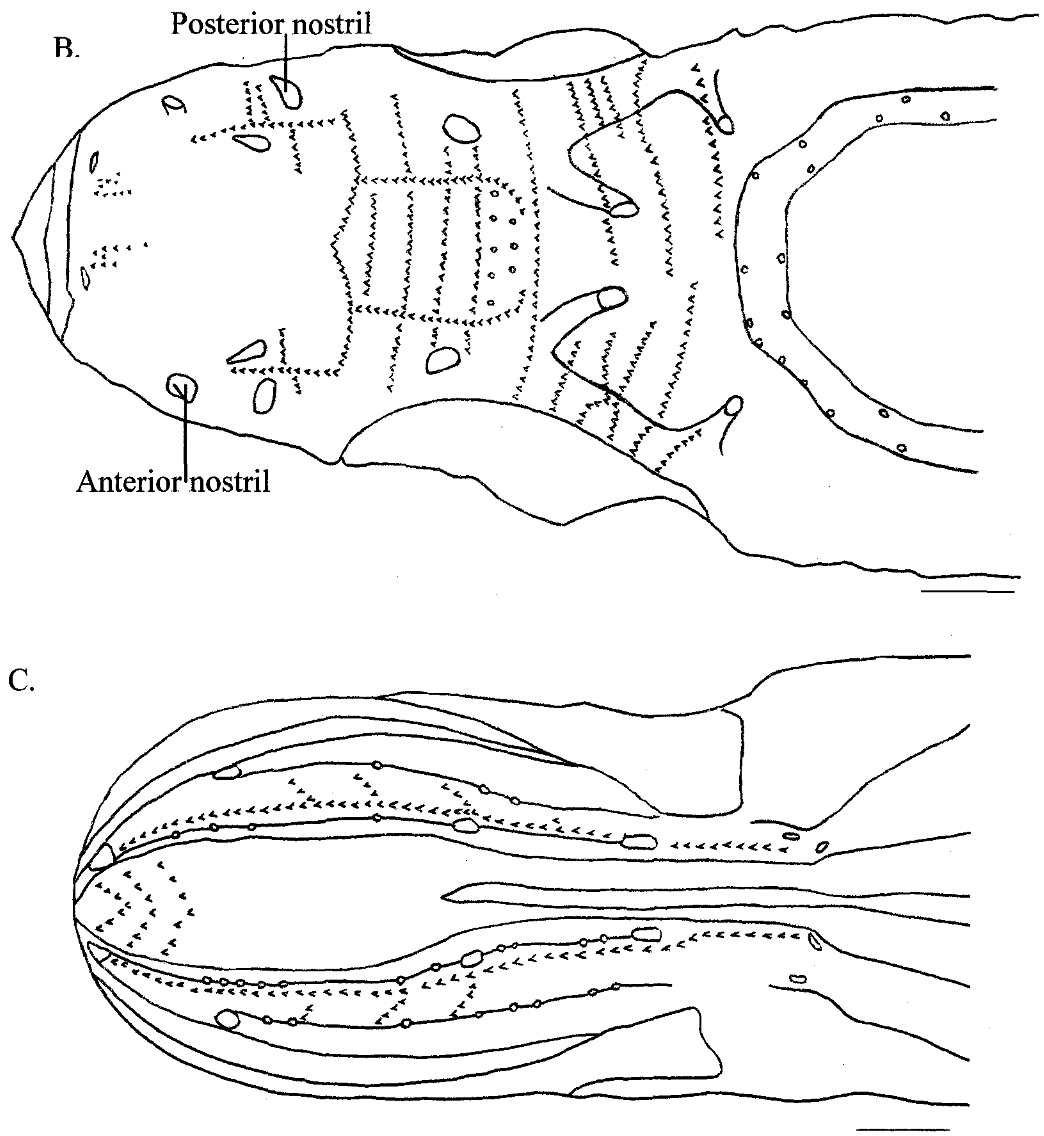


Figure 24 (continued). Cephalic lateralis of *Lachneratus phasmaticus*. B. Dorsal view, C. Ventral view

Neamia Smith & Radcliffe in Radcliffe, 1912

Material Examined

Type species: *Neamia octospina* Smith & Radcliffe in Radcliffe, 1912, by original designation (also monotypic); USNM 268124; 7, 32.3—35.3 mm

Supraorbital Canal

Nasal Portion

- Extends to tip of snout (Figure 25A)
- Terminates anteriorly in a slit-like pore that parallels the premaxilla
- Median and margins perforated by a few small pores anterior of posterior nostril
- Lateral margin perforated by a moderately-sized, round pore perforating just anterior of and medial to posterior nostril (Figure 25B)

Interorbital Portion

- Lateral margin perforated by a relatively-large, slit-like pore near longitudinal midpoint of orbit
- Canal from posterior nostril through postorbital space perforated by small pores
    - Pores concentrated toward margins until mid-interorbital space

Postorbital Portion

- Post-orbital portion of canal formed into several open-ended, posteriorly projecting secondary extensions
    - Margins of extensions perforated by numerous pores

Supratemporal Canal (Figure 25B)

- Anterior margin of canal perforated by several small pores
- Posterior margin formed into a number of open-ended, posteriorly projecting extensions
    - Margins of extensions perforated by a few small pores

Infraorbital Canal (Figure 25A)

<u>Lachrymal Portion</u>

- Terminates anteriorly in a large pore located just posterior of anterior nostril
- Distal margin, along ventral edge of lachrymal, perforated by two, long, slit-like pores

<u>Suborbital Portion</u>

- Proximal margin perforated by a few moderately-sized pores
- Distal margin just anterior of terminus of maxilla perforated by two, moderately-sized pores

<u>Postorbital Portion</u>

- Proximal margin perforated by few moderately-sized pores
- Distal margin of postorbital portion formed into several broad, open-ended projections extending posteriorly onto cheek
    - Margins of projections not perforated

Preoperculomandibular Canal

<u>Mandibular Portion</u> (Figure 25C)

- Terminates anteriorly in a pair of large pores that perforate the dentary

- Canal just posterior of apex of dentary perforated by a relatively large pair of mental pores
- Lateral margin perforated by three relatively-large, equidistant pores
    - Pores not at ends of projections
- Medial margin opposite posterior two lateral pores perforated by a few small pores
- Terminates in a relatively large, slit-like pore adjacent to origin of preopercle

Preopercular Portion (Figure 25A)

- Proximal margin perforated by several moderately-sized pores
- Distal margin formed into numerous open-ended projections extending toward margin of preopercle
    - Margins of projections not perforated
- Dorsal-most portion distal margin formed into a few open-ended projections that extend posteriorly beyond preopercle onto opercle
    - Margins of projections not perforated

Remarks

Neamia is a monotypic genus. The canal system is relatively simple with reduced secondary development and sparse perforations. The primary canals are broad in comparison to other apogonids. A large nasal pore, large interorbital pore, and several secondary postorbital projections characterize the supratemporal canal. The infraorbital canal is broad with few perforations and few postorbital projections. The sparsely perforated mandibular canal is not developed into projections. The projections formed from the distal margin of the preopercular canal are sparsely perforated and quite broad.

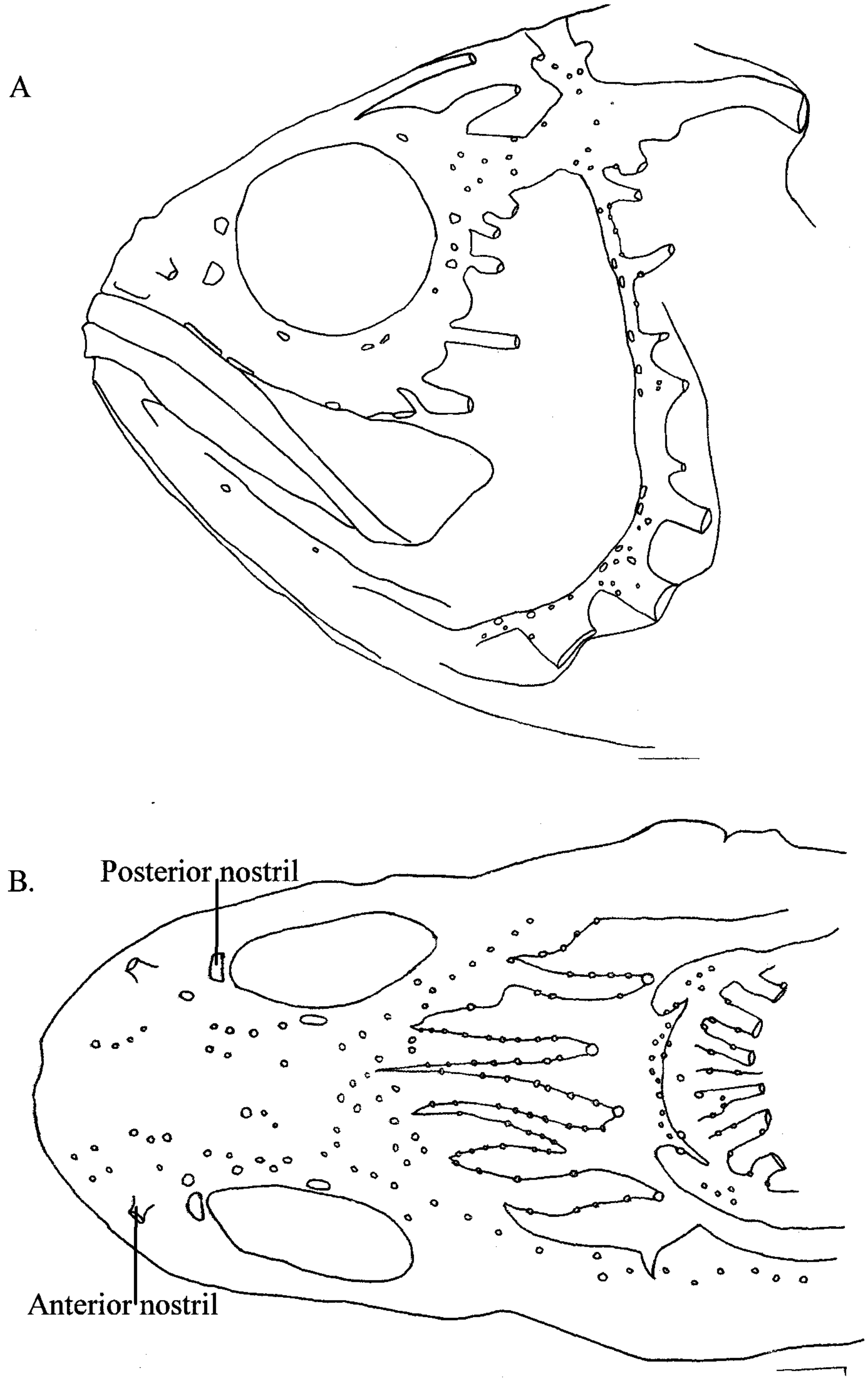


Figure 25. Cephalic lateralis of *Neamia octospina.* A. Lateral view, B. Dorsal view

C.

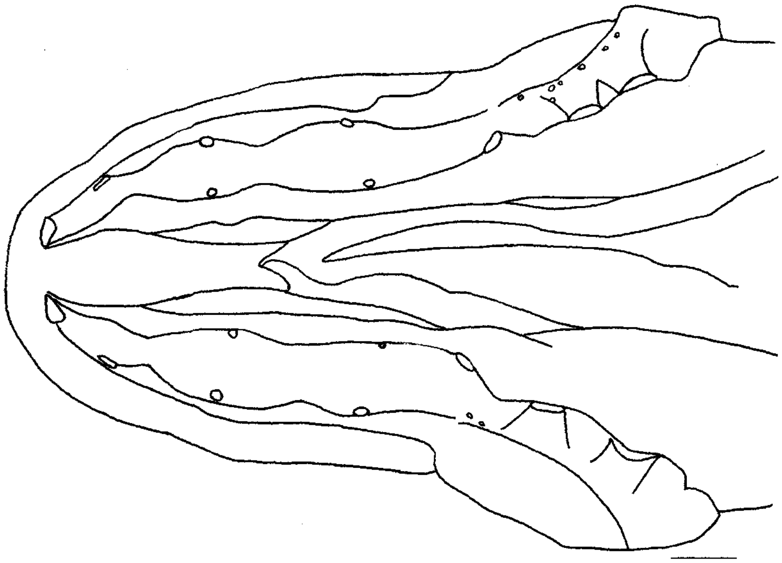


Figure 25 (continued). Cephalic lateralis of *Neamia octospina.* C. Ventral view

Phaeoptyx Fraser & Robins, 1970

Material Examined

Type Species: *Amia conklini* Silvester, 1915 by original designation; USNM 322239; 5, 33.1—42.4 mm

Phaeoptyx xenus (Böhlke & Randall, 1968); BPBM 88617; 1, 41.5 mm

Supraorbital Canal

- Extends almost to tip of snout (Figure 26A)
- Terminates anteriorly in a slit-like pore that parallels the premaxilla
- Lateral margin just medial to posterior nostril perforated by a large, sub-triangular pore (Figure 26B)
- Lateral margin just posterior of posterior nostril perforated by a moderately-sized oval-shaped pore

- Canal from anterior nostril to interorbital space perforated by numerous small pores
    - Pores concentrated toward margins

Interorbital Portion

- Lateral margin just anterior of longitudinal midpoint of orbit perforated by a large, slit-like pore
- Median of interorbital space perforated by several small pores
- Lateral margin perforated by numerous moderately-sized pores along dorsoposterior edge of orbit

Postorbital Portion

- Post-orbital portion of canal formed into several open-ended secondary projections that extend posteriorly to meet supratemporal canal
    - Margins of extensions perforated by numerous pores

Sensory Papillae Pattern

- Two longitudinal rows of sensory papillae extend posteriorly along medial and lateral margins of nasal, preorbital, and anterior interorbital portion of canal
- Longitudinal row of papillae extends along dorsoposterior margin of orbit, beginning in mid-interorbital space and terminating posterior of supratemporal canal
- Two, longitudinal rows of sensory papillae extend along median of head in posterior interorbital space and intersect secondary postorbital extensions
- Numerous transverse rows of papillae covering canal surface from terminal pore through postorbital space
    - From posterior nostril to mid-interorbital space, rows completely traverse dorsal surface

- Rows of sensory papillae radiating from orbit and extend onto postorbital extensions

Supratemporal Canal (Figure 26B)

- Anterior margin perforated by numerous small pores
- Posterior margin formed into numerous open-ended, posteriorly projecting extensions
    - Margins of extensions perforated by numerous pores

Sensory Papillae Pattern

- Transverse row of papillae extends along median portion of canal
- Canal intersected by few longitudinal rows of sensory papillae

Infraorbital Canal (Figure 26A)

Lachrymal Portion

- Terminates anteriorly in a relatively large pore located just posterior of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two, long pores

Suborbital Portion

- Proximal margin perforated by few pores
- Distal margin perforated by numerous small pores

Postorbital Portion

- Proximal margin perforated by numerous moderately-sized pores
- Distal margin formed into open-ended projections that extend posteriorly beyond maxilla onto cheek
    - Margins of projections perforated by a few pores

Sensory Papillae Pattern

- Internarial space with rows of sensory papillae
- Rows of papillae radiate ventrally from terminal pore
- Longitudinal row of papillae extends along suborbital median from first lachrymal pore to terminus of maxilla
- Two transverse rows of sensory papillae parallel posterior margin of maxilla
- Crosshatch pattern of papillae posterior to orbit

Preoperculomandibular Canal

Mandibular Portion (Figure 26C)

- Terminates anteriorly in a pair of small round pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a large pair of subtriangular mental pores
- Medial and lateral margins perforated by numerous moderately-sized pores
- Terminates posteriorly in a slit-like pore adjacent to origin of preopercle

Preopercular Portion (Figure 26A)

- Proximal margin perforated by several moderately-sized pores
- Distal margin formed into several projections that extend toward edge of preopercle
    - Margins of projections perforated by few small pores
- Dorsal-most portion of distal margin formed into several open-ended projections that extend posteriorly onto opercle

Sensory Papillae Pattern

- Sensory papillae form chevron pattern on basihyal
- Mandibular median with two, longitudinal rows of sensory papillae

- Lateral-most row extends onto ventral flange of preopercle

Remarks

The canals of the cephalic lateralis of *Phaeoptyx* are moderately branched and covered with a fairly regular pattern of sensory papillae. The morphologies of the cephalic lateralis of *Phaeoptyx conklini* and *P. xenus* are very similar. The only significant difference being that the secondary postorbital projections of *P. xenus* do not extend to meet the supratemporal canal as they do in *P. conklini.*

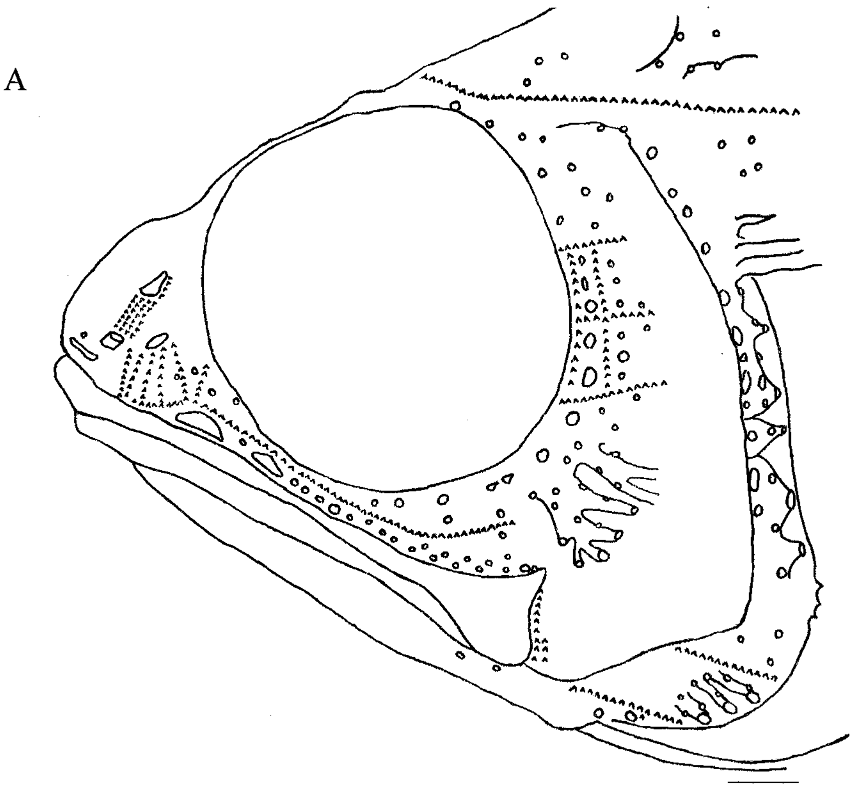


Figure 26. Cephalic lateralis of *Phaeoptyx conklini.* A. Lateral view

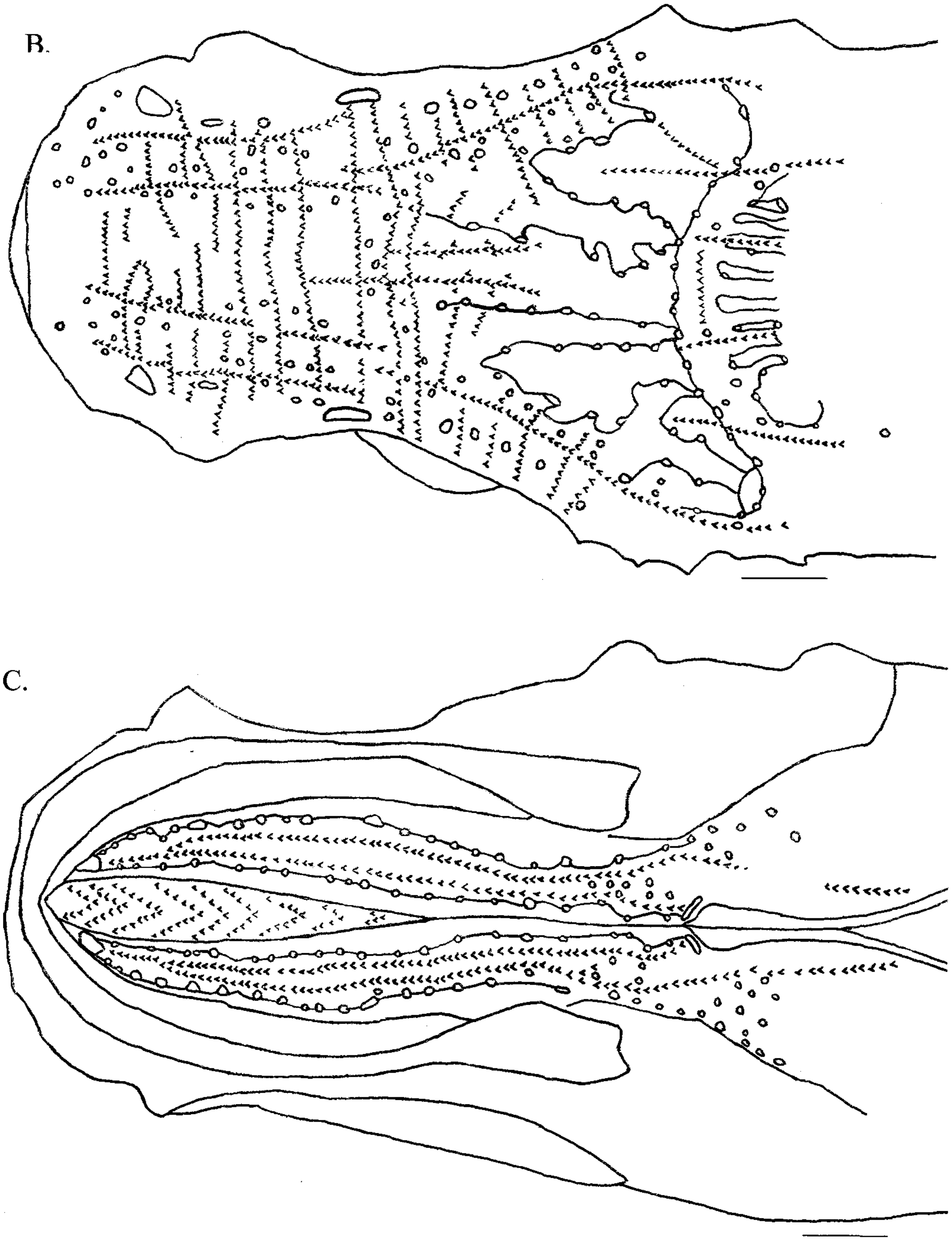


Figure 26 (continued). Cephalic lateralis of *Phaeoptyx conklini*. B. Dorsal view, C. Ventral view

Pterapogon (*Pterapogon*) Koumans, 1933

Material Examined

Type species: *Pterapogon kauderni* Koumans, 1933, by original designation (also monotypic); USNM 351332; 2, 9.9—15.5 mm; NJSA; 3, 21.3—46.8 mm

Supraorbital Canal

Nasal Portion

- Extends almost to tip of snout (Figure 27A)
- Terminates anteriorly in a moderately-sized slit-like pore just anterior of and medial to anterior nostril
- Lateral margin perforated by large pore just medial to posterior nostril (Figure 27B)
- Canal margins, from terminal pore to interorbital pore, perforated by several small pores

Interorbital Portion

- Lateral margin perforated by large, slit-like pore near longitudinal midpoint of interorbital space
- Medial margin perforated by a few small pores in mid-interorbital space

Postorbital Portion

- Post-orbital portion of canal formed into several open-ended secondary projections that extend toward supratemporal canal
    - Margins of projections not perforated

Sensory Papillae Pattern

- Small papillae covering canal median from terminal pore through interorbital space

Supratemporal Canal (Figure 27B)

- Anterior margin perforated by a few pores
- Posterior margin formed into a number of posteriorly projecting extensions that terminate in large round pores
    - Margins along posterior portions of extensions perforated by few moderately-sized pores

Sensory Papillae Pattern

- Several longitudinal rows of small sensory papillae traverse supratemporal canal and extend posteriorly onto secondary projections

Infraorbital Canal (Figure 27A)

Lachrymal Portion

- Terminates anteriorly in a large pore located posterior of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two, large, oval-shaped pores

Suborbital Portion

- Proximal margin perforated by several moderately-sized pores
- Distal margin along posterior of maxilla perforated by a few moderately-sized pores

Postorbital Portion

- Ventroposterior portion of distal margin formed into a number of open-ended projections that extend onto cheek
- Margins perforated by several moderately-sized pores

Sensory Papillae Pattern

- Suborbital median from posterior of lachrymal pores to terminus of maxilla covered by sensory papillae
- Few longitudinal rows of papillae radiate from ventroposterior rim of orbit

Preoperculomandibular Canal

Mandibular Portion (Figure 27C)

- Terminates anteriorly in a pair of small round pores that perforate the dentary (Figure 27B)
- Canal just posterior of apex of dentary perforated by a large pair of subtriangular mental pores
- Margins perforated by numerous pores
- Lateral margin perforated by comparatively large pores one-quarter, two-quarters and three-quarters of the way along then length of the canal
- Median adjacent to terminus of maxilla perforated by a few small pores
- Mandibular portion terminates in a large pore just anterior of and medial to origin of preopercle

Preopercular Portion (Figure 27A)

- Proximal margin along dorsal-most portion of preopercle densely perforated by many moderately-sized pores
- Distal margin formed into extensions that terminate in pores along margin of preopercle
  - Margins of extensions perforated by numerous small and moderately-sized pores

Sensory Papillae Pattern

- Basihyal covered by sensory papillae
- Mandibular median covered by irregular rows of sensory papillae
- Few papillae present on vertical flange of preopercle

Remarks

The canal system of *Pterapogon* (*Pterapogon*) *kauderni* is relatively simple with little secondary canal development. In comparison to other apogonids, the pores perforating the margins of the canals of *P. kauderni* are large relative to the body size of the specimens observed. The supraorbital canal of *P. kauderni* is characterized by a large nasal pore, large interorbital pore, and several simple secondary postorbital projections. The median of the supraorbital canal is covered by small sensory papillae from the terminal pore along the dorsoposterior rim of the orbit; however, these papillae are only visible in the specimens larger than 15 mm. The secondary projections of the supratemporal canal are noteworthy on account of the large size of their terminal pores. Because of the narrow space between the posterior rim of the orbit and preopercular ridge, only the ventral-most portion of the postorbital canal is developed into projections in comparison to the more extensive secondary development of many other apogonid species. The mandibular canal is also not developed into projections.

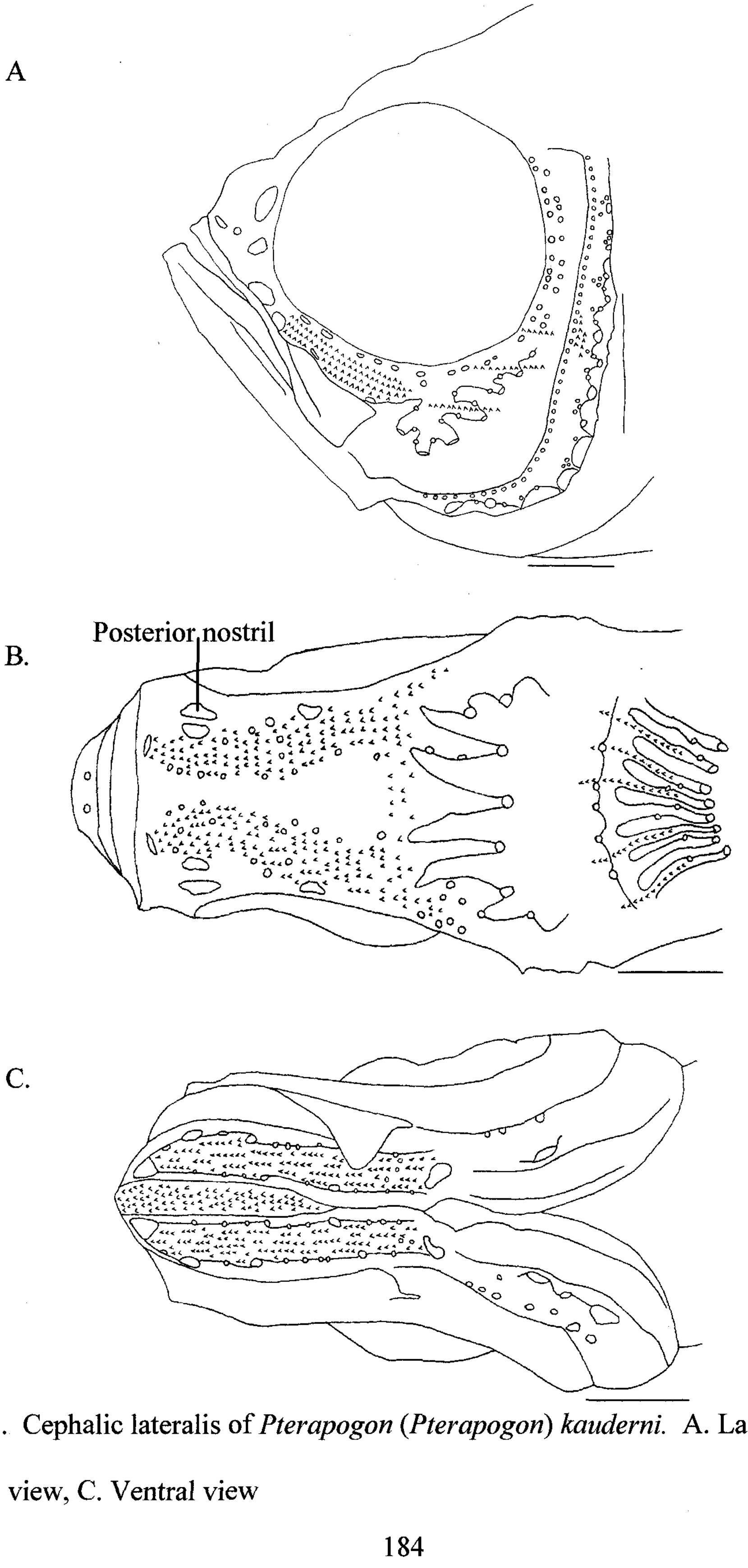


Figure 27. Cephalic lateralis of *Pterapogon* (*Pterapogon*) *kauderni.* A. Lateral view, B. Dorsal view, C. Ventral view

Pterapogon (*Quinca*) Mees, 1966

Material Examined

Type species: *Quinca mirifica* Mees, 1966, by original designation (also monotypic); unnumbered specimen WAM; 2, 49.4—51.8 mm

Supraorbital Canal

Nasal Portion

- Extends to tip of snout (Figure 28A)
- Terminates anteriorly in a long, slit-like pore that parallels the premaxilla
- Lateral margin superior of internarial space perforated by a large slit-like pore (Figure 28B)
- Median from nasal pore to mid-interorbital space perforated by numerous small pores

Interorbital Portion

- Lateral margin between posterior nostril and mid-interorbital space formed into several projections that extend dorsally toward orbit and terminate in pores
- Large interorbital pore absent

Postorbital Portion

- Canal formed into numerous open-ended, posteriorly projecting secondary extensions
    - Margins of canal perforated by small pores
    - Extend nearly to supratemporal canal

Sensory Papillae Pattern

- Sensory papillae densely cover canal from terminal pore to just posterior of nasal pore
- Two longitudinal rows of papillae extend along canal median from posterior nostril to anterior-interorbital space
- Longitudinal row of papillae extends along dorsoposterior margin of orbit
- Several short transverse rows radiate from orbit and intersect longitudinal row

Supratemporal Canal (Figure 28B)

- Anterior margin perforated by numerous small pores
- Posterior margin formed into numerous long, open-ended posteriorly projecting extensions
  - Margins of extensions perforated by many small pores
  - Projections terminate along the edges of scales

Infraorbital Canal (Figure 28A)

Lachrymal Portion

- Terminates anteriorly in a relatively large slit-like pore just posterior of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two long slit-like pores

Suborbital Portion

- Proximal margin perforated by numerous small pores
- Distal margin perforated by several moderately-sized pores along posterior portion of maxilla

Postorbital Portion

- Distal margin formed into numerous open-ended projections that extend posteriorly onto cheek
    - Margins of projections perforated by numerous small pores
    - Projections posterior of maxilla particularly lengthy, extending to preopercle

Sensory Papillae Pattern

- Internarial space with rows of sensory papillae
    - Few extending posteriorly beyond posterior nostril to orbit
- Suborbital median with short, longitudinal, non-continuous rows of papillae, formed into a band, from anterior of lachrymal pores to posterior of maxilla
- Many transverse rows radiate from the ventral rim of orbit

Preoperculomandibular Canal

Mandibular Portion (Figure 28C)

- Terminates anteriorly in a pair of pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a large pair of mental pores
- Medial margin perforated by several pores
- Lateral margin perforated by a moderately-sized pore about one-quarter of the way along its length
    - Pore not located at end of a projection
- Lateral margin formed into a posteriorly projecting extension that terminates in a pore near midpoint of maxilla
- Pores perforating lateral margin adjacent to terminus of maxilla located at ends of small projections

- Mandibular portion terminates in a moderately-sized, oval-shaped pore adjacent to origin of preopercle

Preopercular Portion (Figure 28A)

- Distal margin formed into several projections that terminate in pores along margin of preopercle
- Proximal margin perforated by numerous moderately-sized pores
- Dorsal-most portion of distal margin formed into several projections that terminate in pores and extend posteriorly beyond preopercle onto opercle
    - Margins of projections perforated by numerous small pores

Sensory Papillae Pattern

- Dense chevron pattern of sensory papillae on basihyal
- Short disjunct rows of papillae on mandibular median
- Crosshatch pattern of papillae on ventral flange of preopercle

Remarks

The cephalic lateralis of *Pterapogon* (*Quina*) *mirifica* is relatively complex with extensive secondary canal development and a dense covering of papillae. A large nasal pore and anterior-interorbital projections characterize the supratemporal canal. The secondary projections of the postorbital canal are highly branched and relatively long, reaching nearly to the ridge of the preopercle. The morphology of the cephalic lateralis of *Pterapogon mirifica* appears very similar to that of *Vincentia chrysura.* A notable difference is the absence of projections of the mandibular medial margin in *P. mirifica*; the pores perforating the medial margin of *V. chrysura* are located at the ends of projections.

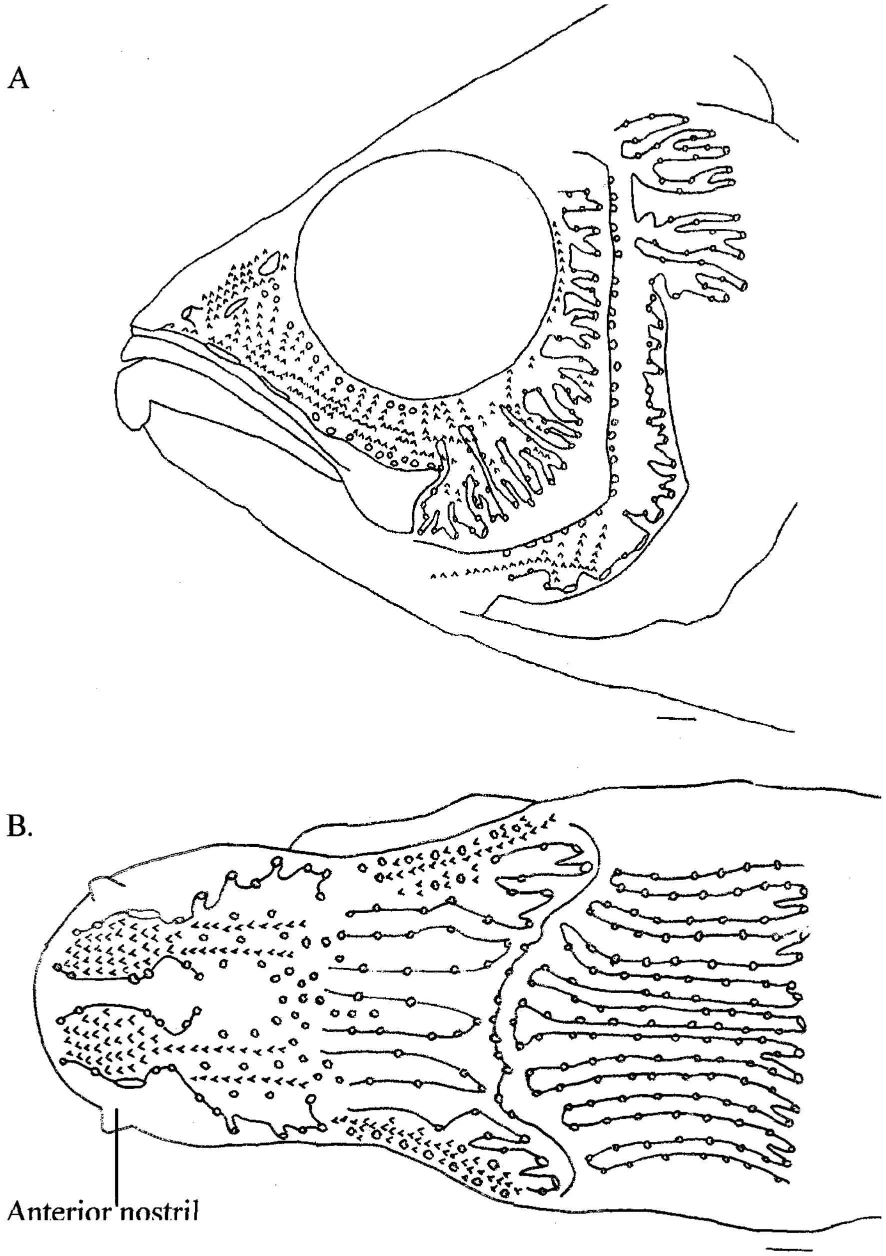


Figure 28. Cephalic lateralis of *Pterapogon* (*Quinca*) *mirifica.* A. Lateral view, B. Dorsal view

C.

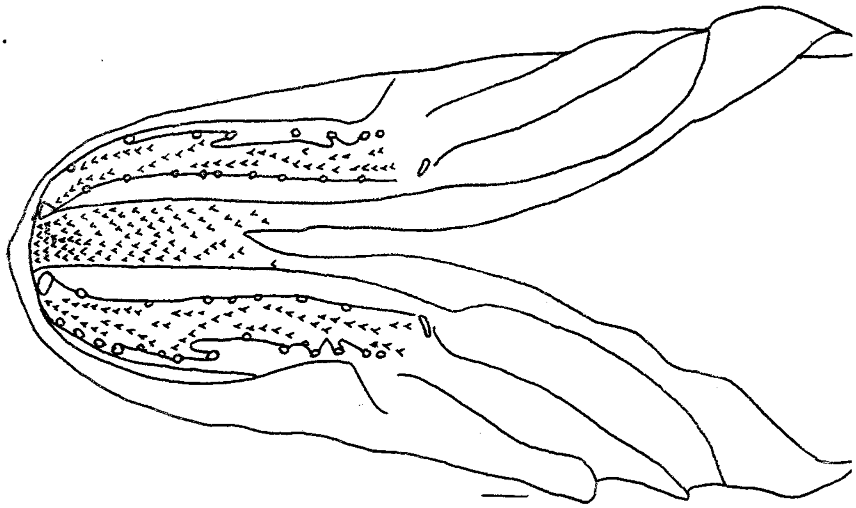


Figure 28 (continued). Cephalic lateralis of *Pterapogon* (*Quinca*) *mirifica.* C. Ventral view

***Rhabdamia* (*Bentuviaichthys*) Smith, 1961**

Material Examined

Type species: *Bentuviaichthys nigrimentum* Smith, 1961, by original designation (also monotypic); BPBM 27389; 4, 53.5—56.1 mm

Supraorbital Canal

<u>Nasal Portion</u>

- Extends almost to tip of snout (Figure 29A)
    - Pore located far forward of anterior nostril
- Terminates anteriorly in a slit-like pore that parallels the premaxilla
- Margins of canal anterior of anterior nostril perforated by a few small pores (Figure 29B)
    - Pore perforating medial margin located at end of a short extension

- Margins between anterior nostril and interorbital space perforated by numerous small pores
  - Pores at ends of short projections
- Lateral margin just anterior of posterior nostril perforated by a pore that is only slightly larger than the other pores along same expanse

Interorbital Portion

- Pores perforating lateral margin in anterior interorbital space located at ends of short projections
- Lateral margin formed into a short projection that terminates in a pore near longitudinal midpoint of orbit
- No large interorbital pore
- Median portion of interorbital space perforated by several small pores

Postorbital Portion

- Proximal margin perforated by numerous small pores
- Canal formed into numerous, highly branched, secondary extensions projecting posteriorly toward supratemporal canal
  - Margins of extensions perforated by numerous pores
  - Median of extensions crossed by transverse rows of papillae
  - Medial-most extension merges with supratemporal canal

Sensory Papillae Pattern

- Crosshatch pattern of papillae extends along canal from anterior nostril through mid-interorbital space
- Longitudinal row of papillae extends posteriorly along dorsoposterior margin of orbit
- Longitudinal row intersected by several transverse rows of papillae that radiate from dorsoposterior rim of orbit
- Rows of papillae radiating from orbit extend across surface of lateral-most postorbital extensions

Supratemporal Canal (Figure 29B)

- Anterior margin of canal formed into numerous secondary, anteriorly projecting extensions
    - Margins of projections perforated by numerous small pores
- Median perforated by a few small pores
- Posterior margin formed into long, posteriorly projecting, open-ended extensions
    - Margins of projections perforated by numerous pores
    - Projections forming finer and finer branches, becoming sequentially smaller posteriorly
        - Individual projections branch on individual scales, with ends of branches reaching toward margins of scales

Infraorbital Canal (Figure 29A)

Lachrymal Portion

- Terminates anteriorly in a relatively large, slit-like pore just ventral of internarial space

- Anterior margin of canal between terminal pore and maxilla formed inot two anteriorly directed projections that terminate in pores
- Distal margin, along ventral edge of lachrymal, perforated by two long, slit-like pores
    - Pores are located at the ends of projections from the primary canal

Suborbital and Postorbital Portions

- Proximal margins of suborbital and postorbital portions perforated by numerous small pores
- Distal margin of suborbital and postorbital portions formed into many, highly-branched, open-ended extensions projecting toward maxilla and posteriorly over cheek to preopercle
    - Margins of canals perforated by numerous small pores

Preoperculomandibular Canal

Mandibular Portion (Figure 29C)

- Terminates anteriorly in a pair of pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a large pair of oval-shaped mental pores
- Lateral and medial margins perforated by numerous small pores
- Lateral margin of canal formed into two short, open-ended, projections roughly one-quarter and one-half of the way along the canal expanse
- Medial margin adjacent to terminus of maxilla formed into several short, open-ended projections
- Terminal pore not present

Preopercular Portion (Figure 29A)

- Proximal margin perforated by several small pores
- Distal margin formed into numerous long, open-ended extensions projecting toward margin of preopercle
    - Margins of extensions perforated by numerous small pores
- Dorsal-most portion of distal margin formed into numerous very long, open-ended projections that extend posteriorly beyond preopercle onto opercle
    - Margins of projections perforated by numerous small pores

Sensory Papillae Pattern

- Sensory papillae forming two longitudinal rows on basihyal
- Disjunct longitudinal rows of papillae on mandibular median

Remarks

The cephalic lateralis of *Rhabdamia* (*Bentuviaichthys*) *nigrimentum* is marked by a high degree of secondary development. The most distinguishing feature of *Bentuviaichthys* is the length and diverticulation of the secondary canal system. The postorbital, infraorbital, supratemporal, and preopercular secondary projections are long and highly branched in comparison to other apogonid genera. The morphology of the supratemporal posterior projections is unique to this taxon in that the lateral-most projections diverticulate and terminate along the margins of sequentially more posterior scales, resulting in the lateral projections becoming more and more medial posteriorly.

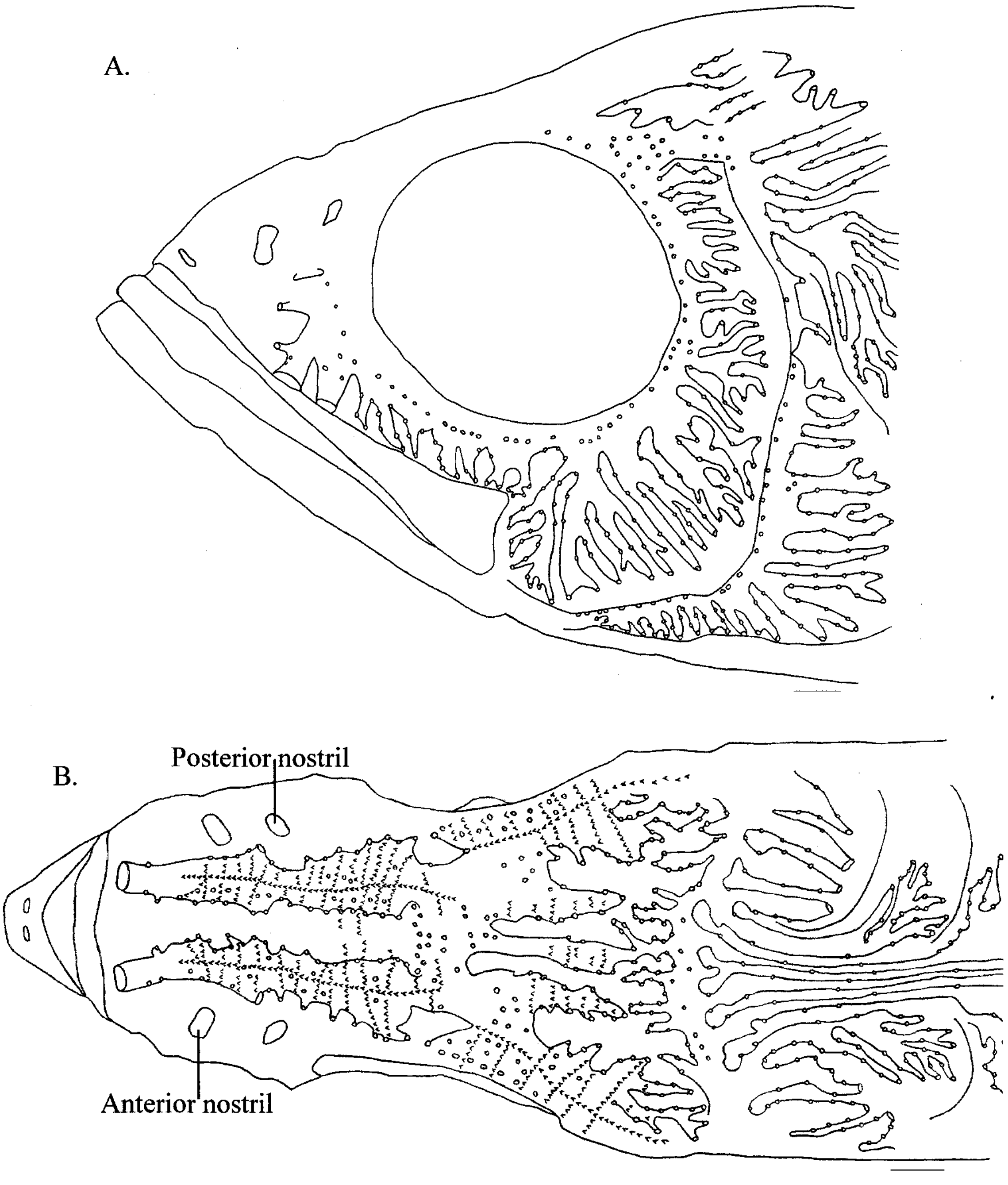


Figure 29. Cephalic lateralis of *Rhabdamia* (*Bentuviaichthys*) *nigrimentum*. A. Lateral view, B. Dorsal view

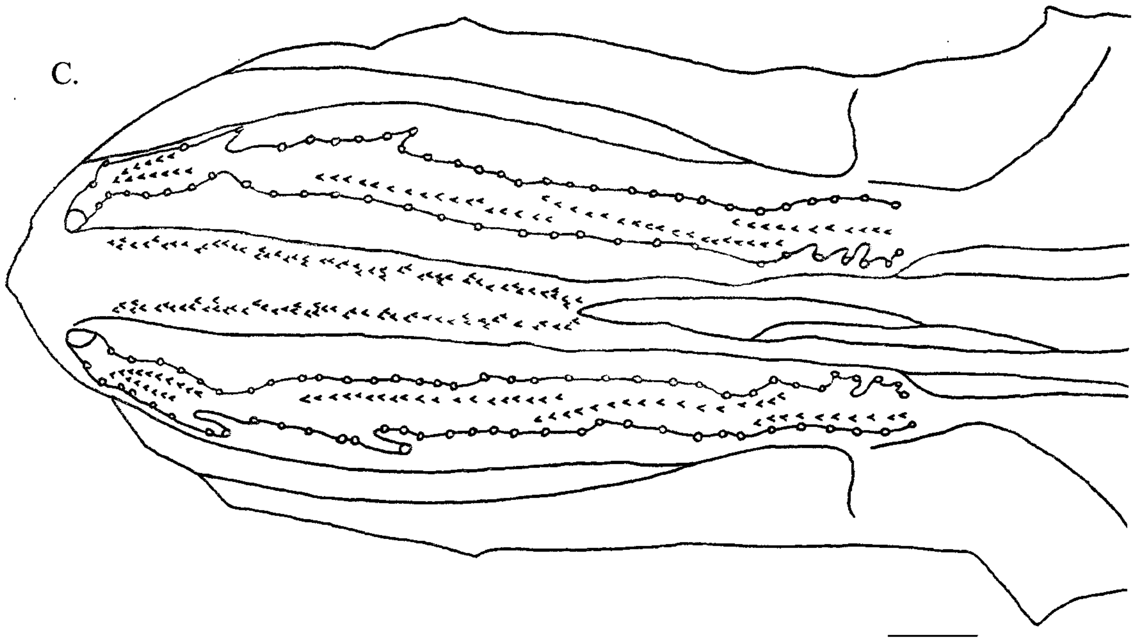


Figure 29 (continued). Cephalic lateralis of *Rhabdamia* (*Bentuviaichthys*) *nigrimentum*. C. Ventral view

Rhabdamia (*Rhabdamia*) Weber, 1909

Material Examined

Type species: *Rhabdamia clupeiformis* Weber, 1909; by subsequent designation of Jordan (1920); no specimens examined

Rhabdamia gracilis (Bleeker, 1856[c]); CAS 17604; 5, 36.3—40.5 mm

Rhabdamia spilota Allen & Kuiter, 1994; BPBM 21516; 2, 51.1—52.3 mm

Supraorbital Canal

Nasal Portion

- Extends almost to tip of snout (Figure 30A)
- Terminates anteriorly in a moderately-sized, oval-shaped pore that parallels the premaxilla

- Lateral margin perforated by a moderately-sized pore just medial to posterior nostril (Figure 30B)

Interorbital Portion

- Proximal margin perforated by small pores in mid-interorbital space
- Lateral margin formed into a short, posteriorly projecting extension that terminates in a pore just posterior of longitudinal midpoint of interorbital space
- Proximal margin perforated by few small pores along dorsoposterior margin of orbit

Postorbital Portion

- Canal formed into several open-ended, posteriorly projecting extensions
    - Margins of extensions perforated by numerous small pores

Sensory Papillae Pattern

- Longitudinal row of papillae extends along median from terminal pore to posterior of orbit

Supratemporal Canal (Figure 30B)

- Anterior margin perforated by a few pores
    - Not formed into extensions
- Canal formed into several open-ended, branched secondary projections extending posteriorly
    - Margins of extensions perforated by numerous pores

Infraorbital Canal (Figure 30A)

Lachrymal Portion

- Terminates in a moderately-sized pore just posterior of anterior nostril
- Distal margin, along ventral edge of lachrymal, perforated by two, short, slit-like pores
    - Pores located at ends of projections

Suborbital Portion

- Proximal margin perforated by few small pores
- Distal margin formed into a few projections that terminate in pores along posterior portion of maxilla

Postorbital Portion

- Distal margin formed into many open-ended projections that extend posteriorly toward preopercle
    - Projections are long, extending almost to preopercular ridge
    - Margins of extensions perforated by a few pores

Preoperculomandibular Canal

Mandibular Portion (Figure 30C)

- Terminates anteriorly in a pair of pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a moderately-large pair of round mental pores
- Medial and lateral margins perforated by several small pores
- Lateral margin of canal formed into two short, open-ended projections roughly one quarter and one half way along expanse of canal

- Medial margin formed into a single projection (on one side of the canal only) near terminus of maxilla
- No terminal pore present

<u>Preopercular Portion</u> (Figure 30A)

- Proximal margin perforated by a few small pores
- Distal margin formed into many open-ended projections extending toward margin of preopercle
    - Margins of projections perforated by few pores
- Dorsal-most portion of distal margin formed into projections that extend posteriorly beyond preopercle onto opercle
    - Margins of projections perforated by few pores

<u>Sensory Papillae Pattern</u>

- Two longitudinal rows of papillae on basihyal

Remarks

Overall the canal system of *Rhabdamia spilota* is more highly branched, particularly the secondary canals, and more densely perforated than is that of *R. gracilis*. The supraorbital canal of *R. gracilis* is characterized by a single projection that terminates in a pore near the longitudinal midpoint of the interorbital space. In contrast, the supraorbital canal of *R. spilota* is characterized by a few projections that terminate in pores anterior and posterior of the posterior nostril, and two projections in the mid-interorbital space.

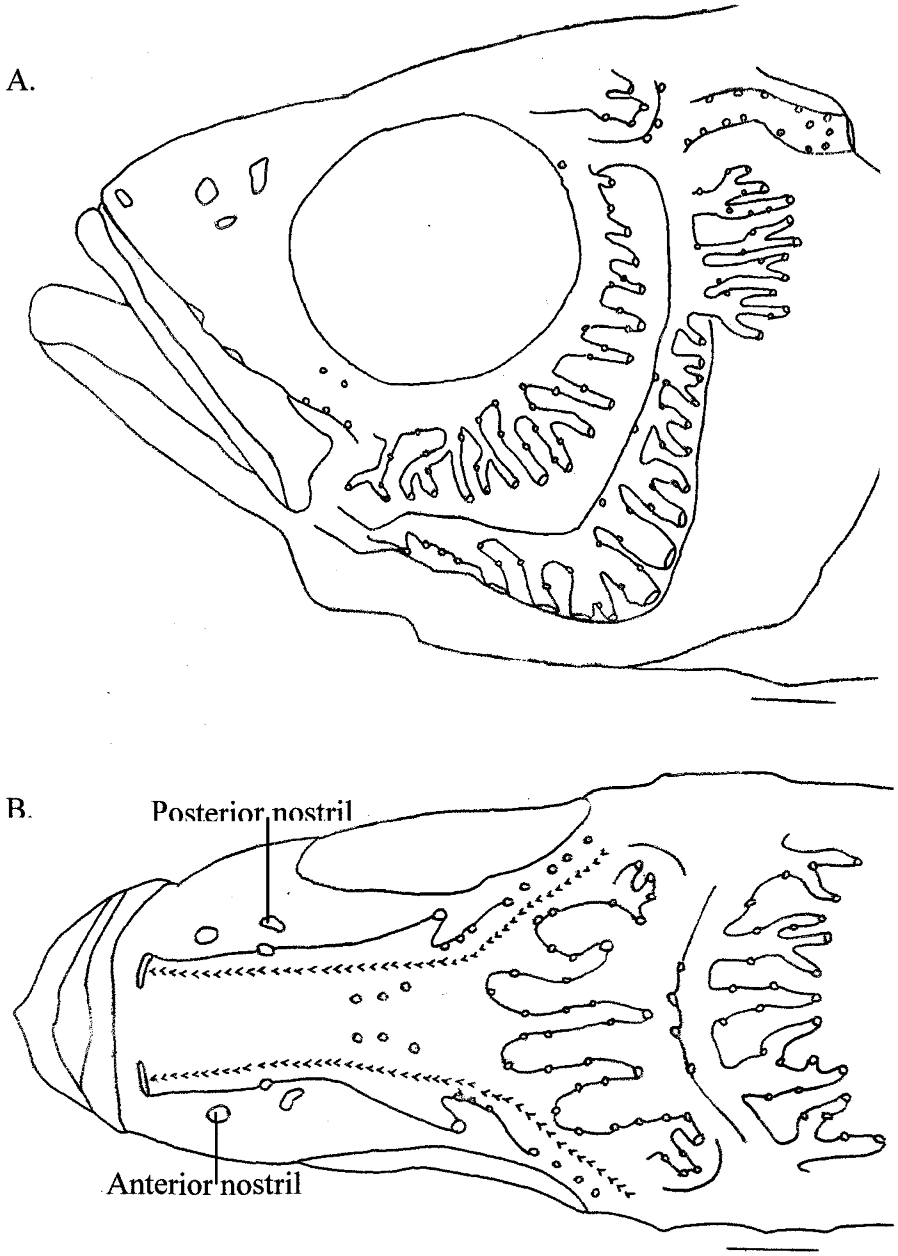


Figure 30. Cephalic lateralis of *Rhabdamia* (*Rhabdamia*) *gracilis*. A. Lateral view, B. Dorsal view

C.

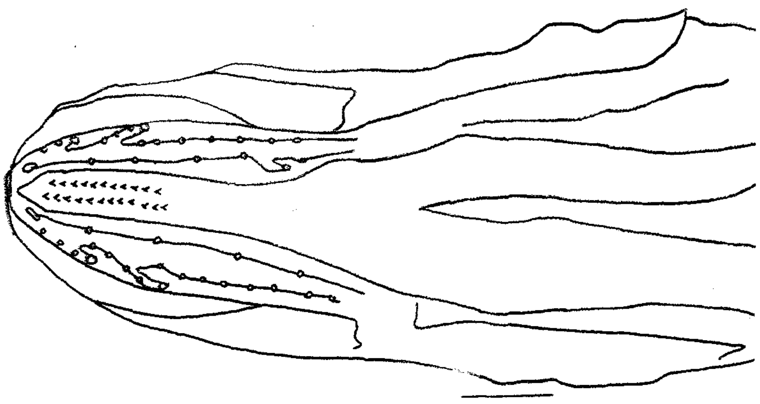


Figure 30 (continued). Cephalic lateralis of *Rhabdamia* (*Rhabdamia*) *gracilis*. C. Ventral view

***Rhabdamia* (*Verulux*) Fraser, 1972**

Material Examined

Type species: *Rhabdamia cypselurus* Weber, 1909, by original designation (also monotypic); USNM 357381; 5, 33.3—37.7 mm

Supraorbital Canal

<u>Nasal Portion</u>

- Extends almost to tip of snout (Figure 31A)
- Terminates anteriorly in a moderately-sized, oval-shaped pore that parallels the premaxilla
- Lateral margin just anterior of and medial to posterior nostril perforated by a moderately-sized pore (Figure 31B)

Interorbital Portion

- Canal perforated by small pores from anterior nostril to area of secondary postorbital canal development
    - Pores concentrated toward margins, with fewer perforating median portion
- Pores perforating lateral margin in anterior interorbital space located at ends of short projections
- Lateral margin formed into a short, posteriorly projecting extension that terminates in a pore near longitudinal midpoint of orbit
- No large interorbital pore

Postorbital Portion

- Canal formed into numerous open-ended, posteriorly projecting extensions
    - Margins of extensions perforated by numerous small pores

Sensory Papillae Pattern

- Longitudinal row of papillae extends along median of canal from anterior nostril to supratemporal canal
- Numerous short transverse rows crossing median of canal from anterior nostril to supratemporal canal
- Transverse rows of papillae radiating from dorsoposterior rim of orbit
- Transverse rows of papillae present on medians of postorbital projections

Supratemporal Canal (Figure 31B)

- Anterior margin formed into a number of short, open-ended, anteriorly projecting extensions
- Canal formed into numerous secondary extensions projecting posteriorly

    - Margins of extensions perforated by numerous pores

Sensory Papillae Pattern

- Two short longitudinal rows of papillae along median of body

Infraorbital Canal (Figure 31A)

Lachrymal Portion

- Canal splits anteriorly to form a U-shape – both termini terminating anteriorly in small, round pores
- Distal margin, along ventral edge of lachrymal, perforated by two, short, slit-like pores

Suborbital Portion

- Proximal margin perforated by several small pores
- Distal margin formed into numerous open-ended extensions that terminate along maxilla

Postorbital Portion

- Proximal margin perforated by few small pores
- Distal margin formed into many open-ended projections that extend posteriorly toward preopercle
    - Margins of projections perforated by very few pores

Sensory Papillae Pattern

- Sensory papillae present in internarial space
    - Row extends posteriorly beyond posterior nostril to orbit

Preoperculomandibular Canal

Mandibular Portion (Figure 31C)

- Terminates anteriorly in a pair of moderately-large, oval-shaped pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a moderately-large pair of round mental pores
- Medial and lateral margins perforated by several small pores
- Lateral margin of canal formed into two short, open-ended projections one quarter and one half way along expanse of canal
- Pores perforating medial margin not at end of projections
- No terminal pore present

Preopercular Portion (Figure 31A)

- Proximal margin perforated by several small pores
- Distal margin highly branched, formed into many open-ended projections that extend to margin of preopercle
    - Projections are short relative to width of primary canal
- Dorsal-most portion of distal margin highly branched, formed into many open-ended projections that extend posteriorly beyond margin of preopercle onto opercle

Sensory Papillae Pattern

- Basihyal with longitudinal rows of papillae on anterior portion, formed into a chevron pattern posteriorly
- Short semi-longitudinal rows of papillae on mandibular median

Remarks

The canal system of *Rhabdamia cypselura* is similar to that of other *Rhabdamia* species in that it is highly branched. The canals are relatively wide with distal margins formed into many narrow, short projections that terminate in pores. *Rhabdamia cypselura* is unique in that there is no single terminal infraorbital pore. The canal splits anteriorly forming a U-shape, both branches of which terminate in moderately-sized pores. An alternative interpretation of this configuration is that a terminal pore is located just posterior of the internarial space, and the anterior canal margin, just ventral of this pore, is formed into a anteriorly directed projection that terminates in a pore. This projection curves dorsally to form a U-shape in relation to the terminal pore and its associated canal.

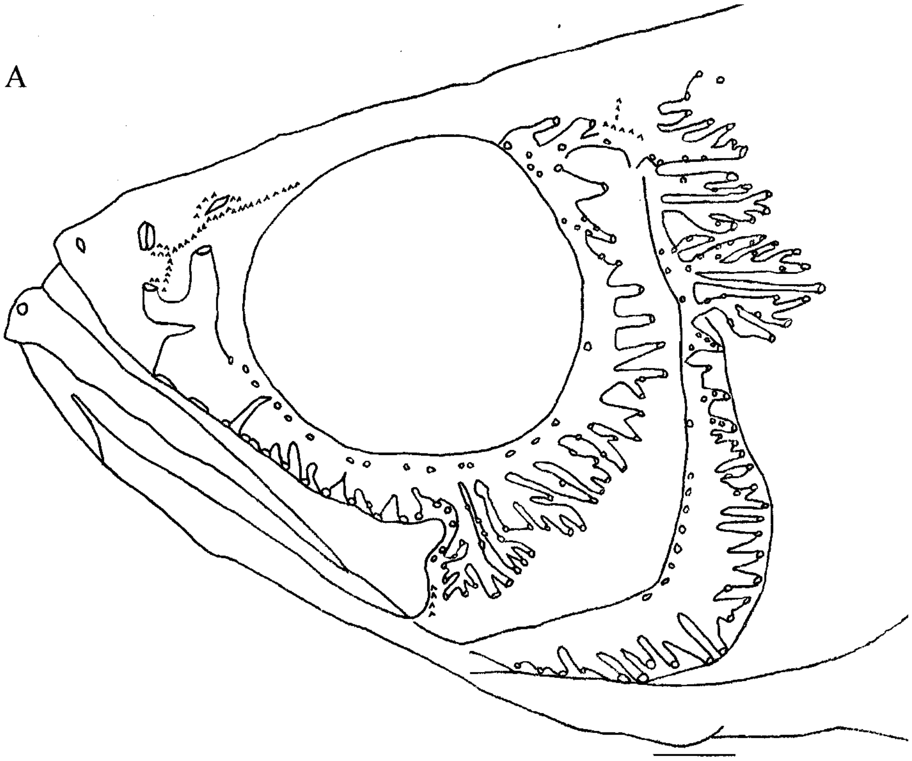


Figure 31. Cephalic lateralis of *Rhabdamia* (*Verulux*) *cypselura*. A. Lateral view

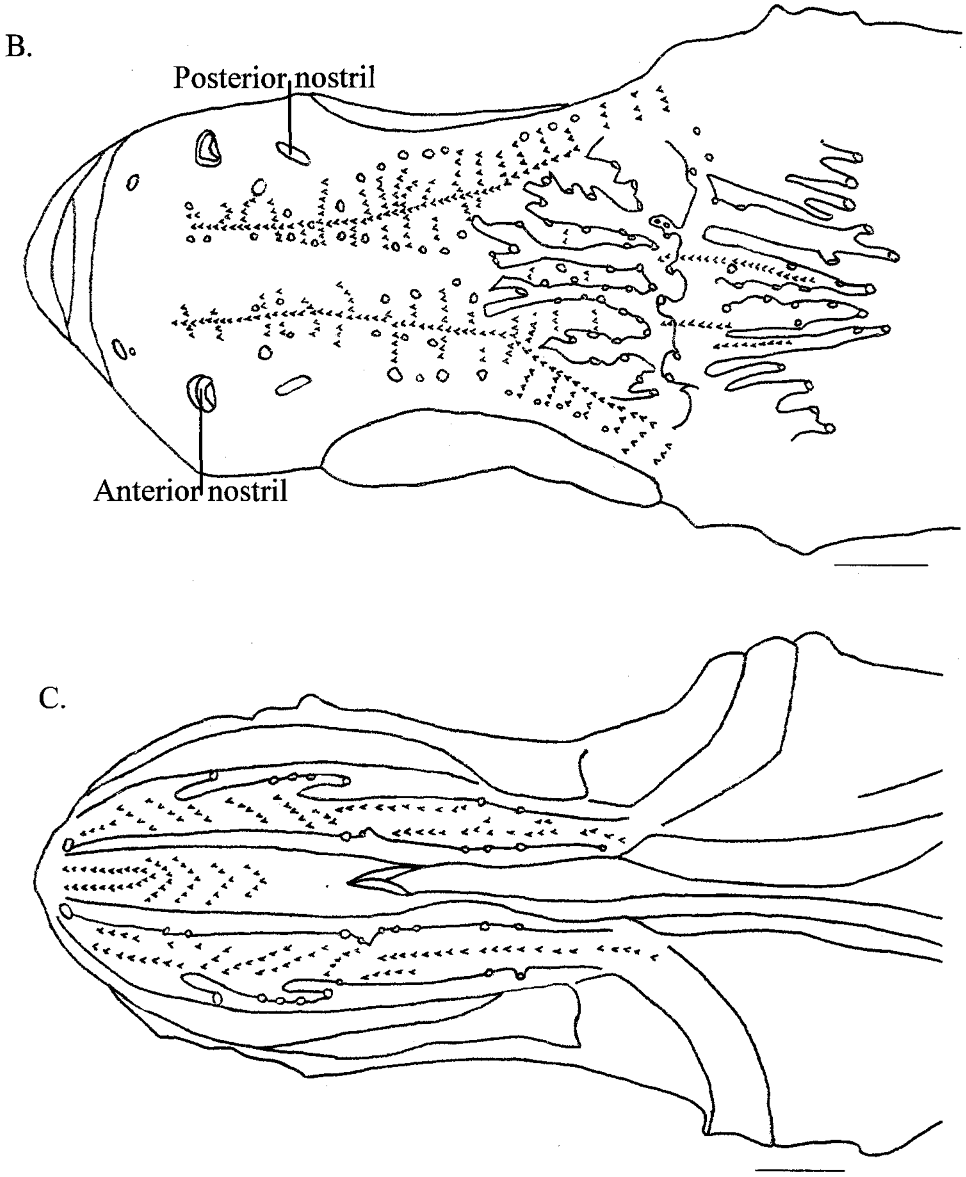


Figure 31 (continued). Cephalic lateralis of *Rhabdamia* (*Verulux*) *cypselura*. B. Dorsal view, C. Ventral view

Siphamia Weber, 1909

Material Examined

Type species: *Siphamia tubifer* Weber, 1909; by monotypy; USNM 341601; 3, 21.3—24.9 mm

Siphamia sp. G02-2-55; 1, 20.6 mm

Siphamia sp. G02-56; 3, 22.7—39.5 mm

Supraorbital Canal

Nasal Portion

- Does not extend to tip of snout (Figure 32A)
- Terminates anteriorly in a moderately-sized, oval-shaped pore located just anterior of and medial to anterior nostril
- Lateral margin perforated by a moderately-sized round pore just medial to posterior nostril (Figure 32B)

Interorbital Portion

- Lateral margin perforated by a large oval-shaped pore in anterior interorbital space

Postorbital Portion

- Canal formed into a few open-ended, posteriorly projecting secondary extensions
    - Margins of projections perforated by few small pores

Sensory Papillae Pattern

- Longitudinal row of sensory papillae extends from just medial of terminal pore to posterior interorbital space
    - Row forks anteriorly between terminal pore and anterior nostril

- Few short, transverse rows of papillae intersect longitudinal row between posterior nostril and large interorbital pore
- Row of papillae along dorsoposterior margin of orbit

Supratemporal Canal (Figure 32B)

- Anterior margin formed into a few relatively long, open-ended, anteriorly projecting extensions
    - Margins of extensions perforated by a few pores
- Posterior margin formed into numerous open-ended, posteriorly projecting extensions
    - Margins of extensions not perforated
- Projections formed from anterior margin as long as those formed from posterior margin

Infraorbital Canal (Figure 32A)

<u>Lachrymal Portion</u>

- Terminates anteriorly in a moderately-sized round pore located just posterior of anterior nostril
- Distal margin perforated by two small pores along ventral edge of lachrymal
- Proximal margin, superior to first lachrymal pore, perforated by a small pore

<u>Suborbital Portion</u>

- Distal margin formed into a number of open-ended projections that extend toward margin of maxilla
    - Margins of projections not perforated

Postorbital Portion

- Distal margin formed into a number of open-ended projections that extend posteriorly onto cheek
    - Margins of projections not perforated

Sensory Papillae Pattern

- Internarial space and area anterior of terminal pore with few rows of sensory papillae
- Longitudinal row of sensory papillae extends along canal median beginning at terminal pore

Preoperculomandibular Canal

Mandibular Portion (Figure 32C)

- Terminates anteriorly in a pair of pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a moderately-sized pair of subtriangular mental pores
- Lateral margin perforated by large pores one-quarter, two-quarters and three-quarters along the length of the canal
- Medial margin adjacent to terminus of maxilla perforated by two pores
    - Pores located at ends of short projections
- Terminates in a relatively large subtriangular pore adjacent to origin of preopercle

Preopercular Portion (Figure 32A)

- Proximal margin perforated by few small pores
- Distal margin formed into a number of open-ended projections that extend toward margin of preopercle

- Dorsal-most portion of distal margin formed into a number of open-ended projections that extend posteriorly beyond margin of preopercle onto opercle

Sensory Papillae Pattern

- Short, disjunct, longitudinal rows of papillae on median of mandibular canal
- Sensory papillae formed into a chevron pattern on anterior portion of basihyal

Remarks

In species of *Siphamia*, the infraorbital canal does not extend as far anteriorly as it does in other apogonid species, resulting in the terminal pore being far posterior of the anterior nostril. The configuration of the lachrymal pores in *Siphamia* is unique among apogonid species. In *Siphamia*, the first lachrymal pore is large and round, as opposed to slit-like, and is located just anterior of the anterior margin of the orbit. The second lachrymal pore, also round, is far back from the first pore, being located one quarter of the distance along the orbit. The development of the supratemporal canal is also distinct in *Siphamia* species. The projections formed from the anterior margin are as long as those formed from the posterior margin. In other apogonid species that exhibit development of the anterior margin, the anterior projections are short and undeveloped in comparison with the projections formed from the posterior margin.

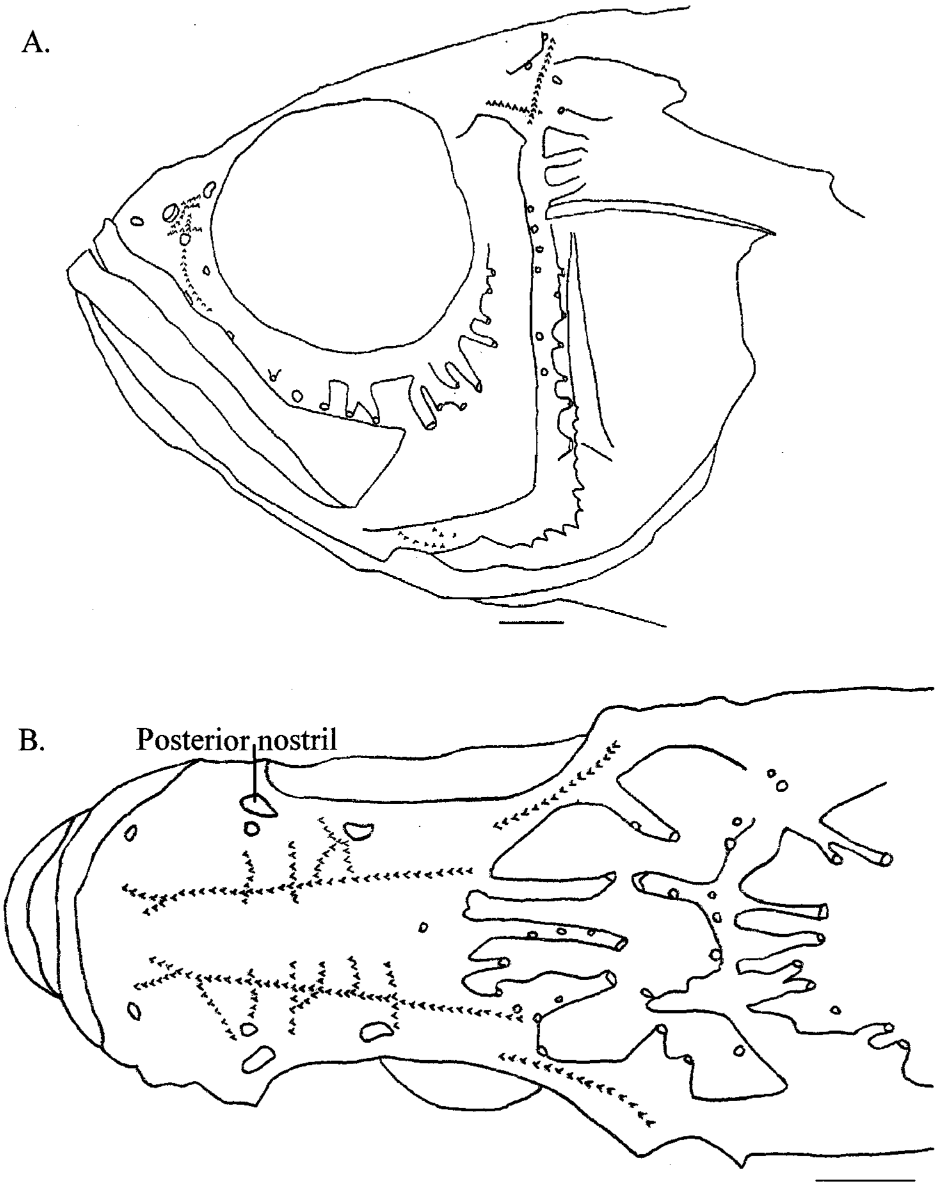


Figure 32. Cephalic lateralis of *Siphamia tubifer*. A. Lateral view, B. Dorsal view

C.

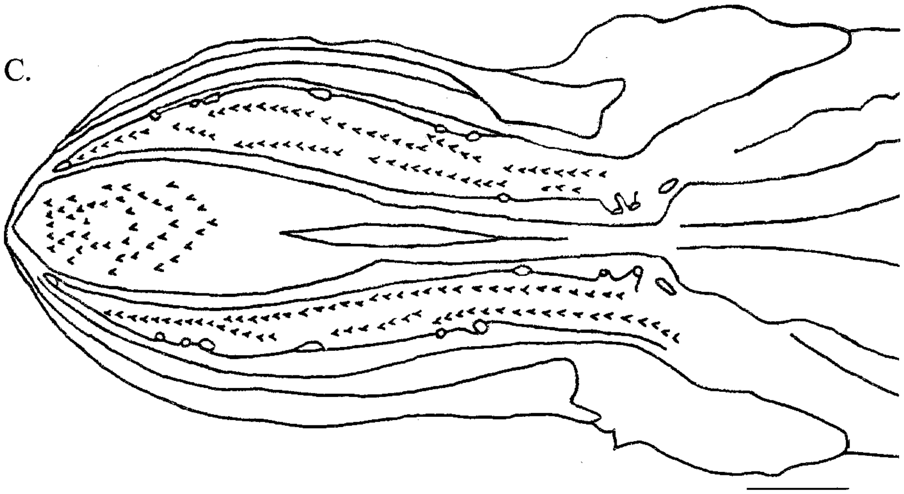


Figure 32 (continued). Cephalic lateralis of *Siphamia tubifer*. C. Ventral view

Sphaeramia **Fowler & Bean, 1930**

Material Examined

Type species: *Apogon nematopterus* Bleeker, 1856[a], by original designation; BPBM 9668; 3, 28.2—44.8 mm

Sphaeramia orbicularis (Cuvier in Cuvier & Valenciennes, 1828); BPBM 24631; 1, 61.8 mm

Supraorbital Canal

<u>Nasal Portion</u>

- Extends almost to tip of snout (Figure 33A)
- Terminates anteriorly in a slit-like pore that parallels the premaxilla
- Lateral margin perforated by a large pore just anterior of and medial to posterior nostril (Figure 33B)
- Median and medial margin of canal perforated by numerous small pores

Interorbital Portion

- Lateral margin perforated by moderately-sized pore in anterior interorbital space
- Median of interorbital space perforated by several small pores

Postorbital Portion

- Posterior interorbital portion of canal formed into several open-ended, posteriorly projecting secondary extensions
    - Margins of extensions perforated by numerous small pores

Sensory Papillae Pattern

- Minute sensory papillae anterior of terminal pore
- Numerous transverse rows of papillae crossing canal from terminal pore to large interorbital pore
- Two rows of papillae cross dorsal surface of head in mid-interorbital space
- Longitudinal row of papillae extends from interorbital pore along dorsoposterior margin of orbit to supratemporal canal
- Transverse rows of papillae radiate from dorsal margin of orbit

Supratemporal Canal (Figure 33B)

- Anterior margin perforated by numerous small pores
- Posterior margin formed into several open-ended, posteriorly projecting extensions

Sensory Papillae Pattern

- Few short longitudinal rows of sensory papillae intersect canal near mid-line of body

Infraorbital Canal (Figure 33A)

Lachrymal Portion

- Terminates anteriorly in a large pore just posterior of midpoint of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two, long, slit-like pores
- Median superior of first lachrymal pore perforated by numerous small pores

Suborbital Portion

- Posterior half of distal and proximal margins perforated by several moderately-sized pores
    - Canal not formed into projections

Postorbital Portion

- Proximal and distal margins perforated by numerous small pores
- Canal relatively narrow
- Distal margin of ventroposterior portion formed into several open-ended projections that extend onto check
    - Margins of projections perforated by numerous small pores

Sensory Papillae Pattern

- Rows of sensory papillae in internarial space
    - Few rows extend beyond posterior nostril to orbit
- Two longitudinal rows of papillae, forming a band, extend along suborbital median from first lachrymal pore to terminus of maxilla
- Short transverse row of sensory papillae extends posteriorly from ventroposterior margin of orbit

Preoperculomandibular Canal

Mandibular Portion (Figure 33C)

- Terminates anteriorly in a pair of moderately-sized, oval-shaped pores that perforate the dentary (Figure 33B)
- Canal just posterior of apex of dentary perforated by a relatively large pair of subtriangular mental pores
- Lateral margin perforated quarterly by three, large pores
- Medial margin adjacent to terminus of maxilla perforated by moderately-sized round pore
- Lateral margin posterior of terminus of maxilla formed into two short projections that terminate in pores
- Terminates in a large oval-shaped pore adjacent to origin of preopercle

Preopercular Portion (Figure 33A)

- Proximal margin perforated by numerous small pores
- Distal margin formed into numerous short, open-ended projections that extend toward margin of preopercle
- Dorsal-most portion of distal margin formed into a few projections that terminate in pores and extend posteriorly beyond preopercle onto opercle
    - Margins of projections not perforated

Sensory Papillae Pattern

- Sensory papillae formed into a chevron pattern on basihyal
- Two longitudinal rows of papillae on mandibular median extend from mental pores to terminal pore

Remarks

The canal structures of *Sphaeramia nematoptera* and *Sphaeramia orbicularis* are generally similar. The only significant difference is that the canals of *S. orbicularis* are more densely covered by sensory papillae. Both species have a longitudinal band of papillae along the suborbital canal median, but *S. orbicularis* also has numerous transverse rows of papillae radiating from the ventral margin of the orbit. *Sphaeramia orbicularis* also has two widely spaced rows of sensory papillae on the vertical flange of the preopercle, whereas the preopercle of *S. nematoptera* lacks papillae. The canal structure of *Sphaeramia* is very similar to that of *Pterapogon* (*Pterapogon*) *kauderni.* Both taxa are characterized by the development of the ventroposterior portion of the postorbital distal margin into projections that terminate in pores. Some characteristics of *S. nematoptera* that distinguish it from *P. kauderni* include the presence of papillae in the internarial space, the branching pattern characteristic of the posterior supratemporal margin, the distinct crosshatch pattern of papillae along the posteriodorsal margin of the orbit, and the two rows of papillae on the vertical preopercular flange. Other than these relatively minor differences, the cephalic lateralis systems of the two species are identical.

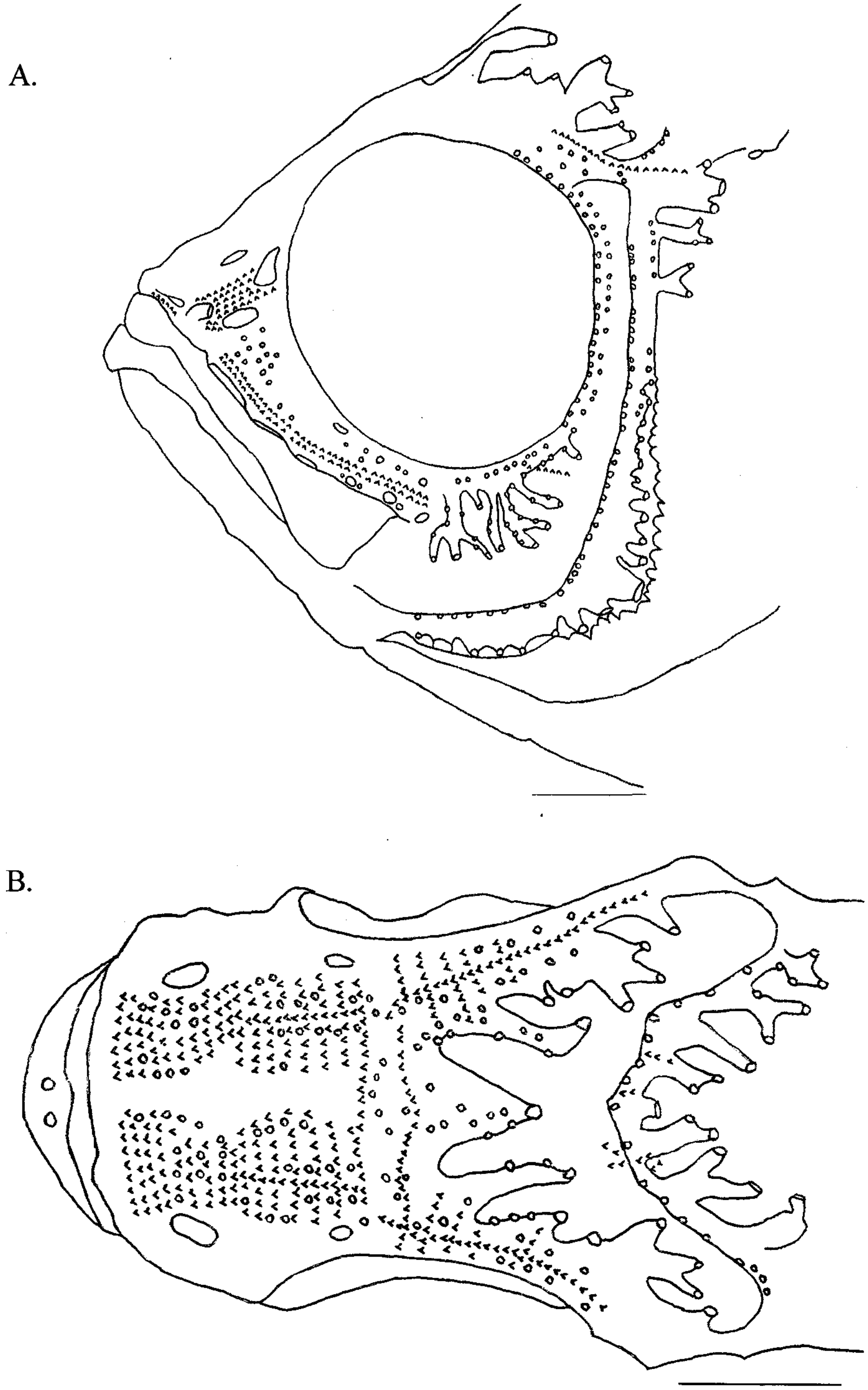


Figure 33. Cephalic lateralis of *Sphaeramia nematoptera*. A. Lateral view, B. Dorsal view

C.

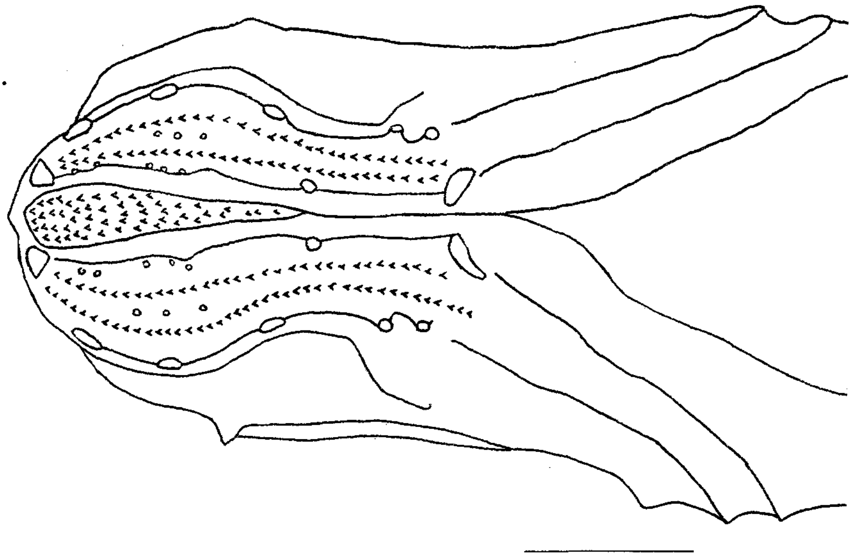


Figure 33 (continued). Cephalic lateralis of *Sphaeramia nematoptera*. C. Ventral view

***Vincentia* Castelnau, 1872**

Material Examined

Type species: *Vincentia waterhousii* Castelnau, 1872 [= *Vincentia chrysura* (Ogilby, 1889) according to Paxton et al. (1989)], by monotypy; USNM 21337; 6, 43.4—50.0 mm

Supraorbital Canal

<u>Nasal Portion</u>

- Extends to tip of snout (Figure 34A)
- Terminates anteriorly in a long, slit-like pore that parallels the premaxilla
- Lateral margin perforated by a large slit-like pore just medial to internarial space (Figure 34B)
- Medial margin perforated by numerous small pores from terminal pore through anterior interorbital space

- Lateral margin of canal between posterior nostril and orbit formed into several projections that extend toward orbit and terminate in pores

Interorbital Portion

- Lateral margin perforated by relatively large slit-like pore just anterior of longitudinal midpoint of orbit
- Pores in median of interorbital area do not perforate all the way into canal space

Postorbital Portion

- Proximal margin along dorsoposterior half of orbit perforated by numerous moderately-sized pores
- Posterior portion of canal formed into numerous open-ended, posteriorly projecting secondary extensions
    - Margins of extensions perforated by many small pores
    - Median-most projection confluent with supratemporal canal

Sensory Papillae Pattern

- Canal median densely covered by sensory papillae from terminal pore to anterior interorbital space

Supratemporal Canal (Figure 34B)

- Anterior margin and median perforated by numerous small pores
- Anterior margin formed into a few anteriorly projecting extensions
    - Margins of extensions perforated by numerous small pores
- Posterior margin formed into numerous relatively long, open-ended posteriorly projecting extensions
    - Margins of extensions perforated by numerous small pores

Infraorbital Canal (Figure 34A)

Lachrymal Portion

- Terminates anteriorly in a relatively large slit-like pore just posterior of internarial space
- Distal margin, along ventral edge of lachrymal, perforated by two long, slit-like pores
- Median superior of lachrymal pores perforated by several small and moderately-sized pores

Suborbital Portion

- Proximal margin perforated by numerous small and moderately-sized pores
- Distal margin and median of posterior half perforated by rows of small pores

Postorbital Portion

- Proximal margin perforated by numerous small pores
- Distal margin formed into numerous open-ended projections that extend posteriorly onto cheek
    - Margin of projections perforated by numerous small pores

Sensory Papillae Pattern

- Internarial space with rows of sensory papillae
- Row of sensory papillae along anterior rim of orbit
- Suborbital median with a longitudinal band of papillae and few short transverse rows
    - Not formed into a crosshatch pattern

Preoperculomandibular Canal

Mandibular Portion (Figure 34C)

- Terminates anteriorly in a pair of moderately-sized pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a large pair of subtriangular mental pores
- Lateral margin formed into two short, posteriorly projecting extensions, that terminate in pores one near first quarter and one near midpoint of canal
- Margins of posterior half formed into numerous projections that terminate in pores
- Mandibular portion terminates in a moderately-sized, oval-shaped pore adjacent to origin of preopercle

Preopercular Portion (Figure 34A)

- Proximal margin and median perforated by numerous moderately-sized pores
- Distal margin of ventral flange formed into a few projections that terminate in large pores along margin of preopercle
- Distal margin of vertical flange perforated by numerous moderately-sized pores

Sensory Papillae Pattern

- Chevron pattern of relatively-large sensory papillae on basihyal
- Longitudinal rows of papillae extend along median of mandibular canal
- Semi-transverse rows of papillae diagonally cross ventral flange of preopercle
- Column of sensory papillae extends along median of vertical flange of preopercle

Remarks

The cephalic lateralis of *Vincentia chrysura* is relatively complex with extensive secondary canal development and a dense covering of papillae. A large nasal pore and anterior-interorbital projections characterize the supratemporal canal. The secondary postorbital projections of *V. chrysura* extend posteriorly to fuse with the anterior projections of the supratemporal canal. The morphology of the cephalic lateralis of *V. chrysura* appears very similar to that of *Pterapogon* (*Quinca*) *mirifica.* Notable differences include the absence of projections of the mandibular medial margin and less extensive branching of the postorbital secondary extensions in *P. mirifica.*

A.

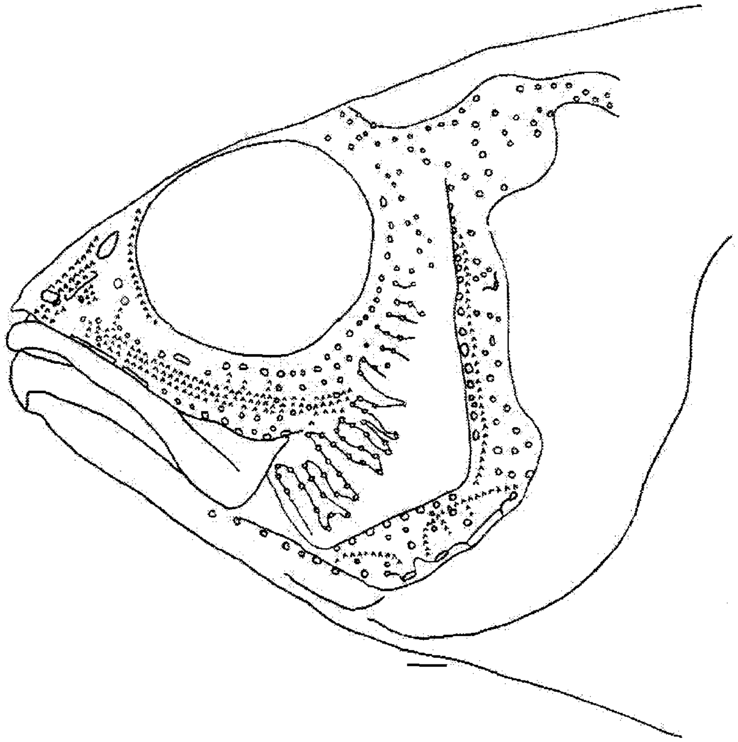


Figure 34. Cephalic lateralis of *Vincentia chrysura.* A. Lateral view

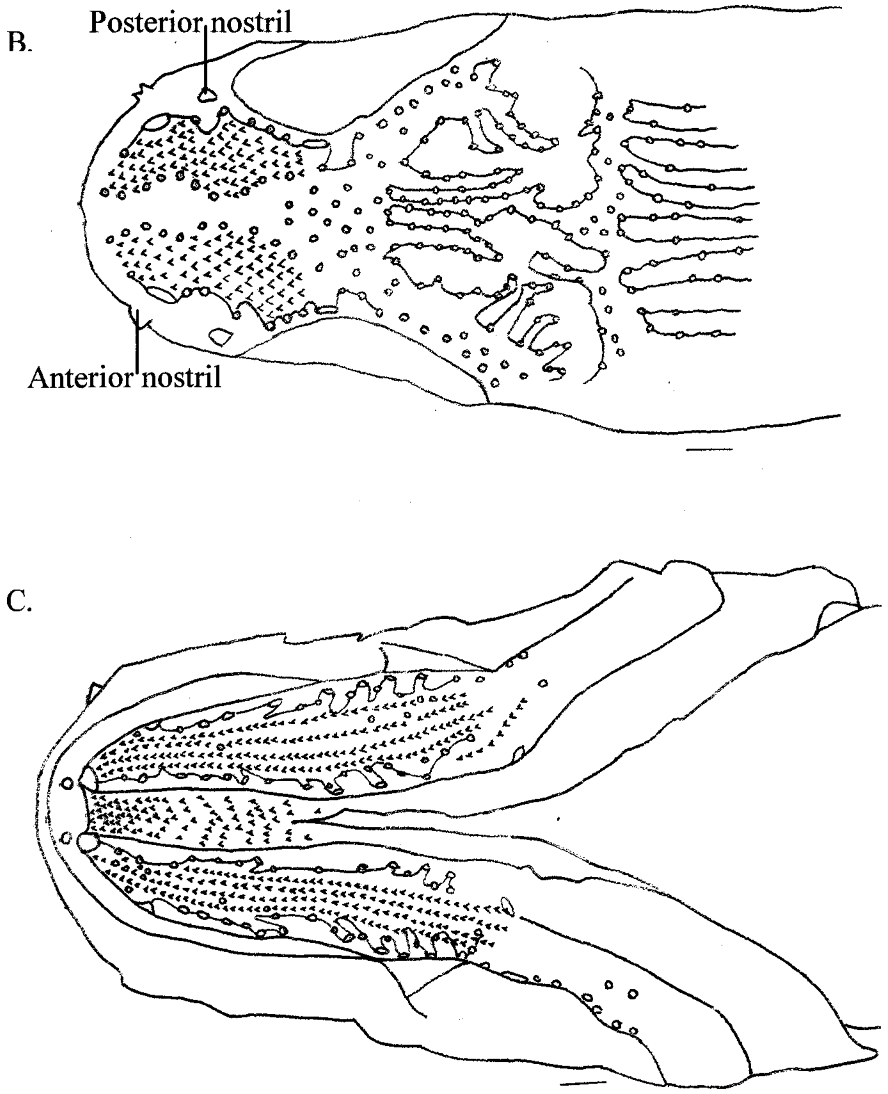


Figure 34 (continued). Cephalic lateralis of *Vincentia chrysura*. B. Dorsal view, C. Ventral view

Subfamily Pseudaminae

Gymnapogon Regan, 1905

Material Examined

Type species: *Gymnapogon japonicus* Regan, 1905, by monotypy; USNM 108821 paratype; 1, 30.5 mm

Gymnapogon urospilotus Lachner, 1953; BPBM 37514; 3, 27.2—32.8 mm

Gymnapogon sp.; BPBM 33343; 3, 25.6—28.3 mm

Supraorbital Canal

Nasal Portion

- Extends almost to tip of snout (Figure 35A)
- Terminates anteriorly in a moderately-sized, round pore
    - Located medial to anterior nostril
- Lateral margin anterior of and superior to posterior nostril perforated by a moderately-sized pore (Figure 35A, B)
- Lateral margin posterior of posterior nostril perforated by a moderately-sized pore

Interorbital Portion

- Median near the medial margin in the posterior interorbital space perforated by three, relatively large pores (Figure 35B)

Postorbital Portion

- Canal median perforated by two moderately-sized round pores posterior of orbit
- No secondary canal development

Sensory Papillae Pattern

- Longitudinal row of papillae extends from terminal pore to anterior interorbital space
- Four transverse rows of papillae span dorsal surface of head from terminal pore to anterior interorbital space
- Longitudinal row of papillae, medial to nasal longitudinal row, extends from mid-interorbital space to supratemporal canal
- Eight, nearly equidistant, transverse rows of sensory papillae span the dorsal portion of the head from anterior of the posterior nostril to supratemporal canal
- Several transverse rows of papillae radiate dorsally from orbit
    - Do not completely cross dorsal surface of head
- Several transverse rows of papillae extend ventrally from medial longitudinal row to intersect a second longitudinal row just dorsal and posterior of posterior margin of orbit

Supratemporal Canal (Figure 35B)

- Posterior margin of canal perforated by a few moderately-sized pores
- Posterior margin not developed into projections

Sensory Papillae Pattern

- Canal intersected by a few short, transverse rows of sensory papillae

Infraorbital Canal (Figure 35A)

Lachrymal Portion

- Terminates anteriorly in a moderately-sized pore posterior of internarial space
- Distal margin below terminal pore perforated by one slit-like pore

Suborbital Portion

- Proximal margin not perforated
- Distal margin perforated by three moderately-sized pores
    - Pores located at ends of projections

Postorbital Portion

- Proximal margin not perforated
- Distal margin perforated by a few moderately-sized pores

Sensory Papillae Pattern

- Few sensory papillae in internarial space
- Few transverse rows of papillae radiate from ventral margin of orbit
- Cheek covered by a crosshatch pattern of sensory papillae
    - Crosshatch pattern is wide-spaced, formed from only a few transverse and longitudinal rows of papillae
    - Crosshatch pattern extends posteriorly onto opercle

Preoperculomandibular Canal

Mandibular Portion (Figure 35C)

- Terminates anteriorly in a pair of relatively large pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a moderately-sized pair of mental pores
- Lateral margin perforated by six moderately-sized pores
    - Pores occur in three equidistant pairs of two
    - First pair located one-quarter of the way along the canal length
- Medial margin perforated by four pores

    - Two opposite first pair of lateral pores
    - One, each, opposite the second and third pairs of lateral pores
- Terminates in a moderately-sized pore adjacent to origin of preopercle

<u>Preopercular Portion</u> (Figure 35A)

- Proximal margin not perforated
- Distal margin formed into a few short projections terminating in relatively large pores along posterior edge of preopercle
    - Few short projections extending onto preopercular flap

<u>Sensory Papillae Pattern</u>

- Sensory papillae absent from basihyal
- One longitudinal row of sensory papillae extends along mandibular median
- Several irregularly spaced transverse rows of papillae intersect longitudinal row along mandibular median
- Preopercular flap with crosshatch pattern of papillae

Remarks

The canal structure of *Gymnapogon* is simple, being relatively narrow, sparsely perforated and with minimal secondary development. The presence of sensory papillae on the basihyal is a variable characteristic: present in *Gymnapogon urospilotus* and absent in *G. japonicus* and the unidentified species of *Gymnapogon* that was examined. The cephalic lateralis system of *Gymnapogon* is very similar to that of *Pseudamiops*. A notable exception being that the preopercular and mandibular canal portions are confluent in *Gymnapogon* species.

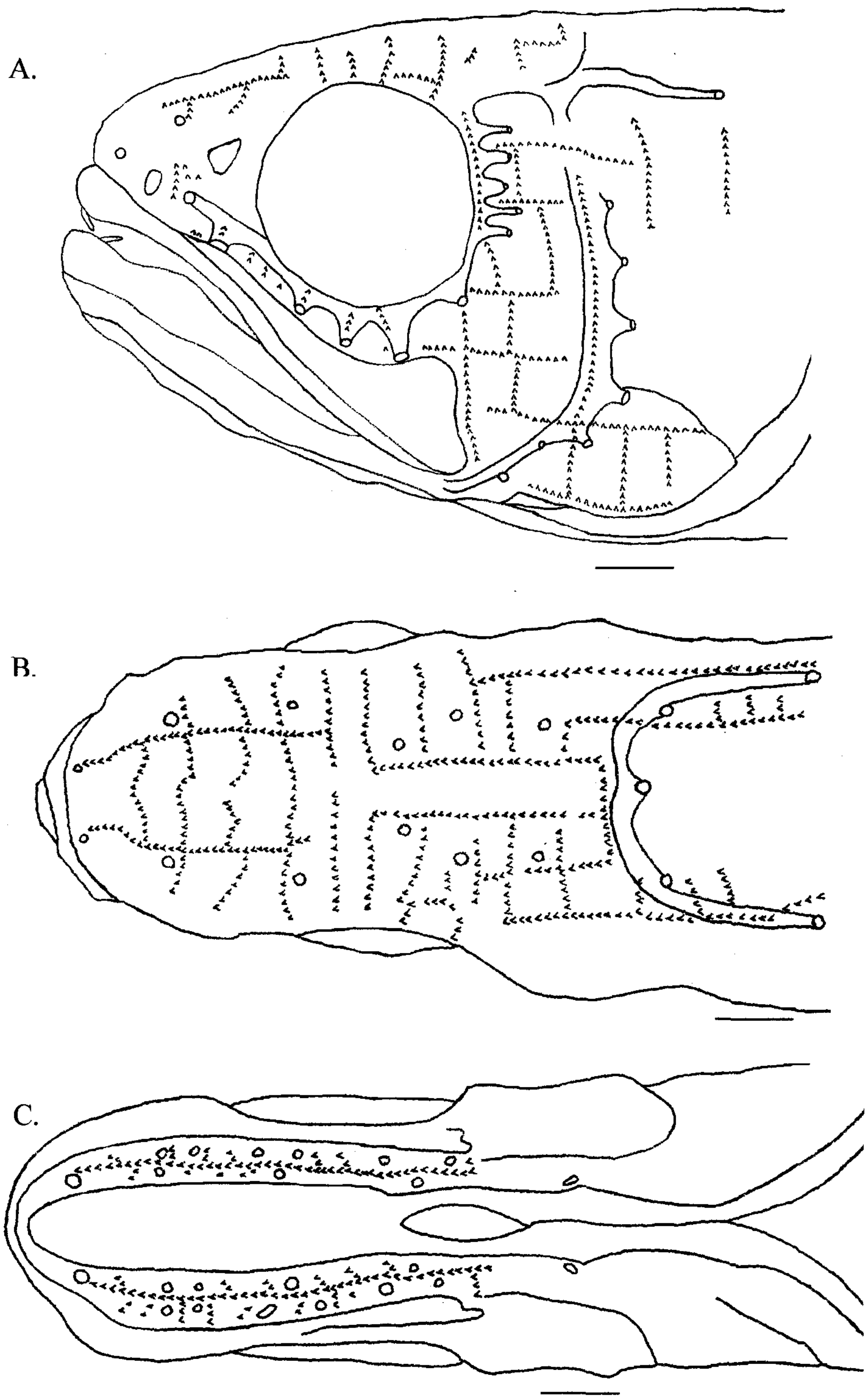


Figure 35. Cephalic lateralis of *Gymnapogon japonicus.* A. Lateral view, B. Dorsal view, C. Ventral view

Paxton Baldwin & Johnson, 1999

Material Examined

Type species: *Paxton concilians* Baldwin & Johnson, 1999, by original designation (also monotypic); WAM P.27219.035 paratype; 1, 66.5 mm

Supraorbital Canal

Nasal Portion

- Snout covered by minute papillae
- Extends to tip of snout (Figure 36A)
- Terminates anteriorly in a small round pore located medial of anterior nostril
- Lateral margin medial of posterior nostril perforated by a small pore (Figure 36A, B)
- Longitudinal row of sensory papillae extends along canal median from terminal pore to posterior of supratemporal canal
- Numerous short semi-transverse rows of papillae variously intersect the longitudinal row

Interorbital Portion

- Lateral margin in anterior interorbital space perforated by a small, round pore (Figure 36B)
- Lateral margin in posterior interorbital space perforated by a small pore

Postorbital Portion

- No secondary canal development

Sensory Papillae Pattern

- Longitudinal row of papillae extends along proximal margin from anterior interorbital space to supratemporal canal
- Disjunct longitudinal row of papillae extends from posterior interorbital space to supratemporal canal
    - Medial to row originating in anterior interorbital space
- Numerous short semi-transverse rows of papillae variously intersect the longitudinal rows to form an irregular crosshatch pattern

Supratemporal Canal (Figure 36B)

- No secondary canal development

Sensory Papillae Pattern

- Irregular crosshatch pattern of papillae continues onto supratemporal canal from interorbital space

Infraorbital Canal (Figure 36A)

Lachrymal Portion

- Terminates anteriorly in a small pore just posterior of internarial space

Suborbital Portion

- Proximal margin not perforated
- Distal margin perforated by two small pores
    - One just below anterior edge of orbit
    - One near midpoint of orbit

Postorbital Portion

- Margins not perforated

Sensory Papillae Pattern

- Internarial space with rows of sensory papillae
- Longitudinal row of papillae from just posterior or anterior nostril to posterior of preopercle
- Numerous rows of papillae radiate from ventral margin of orbit extending to intersect longitudinal row
- Cheek covered by a crosshatch pattern of sensory papillae

Preoperculomandibular Canal

Mandibular Portion (Figure 36C)

- Terminates anteriorly in a pair of small round pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a small pair of round mental pores
- Medial margin perforated by two small pores
    - One near midpoint of maxilla
    - One just anterior of terminus of maxilla
- No terminal pore present

Preopercular Portion (Figure 36A)

- Distal margin formed into one small projection that terminates in a pore near middle of preopercle
- Crosshatch pattern of papillae continuing from cheek onto preopercle and posteriorly onto opercle

Sensory Papillae Pattern

- Sensory papillae formed into a sparse chevron pattern on basihyal
- One longitudinal row of sensory papillae extends along median of canal
- Numerous semi-transverse rows originate along expanse of longitudinal row and extend to margin of dentary
- Semi-longitudinal rows of papillae present on branchiostegal membrane

Remarks

The cephalic lateralis of *Paxton*, despite its simple canal structure, few perforations and, lack of secondary canal development, is characterized by an extensive network of sensory papillae. This characteristic, in combination with the lack of perforation, distinguishes *Paxton* from all other apogonids.

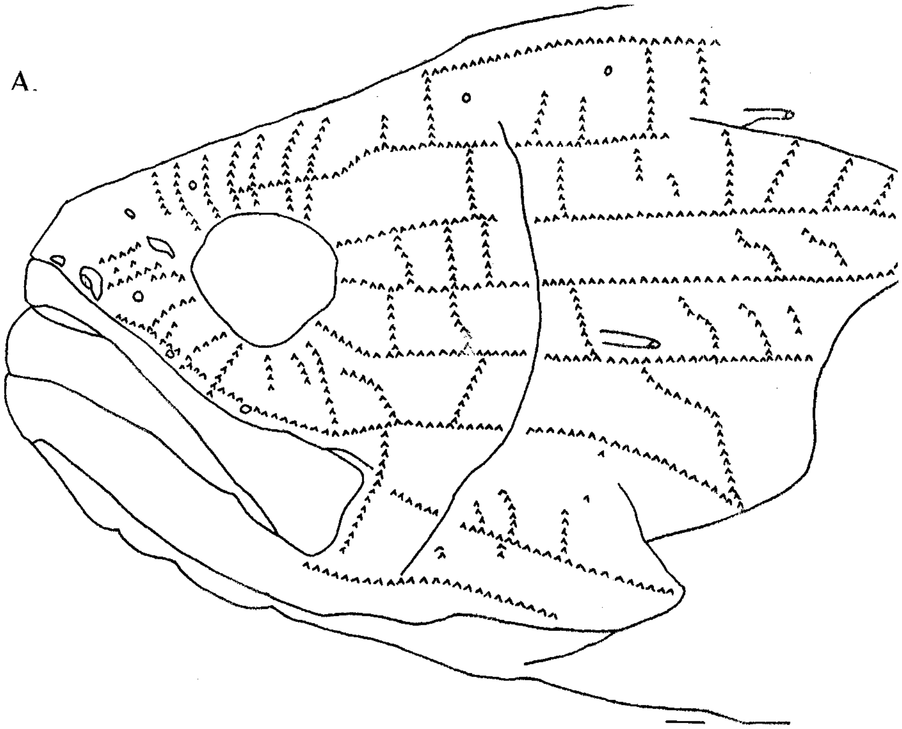


Figure 36. Cephalic lateralis of *Paxton concilians*. A. Lateral view

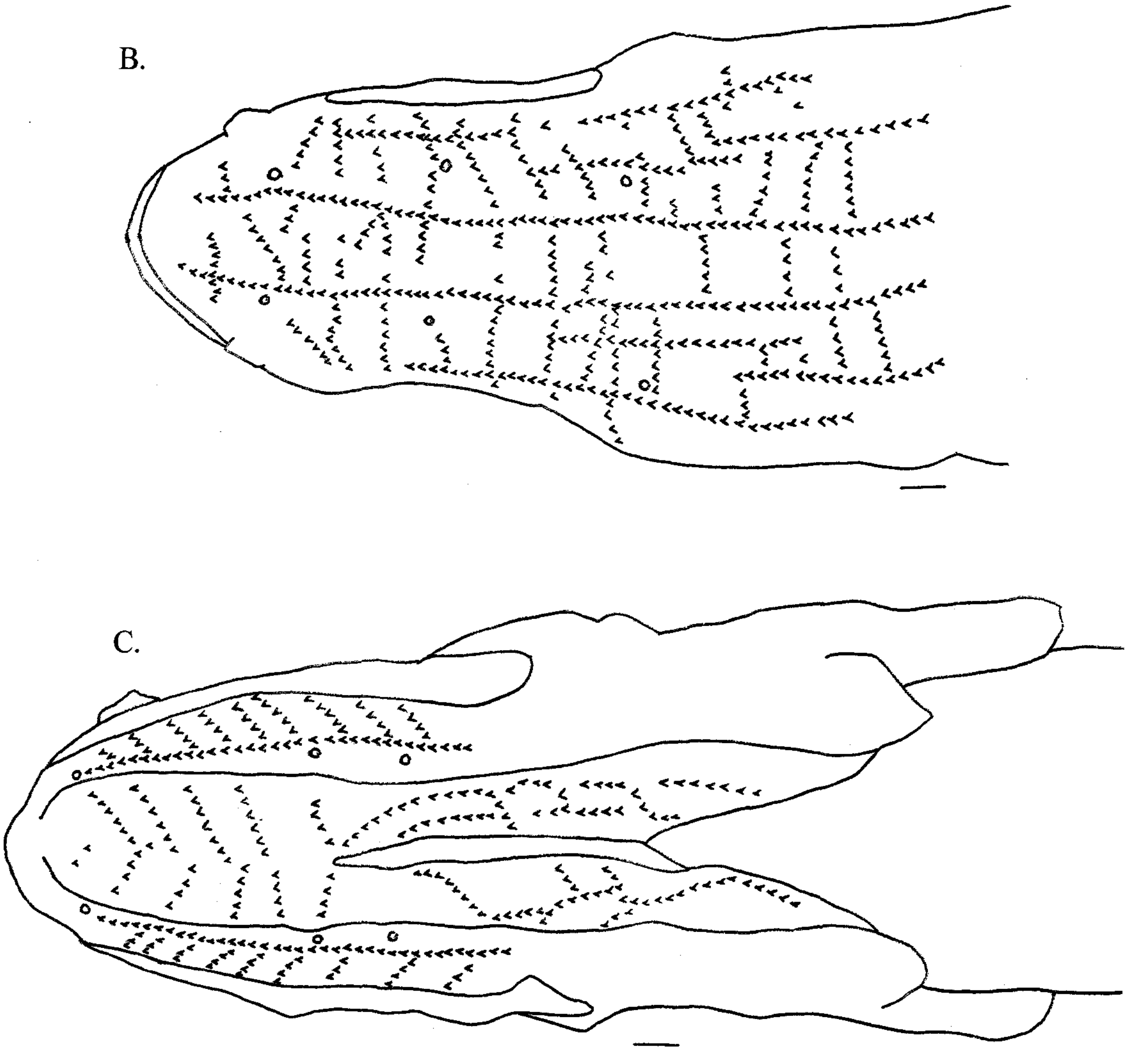


Figure 36 (continued). Cephalic lateralis of *Paxton concilians*. B. Dorsal view, C. Ventral view

Pseudamia Bleeker, 1865

Material Examined

Type species: *Cheilodipterus polystigma* Bleeker, 1859 [= *Cheilodipterus amblyuropterus* Bleeker, 1856[b] according to Randall et al. (1985)], by monotypy; USNM 210516; 1, 82.3 mm; USNM 357440; 2, 32.8—13.8 mm

Pseudamia gelatinosa Smith, 1955; BPBM 28223; 3, 37.8—46.8 mm

Pseudamia hayashii Randall, Lachner & Fraser, 1985; BPBM 36901; 2, 56.1—61.0 mm

Supraorbital Canal

Nasal Portion

- Extends almost to tip of snout (Figure 37A)
- Terminates anteriorly in a small round pore located anterior of and medial to base of anterior nostril
- Canal median perforated by a few small pores anterior of posterior nostril (Figure 37B)
- No large nasal pore

Interorbital Portion

- Medial margin and canal median perforated by several small pores along margin of orbit
- No large interorbital pore

Postorbital Portion

- Few small pores scattered across dorsal surface
- Secondary canal development absent

Sensory Papillae Pattern

- Longitudinal row of sensory papillae extends along canal median from tip of snout to posterior of supratemporal canal
- Longitudinal row of papillae extends posteriorly from dorsoposterior margin of orbit
- Two longitudinal rows of sensory papillae extend posteriorly from posterior interorbital space
- Many transverse rows cross dorsal surface of head from snout through supratemporal canal
    - Forms irregular crosshatch pattern on head

Supratemporal Canal (Figure 37B)

- Few small pores perforating canal area
- Canal formed into a short, open-ended posteriorly projecting extension

Infraorbital Canal (Figure 37A)

Lachrymal Portion

- Terminates anteriorly in a small, oval-shaped pore just ventral to and posterior of posterior nostril
- Distal margin, along ventral edge of lachrymal, perforated by two small pores

Suborbital Portion

- Proximal margin perforated by few small pores
- Distal margin formed into numerous projections that terminate in pores and extend toward maxilla

Postorbital Portion

- Ventroposterior distal margin formed into several open ended projections

Sensory Papillae Pattern

- Longitudinal row of papillae extends along canal median from anterior margin of orbit to preopercular edge
- Numerous transverse rows of papillae radiate from ventral margin of orbit
  - Intersect longitudinal row
- Irregular crosshatch pattern of papillae covering cheek and postorbital area
  - Longitudinal rows radiating posteriorly from posterior margin of orbit
  - Many short transverse rows covering postorbital and cheek areas

Preoperculomandibular Canal

Mandibular Portion (Figure 37C)

- Terminates anteriorly in a pair of small round pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a small pair of mental pores
- Margins of canals perforated by numerous small pores
- Lateral margin formed into a projection that terminates in a pore near midpoint of maxilla
- No terminal pore

Preopercular Portion (Figure 37A)

- Distal margin formed into numerous open-ended projections that extend toward margin of preopercle

Sensory Papillae Pattern

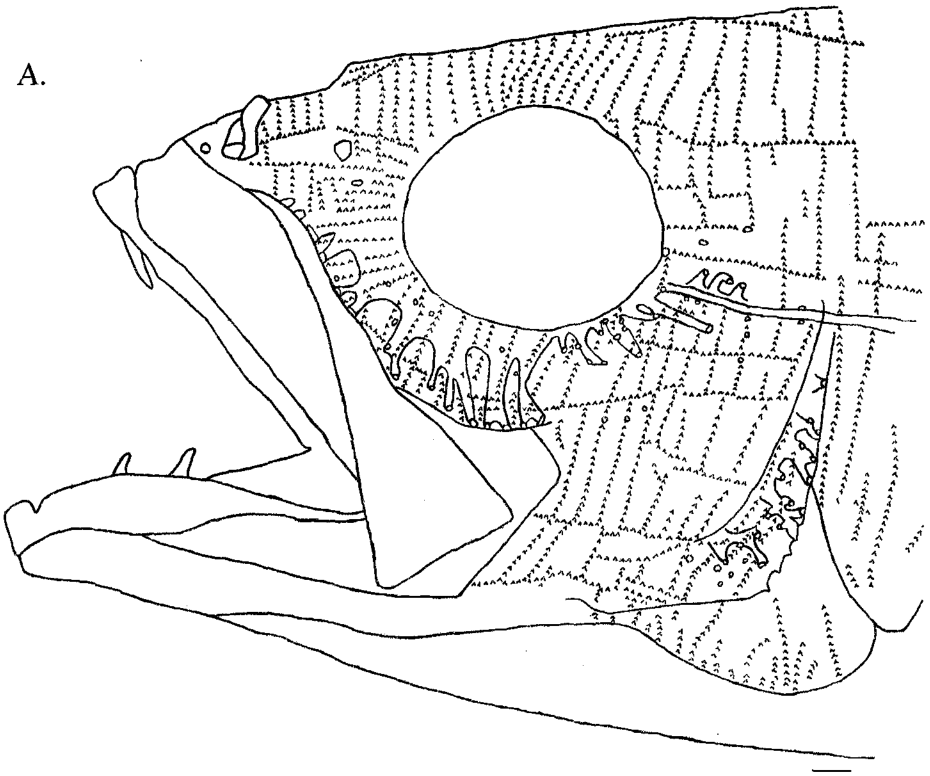
- Papillae formed into chevron pattern on basihyal
- Longitudinal row of papillae extends from mental pore to end of mandibular portion of canal

- Mandibular median with many transverse rows of papillae
    - Extend beyond margins of canal
    - Form irregular crosshatch pattern with longitudinal row
- Crosshatch pattern of papillae on ventral preopercular flange
- Rows of papillae along ventral portion of vertical preopercular flange
- Sensory papillae also present on ventral portions of opercle and interopercle

Remarks

In comparison to other apogonid species, the canals of the cephalic lateralis of *Pseudamia* species are narrow. The cephalic lateralis of *Pseudamia* displays a considerable amount of variability in both the pore and papillae patterns. The supraorbital canal of *P. amblyuroptera* is relatively simple with a few small pores perforating the median near the nostrils and in the interorbital space. The supraorbital canals of *P. gelatinosa* and *P. hayashii* are more complex, with a moderately-sized pore perforating the lateral margin adjacent to the posterior nostril and three pores perforating the lateral margin in the anterior interorbital space. The perforation of the mandibular portion varies from complete absence, with the exception of the dentary and mental pores, in *P. hayashii* to the three regularly spaced pores in the lateral margin in *P. gelatinosa*. *Pseudamia amblyuroptera* represents an intermediate form with its scattered, irregular perforations of the median and short lateral projection near the midpoint of the maxilla. All species of *Pseudamia* have a crosshatch pattern of papillae covering the head, but the density of the rows varies among the species. The pattern ranges from very dense in *P. amblyuroptera* to sparse in *P. gelatinosa*, with only twelve transverse rows crossing the dorsal surface of the head.

A.



B.

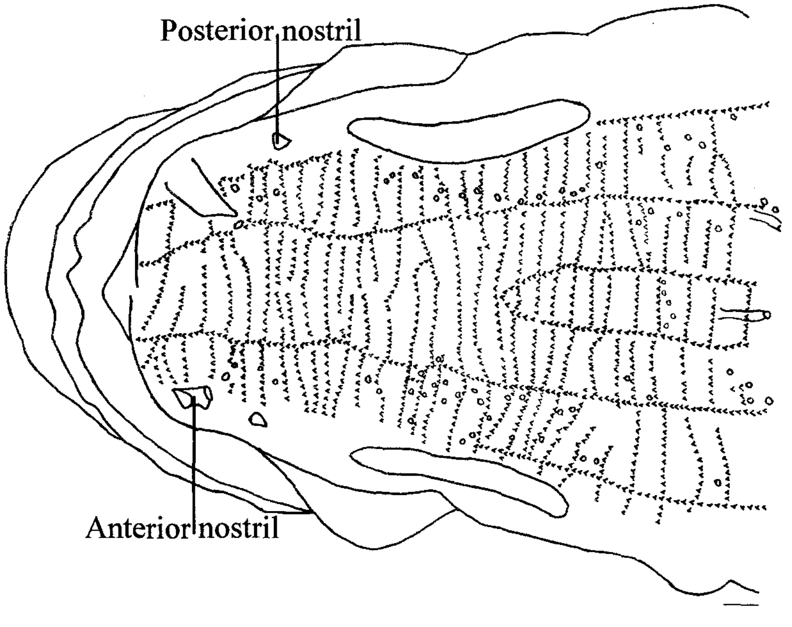


Figure 37. Cephalic lateralis of *Pseudamia amblyuroptera*. A. Lateral view, B. Dorsal view

C.

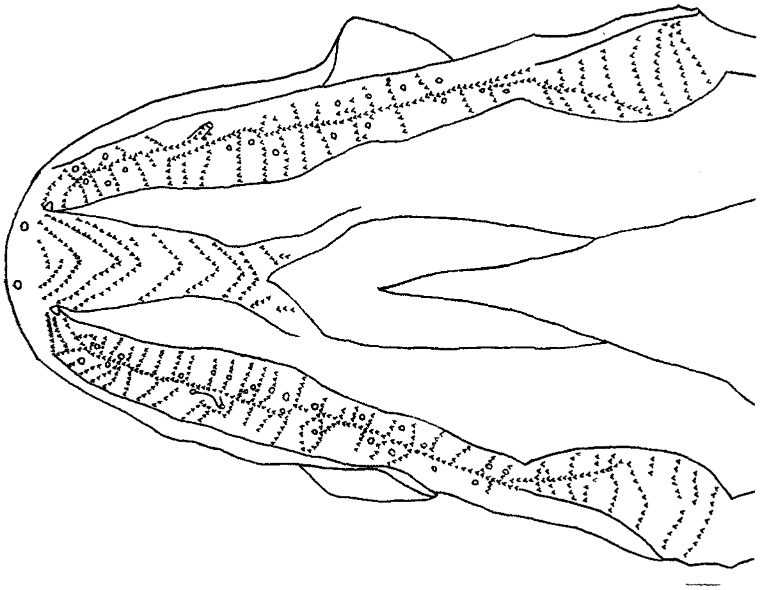


Figure 37 (continued). Cephalic lateralis of *Pseudamia amblyuroptera.* B. Dorsal view, C. Ventral view

Pseudamiops **Smith, 1954**

Material Examined

Type species: *Pseudamiops pellucidus* Smith, 1954, by original designation (also monotypic); USNM 349773; 1, 31.2 mm

Pseudamiops gracilicauda (Lachner, 1953); BPBM 17311; 1, 44.2 mm

Supraorbital Canal

Nasal Portion

- Extends almost to tip of snout (Figure 38A)
- Terminates anteriorly in a moderately-sized, round pore medial to anterior nostril
- Lateral margin of canal anterior of and superior to posterior nostril perforated by a moderately-sized pore (Figure 38A)

Interorbital Portion

- Lateral margin perforated by three, relatively large pores in the anterior, medial, and posterior portions of the interorbital space (Figure 38B)

Postorbital Portion

- No secondary canal development

Sensory Papillae Pattern

- Eight, nearly equidistant, transverse rows of sensory papillae span the dorsal portion of the head from anterior of the posterior nostril to supratemporal canal

Supratemporal Canal (Figure 38B)

- Canal perforated by few moderately-sized pores
- Posterior margin not formed into projections

Sensory Papillae Pattern

- Canal traversed by row of sensory papillae

Infraorbital Canal (Figure 38A)

Lachrymal Portion

- Terminates anteriorly in a moderately-sized pore just ventral to posterior nostril
- Distal margin perforated by one, slit-like pore below terminal pore

Suborbital Portion

- Distal margin perforated by few moderately-sized pores

Postorbital Portion

- Distal margin perforated by few moderately-sized pores

Sensory Papillae Pattern

- Rows of papillae that traverse the dorsal surface of head extend ventrally on both sides of the posterior nostril
- Cheek covered by crosshatch pattern of sensory papillae
    - Crosshatch pattern is wide-spaced, formed from only a few transverse and longitudinal rows

Preoperculomandibular Canal

Mandibular Portion (Figure 38C)

- Terminates anteriorly in a pair of pores that perforate the dentary
- Canal just posterior of apex of dentary perforated by a relatively large pair of subtriangular mental pores
- Lateral margin perforated by four relatively large, nearly equidistant pores
    - Fourth pore is terminal pore of mandibular portion

Preopercular Portion (Figure 38A)

- Posterior margin formed into a few short projections that terminate in relatively large pores along posterior edge of preopercle
- Canal perforated by a large pore at the bend in the preopercle
    - Pore prevents confluency of the mandibular and preopercular canal portions

Sensory Papillae Pattern

- Sensory papillae formed into a sparse chevron pattern on basihyal
- Longitudinal row of sensory papillae extends along median of mandibular canal
- Row of papillae along preopercular median extends dorsally beyond margin of preopercle

- Transverse row of papillae present on opercle, posterior of edge of preopercle

Remarks

The canal structure of *Pseudamiops* is simple with no secondary development and relatively few large pores. The presence of a large pore perforating the distal margin near the base of the preopercle distinguishes these species. The pore is so large in comparison to the width of the canal that it disrupts the confluence of the preoperculomandibular canal, effectively creating two separate canals. This genus is the only apogonid genus in which the mandibular and preopercular canal portions are not confluent. Another characteristic unique to this genus is the presence of only one pore perforating the distal margin along the ventral edge of the lachrymal, in contrast to other apogonids that typically have two lachrymal pores. The pore patterns are consistent between *Pseudamiops pellucidus* and *P. gracilicauda*. Variation occurs in the sensory papillae patterns, with *P. gracilicauda* having more rows of sensory papillae than *P. pellucidus*. Several transverse rows of papillae radiate from the ventral margin of the orbit in *P. gracilicauda*, whereas papillae are absent on the suborbital canal of *P. pellucidus*. The supratemporal and mandibular canals of *P. gracilicauda* are characterized by crosshatch patterns of papillae; *P. pellucidus* has only transverse rows crossing the dorsal surface of the head and a single longitudinal row along the mandibular canal median.

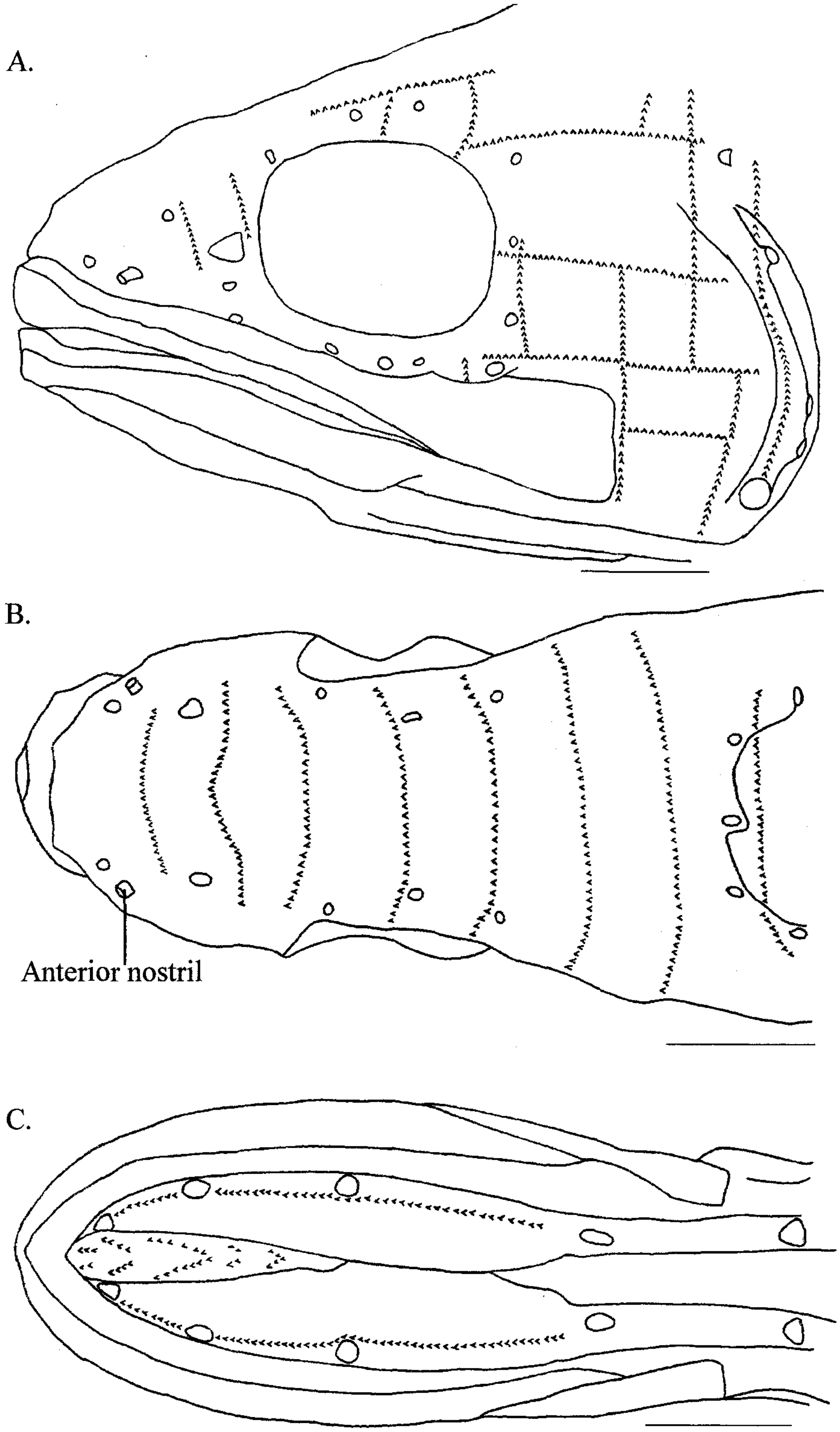


Figure 38. Cephalic lateralis of *Pseudamiops pellucidus*. A. Lateral view, B. Dorsal view, C. Ventral view

CHAPTER 3: PHYLOGENY OF CARDINALFISHES

The Apogonidae is one of the most speciose coral reef fish families. Members of this family are found on every coral reef in all tropical and subtropical waters worldwide and yet, despite this apparent ubiquity, the systematic relationships of its species are poorly understood. Few studies have attempted to address the question of the family's evolutionary history and, as a result, little is known about the evolution of this major group of coral reef fish.

Fraser (1972) completed what is to date, the most comprehensive study of the Apogonidae. One of the figures in his manuscript is the only published hypothesis of the family's evolutionary history (Figure 39). His study preceded the widespread acceptance and use of cladistic methods to elucidate phylogenetic histories, and therefore he used phenetic, rather than cladistic, methodologies to estimate the degree of relatedness among taxa. Fraser separated the apogonine genera into two phenetic groups and within these groups, placed the genera in the direction of one of two extremes, between the more "advanced" and "primitive" genera with which they shared the largest number of characters. He then collated these sequences into a phenogram (Figure 39).

Fraser considered *Glossamia* and *Coranthus* the most primitive, as they retained the largest number primitive characters. In the line of descent from *Glossamia* to *Vincentia* the tendency is to lose the basisphenoid, retain a small supramaxilla, have a rounded caudal fin, to be somberly colored, and to have more cryptic habitats. In the other major line of descent, from *Coranthus* to *Rhabdamia*, the trend is to retain the basisphenoid, lose the supramaxilla, have a forked caudal fin, brighter color patterns, and to have less cryptic habitats. This hypothesis was plagued by interpretational difficulties,

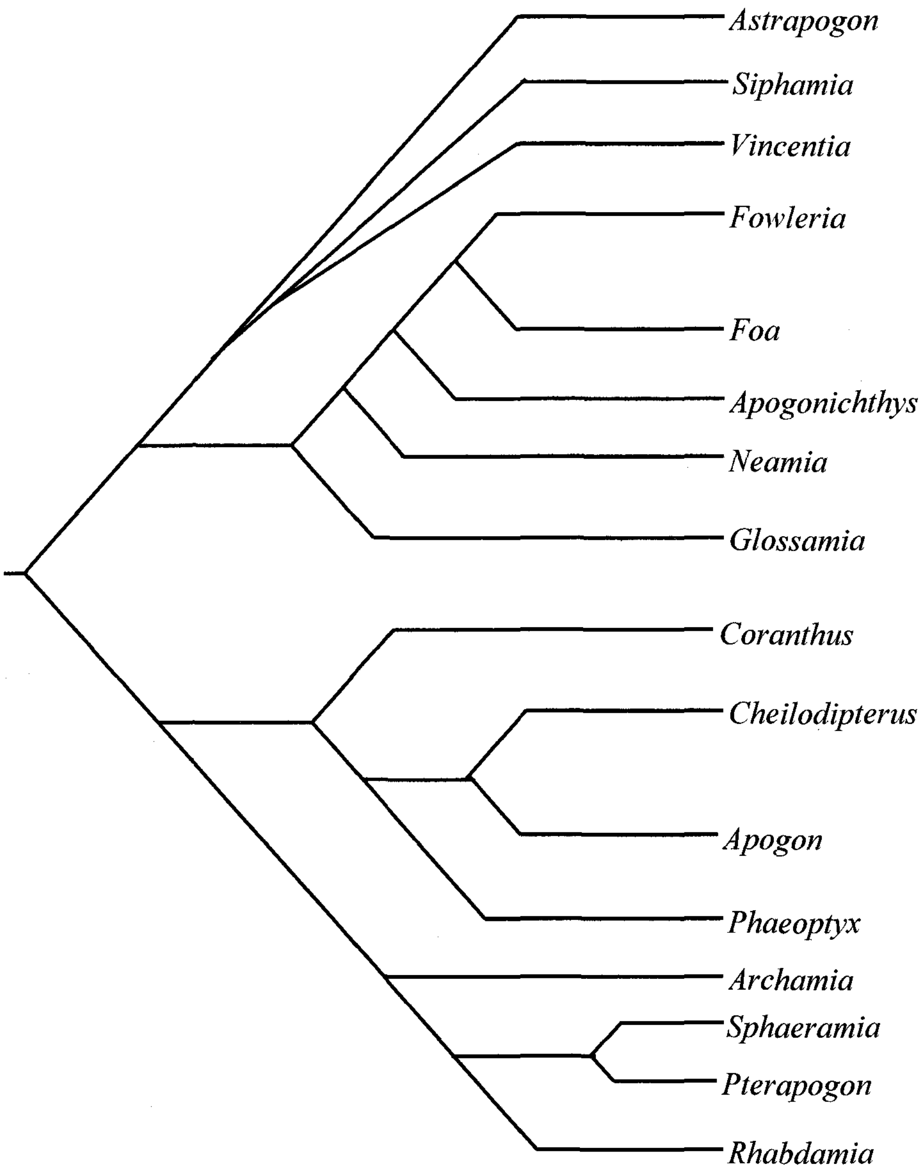


Figure 39. Fraser's (1972) hypothesis of the evolutionary relationships among the apogonine genera, as presented in Plate 44.

such as character reversals, parallel evolution of hypothetically advanced characters, and independent losses of characters within multiple lineages. Fraser found that the evolutionary path was more obvious for some character sets than for others; and often, character sets suggested conflicting evolutionary histories.

The shortcomings of phenetic methodologies led to the apparent inconsistencies of Fraser's evolutionary hypothesis. The phenetic approach to taxonomy is based on the assumption that the more similar two organisms are, the more likely they are to be related (Quicke, 1993). Phenetics depends upon overall similarity and makes no distinction between derived and ancestral character states. And thus, the risk of creating unnatural (i.e., non-monophyletic) taxa and taxonomic hierarchies, being based upon pleisiomorphpic characters, is high. In such a classification, when a character undergoes a change in multiple taxa, it often appears anomalous in the evolutionary scheme, and a mosaic distribution of character states results.

In contrast to phenetics, cladistic methodologies consider only shared derived characters in phylogenetic reconstruction (Quicke, 1993). The publications of Willi Hennig (1950, 1957, 1966) laid the foundation for this approach to systematic studies. In his writings, Hennig explained that during evolution, characters evolve from one state to the next. And so, when a group of related organisms exhibits more than one condition of a particular character, only one of those can be the ancestral state. The other condition(s) must have evolved within the group from the ancestral state. He put forth that this must be considered when attempting to construct evolutionary trees. Only those organisms that share the derived character states are grouped together. This approach reduces the risk of creating non-monophyletic taxa because organisms that share derived characteristics are more likely to have shared a more recent common ancestor. His rationale and methodology continues to be the most widely accept method of phylogentic reconstruction.

This chapter attempts to fill the gap in our knowledge of the evolution of the Apogonidae by presenting a cladistically derived hypothesis of the family's evolutionary history based on an analysis of Fraser's (1972) morphological and osteological data. The family's largest genus, *Apogon,* is considered first, followed by the presentation of the results for the family as a whole. These analyses resulted in a number of well-resolved, but not well-supported (as indicated by the consistency and retention indices), equally parsimonious cladograms. Homoplasies aside, all of the cladograms suggest that the genus *Apogon* is not monophyletic as it is currently defined. The results of this research highlight the need for revision of the family's classification in order more accurately reflect the group's phylogenetic history.

Methods for Cladistic Analysis

Assessment of the Monophyly of *Apogon*

An initial cladistic analysis of Fraser's (1972) osteological data was completed in order to assess the monophyly of the genus *Apogon.* Because the sister group of the genus is unknown, three outgroups were selected from within the family for the analysis: *Cheilodipterus,* a putative sister group of the genus *Apogon; Phaeoptyx,* another genus Fraser (1972) suspected is closely related to *Apogon;* and *Holapogon,* reputedly the most primitive apogonid genus based upon the similarity between its skeleton and the skeleton of primitive percoids.

Fraser's (1972) monograph was used to compile a data matrix of 44 osteological and morphological characters. Additional references were used to gather equivalent data for the 9 taxa described since, or not included in, the monograph (Fraser, 1973; Randall and Smith, 1988; Fraser and Struhsaker, 1991; Hayashi, 1991; Gon, 1996; Baldwin and Johnson, 1999). Eighteen of the 44 characters were informative at the level necessary for assessment of the monophyly of *Apogon.* The 18-character data matrix was analyzed with PAUP (Swofford, 1998) using 100 replicates of a heuristic search. Thirteen of the 18 characters were multi-state (characters 2, 6, 7, 10 and14 were binary). In order to remove bias from the coding and/or to avoid imposing preconceived models of evolution on the characters, the multi-state characters were treated as unordered. The consistency, retention, and rescaled consistency indices were generated for the phylogeny as a whole.

Cladistic Analysis of Fraser's Data for the Entire Family

There is no single, clear choice for the appropriate apogonid outgroup. The interfamilial relationships among the families in the Percoidei are unknown and although the kurtids have been suggested as the sister group to the apogonids (Johnson, 1993) this putative relationship is not well supported. The sister group relationship between the Apogoninae and Pseudaminae is, however, well supported, as described by Baldwin and Johnston (1999). And thus, the most conservative approach was to use the four pseudamine genera as outgroups to analyze the phylogenetic relationships among the apogonine genera and subgenera. Since no evidence exists to support the assumption that the apogonid subgenera, as currently defined, are of lesser taxonomic rank than are the family's genera, all super-specific taxa were treated as equally ranked for the analysis.

Fraser's 1972 monograph was used to compile a data matrix of 44 osteological and morphological characters. Forty-one of these characters were parsimony informative at the family level. The data matrix was analyzed with PAUP (Swofford, 1998) using 100 replicates of a heuristic search. Thirty of the 43 characters were multi-state (characters 2, 4, 7-10, 12, 14-18, 20, 22-23, 25-27, 29-30, 32-34, 36-37, 39-40, 42-44). Multi-state characters were run unordered per reasons given above. The remaining characters were binary. A "?" in the matrix is used to represent missing data and a "-" in the data matrix is used when that character or character state is inappropriate for, or inapplicable to, a given taxon. Missing data indicate that the character state could not accurately be determined due to problems stemming from compilation of the data matrix from a pre-existing data set, and not from the specimens themselves. Inappropriate or inapplicable data most frequently indicate the absence of a character, and thus, coding the condition of that character was impossible, e.g., absence of scales and scale type. The consistency and retention indices were generated for the phylogeny as a whole.

Results

Characters Compiled from Fraser's (1972) Monograph

Fraser's (1972: Table 5) data were used to compile a set of 44 osteological, morphological, and morphometric transformation series. They are listed below, grouped into traditional anatomical units from anterior to posterior, and numbered (in parentheses following the character name) in correspondence with the numbering in the data matrices (Appendices A, B, C). None of the 44 characters was informative at every level of analysis. This is reflected in the numbering following the character name. The Appendix

(A, B, or C) is referenced first, followed by the number to which the character corresponds in that matrix. Appendix A contains the osteological and morphological characters that were used to assess the monophyly of the genus *Apogon*. Appendix B contains the osteological and morphological characters that were used in the cladistic analysis of the entire family. Appendix C contains the osteological and morphological characters derived from Fraser's (1972) data set plus the cephalic lateralis characters generated from the current examination of the species' cephalic lateralis systems. Although the analysis of the combined data set, i.e. the osteological, morphological and cephalic lateralis data, is not the focus of this chapter, the references to Appendix C are included to avoid redundancy in Chapter 4.

The account of each transformation series includes a description of each character state and a short discussion of the historic treatment of the transformation series, if applicable. Because the sister group of the Apogonidae is unknown, the ancestral states for each transformation series are also unknown, precluding the accurate estimation of the relative apomorphy of the character states. As a result, the transformation series have been treated as unpolarized and unordered. The Beryciformes are considered to be basal to the Perciformes (Gregory, 1933; Gosline, 1961; Patterson 1964, 1967, 1968; Johnson, 1984, 1993; Nelson, 1994) and beryciform character states have previously been used to estimate the degree of primitiveness of apogonid characters (Fraser, 1972). But, because apogonids are not directly derived from a beryciform ancestor, there is not always an obvious direction of character evolution suggested by the comparisons of apogonid and beryciform character states. These comparisons were therefore not used to polarize and order the transformation series included in this analysis. Discussions of these apogonid—beryciform comparisons have been included, when applicable, in the historical treatment of the transformation series and character state distributions.

Neurocranium

Supraoccipital crest (A.1, B.1, C.1). – (0) absent; (1) present. Several apogonids have developed large supraoccipital crests (Fraser, 1972). This character is present in *Apogon* (*Zoramia*), *Archamia*, *Pterapogon*, and *Sphaeramia.*

Villiform teeth on vomer (B.2, C.2). – (0) wide band; (1) medium width band; (2) narrow band; (3) single row; (4) absent. Beryciforms have a wide band of villiform teeth on the vomer (Patterson, 1964). In apogonids, the presence of villiform teeth on the vomer varies from a wide band to a single row to absent (Fraser, 1972). *Fowleria* is the only apogonid to have a wide band of villiform teeth on the vomer. *Apogon* (*Apogon*), *Apogon* (*Lepidamia*), *Astrapogon*, *Phaeoptyx*, and *Pterapogon* (*Quinca*) all have vomerine villiform teeth in a band of medium width. *Apogon* (*Jaydia*), *Apogon* (*Pristicon*), *Apogon* (*Ostorhinchus*), *Apogon* (*Yarica*), *Apogon* (*Zapogon*), *Apogon* (*Zoramia*), *Foa*, *Glossamia Holapogon*, *Sphaeramia*, and *Vincentia* all have a narrow band of villiform teeth on the vomer. *Apogon* (*Brephamia*), *Apogon* (*Paroncheilus*), *Apogon* (*Pristiapogon*), *Archamia*, *Coranthus*, *Pterapogon* (*Pterapogon*), *Rhabdamia* (*Bentuviaichthys*), *Rhabdamia* (*Rhabdamia*), *Rhabdamia* (*Verulux*), *Siphamia*, *Gymnapogon*, and *Paxton* have a single row of villiform teeth on the vomer. Species in *Apogonichthys*, *Cheilodipterus*, and *Neamia* possess either a narrow band or single row of villiform teeth on the vomer. Villiform teeth are absent in *Cercamia*, *Lachneratus*, *Pseudamia*, and *Pseudamiops*. A reduction in the presence of villiform teeth has traditionally been considered derived among the Apogonidae (Fraser, 1972). Taxa with 2-3 rows of villiform teeth on the vomer are included in the "narrow band" category.

Canines on vomer (*B.3*, *C.3*). – (0) absent; (1) present. The presence of canines on the vomer varies in the Apogonidae. Some apogonids have one or more canines present on the vomer (Fraser, 1972). Canines are present on the vomer in *Cercamia*, *Cheilodipterus*, *Coranthus*, *Lachneratus*, and in all pseudamine genera. Canines have been treated as derived, as they are thought to have evolved secondarily from villiform teeth (Fraser, 1972).

Basisphenoid (*B.4*, *C.4*). – (0) present; (1) reduced; (2) absent. The basisphenoid is a single, median, Y-shaped bone located in the posterior part of the orbit. When present, the bone articulates posteriorly with the prootics and anteroventrally with the parasphenoid (Bond, 1996). As the major bite has shifted anteriorly during the course of teleost evolution, from the parasphenoid-basihyal area to the dentary-premaxilla, the need for the basisphenoid and other orbitosphenoids to support the parasphenoid has decreased (Patterson, 1964; Fraser, 1972). As a result, the basisphenoid has undergone reduction in size and its complete loss has occurred in some apogonid species. The basisphenoid is reduced in *Apogonichthys* and *Foa* and is absent in all pseudamine genera, *Astrapogon*, *Cercamia*, *Fowleria*, *Gymnapogon*, *Neamia*, *Rhabdamia* (*Bentuviaichthys*), *Siphamia*, and *Vincentia*. In *Glossamia* and *Phaeoptyx* it is reduced or absent, depending on the species. The basisphenoid is present and not reduced in all of the *Apogon* subgenera, *Archamia*, *Cheilodipterus*, *Coranthus*, *Holapogon*, the *Pterapogon* subgenera, *Rhabdamia* (*Rhabdamia*), *Rhabdamia* (*Verulux*), and *Sphaeramia.*

Inclusion of intercalary facet on the otic bulla (A.2, B.5, C.5). – (0) not included on otic bulla; (1) included on otic bulla. The intercalar is the skull bone onto which the lower fork of the posttemporal bone attaches (Gosline, 1966; Tominaga, 1968; Bond, 1996). This bone may or may not be included among the bones forming the posterior portion of the otic capsule. In most apogonids, a large portion of the intercalary forms a part of the otic bulla (Fraser, 1972). The intercalary facet (the point of articulation between the intercalary and the posttemporal), however, may or may not be included on the otic bulla (Baldwin and Johnson, 1999). The location of the intercalary facet relative to the otic bulla is a reflection of the degree to which the intercalar is included among the bones forming the otic capsule. In species with the intercalary facet included on the otic bulla, the intercalar forms a large portion of the capsule, being positioned between the prootic and exoccipital. In those species in which the intercalary facet is not included on the otic bulla, a space exists between the ventrolateral portions of the prootic and exoccipital and the intercalar lies dorsal to these two bones. In this situation, the intercalar forms but a small portion of the otic capsule and the intercalary facet is dorsal of, and therefore not included on, the otic bulla. The intercalary facet is not included on the otic bulla in any of the pseudamine genera or in *Apogon* (*Yarica*), *Glossamia*, and *Holapogon.*

Parasphenoid and pterosphenoid (*B.6, C.6*). – (0) separated by prootic; (1) not separated by prootic. The pterosphenoids are fused in kurtids, meet along the midline in beryciforms, serranids, pempherids, pomatomids, and have been suggested by Fraser (1972) to meet secondarily in percoids. In the pseudamine genera, the anterior projection of the prootic bone that separates the parasphenoid and the pterosphenoid in apogonine species is reduced or absent, resulting in the juxtaposition of the parasphenoid and pterosphenoid bones (Baldwin and Johnson, 1999). This condition does not occur in other apogonids, and may be rare among percoids (Fraser, 1972).

Circumorbital Bones

Infraorbital shelf (*A.3, B.7, C.7*). – (0) shelf on all infraorbitals; (1) shelf only on third, fourth, and fifth infraorbitals; (2) shelf only on third infraorbital; (3) shelf only on third infraorbital, but reduced; (4) shelf absent. Beryciforms have six infraorbitals and a well-developed subocular shelf on the third bone, and sometimes shelves on other infraorbitals (Fraser, 1972). Lower percoids have a well-developed shelf on the third infraorbital (Baldwin and Johnson, 1999). In the Apogonidae the presence of shelves on the infraorbitals varies. The infraorbitals of *Cercamia* all have a subocular shelf, as do the third, fourth and fifth infraorbital bones of *Fowleria.* A shelf is present but reduced on the third infraorbital in *Rhabdamia* (*Rhabdamia*) and *Gymnapogon. Apogon* (*Zoramia*), *Paxton, Pseudamia, Pseudamiops, Rhabdamia* (*Bentuviaichthys*), *Rhabdamia* (*Verulux*), and *Sphaeramia* lack a shelf on any infraorbital. The remaining apogonid taxa have a fully formed shelf present only on the third infraorbital; the remaining ocular bones are without shelves.

Upper edge of infraorbitals (*A.4*, *B.8*, *C.8.*). – (0) smooth; (1) weakly serrate; (2) serrate. The edges of the infraorbitals in apogonids may be smooth to serrate. The infraorbitals are weakly serrate in *Apogon* (*Jaydia*) and are serrate in *Apogon* (*Pristiapogon*) and *Apogon* (*Pristicon*). The upper edge of the infraorbitals is smooth in all other apogonids.

Jaws, suspensorium, opercular series

Supramaxillae (*A.5*, *B.9*, *C.9*). – (0) present; (1) reduced; (2) absent. The supramaxillae are small bones of dermal origin attached to the maxillary bones posterodorsally in teleosts (Lagler et al., 1962). Beryciform fishes possess two supramaxillae above each maxilla (Patterson, 1967). No percoid has been found to possess both supramaxillae (Fraser, 1972). The shape of the single supramaxilla of percoid fishes is similar in structure to the posterior supramaxilla of beryciforms, suggesting that the anterior supramaxilla of beryciforms has been lost (Fraser, 1972). A single supramaxilla is present in some apogonids but is usually reduced or absent; it is well-developed only in *Coranthus*, *Glossamia*, *Holapogon*, and *Apogon* (*Yarica*). A reduced supramaxilla is present in *Apogonichthys*, *Cheilodipterus*, *Foa*, *Fowleria*, and *Neamia*. The remaining apogonid taxa do not have a supramaxillary bone.

Villiform teeth on jaws (*A.6*, *B.10*, *C.10*). – (0) wide band; (1) medium width band; (2) narrow band; (3) single row. The major teeth-bearing surfaces in higher teleosts are the premaxilla, in the upper jaw, and the dentary, in the lower jaw (Bond, 1996). Beryciforms have wide bands of villiform teeth on the premaxilla and dentary bones (Patterson, 1964). In apogonids, dentition of the jaws varies from the presence of a wide band to a single row of villiform teeth. *Apogon* (*Pristiapogon*), *Apogon* (*Pristicon*), *Apogon* (*Zapogon*), *Apogonichthys*, *Astrapogon*, *Foa*, *Fowleria*, *Glossamia*, *Lachneratus*, *Sphaeramia*, and *Vincentia* have a wide band of villiform teeth on the jaws. A medium width band of villiform teeth is present in the jaws of *Apogon* (*Apogon*), *Apogon* (*Jaydia*), *Apogon* (*Lepidamia*), *Apogon* (*Yarica*), *Cheilodipterus*, *Holapogon*, *Neamia*, *Pterapogon* (*Quinca*), and *Siphamia*. *Zoramia*, *Archamia*, *Cercamia*, *Coranthus*, *Phaeoptyx*, *Pterapogon* (*Pterapogon*), *Rhabdamia* (*Bentuviaichthys*), and all of the pseudamine genera have a narrow band of villiform teeth on the jaws. A single row of villiform teeth is present on the jaws of *Apogon* (*Brephamia*), *Apogon* (*Paroncheilus*), *Rhabdamia* (*Rhabdamia*), and *Rhabdamia* (*Verulux*). The species in the *Apogon* (*Ostorhinchus*) subgenus display all of the different states for this character. A reduction in the presence of villiform teeth has been treated as derived among the Apogonidae (Fraser, 1972). Taxa with 2-3 rows of villiform teeth on the jaws are placed into the "narrow band" category.

Canines on jaws (*A.7*, *B.11*, *C.11*). – (0) absent; (1) present. Canines are present on the jaws of some apogonid species. Canines have been treated as derived as they are thought to have evolved secondarily from villiform teeth (Fraser, 1972). Taxa with canines in their jaws are: *Apogon* (*Paroncheilus*) *affinis*, *Cheilodipterus*, *Coranthus*, *Gymnapogon*, *Lachneratus*, *Paxton*, *Pseudamia*, *Pseudamiops*, and *Rhabdamia* (*Bentuviaichthys*), *Rhabdamia* (*Rhabdamia*), and *Rhabdamia* (*Verulux*).

Villiform teeth on palatine (*A.8*, *B.12*, *C.12*). – (0) wide band; (1) narrow band; (2) single row; (3) absent. Beryciforms have a wide band of villiform teeth on the palatine (Patterson, 1964). In apogonids, dentition of the palatine varies from the presence of a wide band of teeth to an absence of villiform teeth. *Apogon* (*Pristicon*), *Apogon* (*Yarica*), *Apogon* (*Zapogon*), *Glossamia*, *Sphaeramia*, and the pseudamine genera *Gymnapogon*, *Pseudamia*, and *Pseudamiops* have a wide band of villiform teeth on the palatine. A narrow band of villiform teeth is present on the palatine in *Apogon* (*Jaydia*), *Apogon* (*Lepidamia*), *Archamia*, *Holapogon*, and *Pterapogon* (*Quinca*). A single row of villiform teeth is present on the palatine in *Apogon* (*Apogon*), *Apogon* (*Paroncheilus*), *Apogon* (*Ostorhinchus*), *Apogon* (*Zoramia*), *Astrapogon*, *Coranthus*, *Phaeoptyx*, *Rhabdamia* (*Bentuviaichthys*), *Siphamia*, *Vincentia*, and the pseudamine genus *Paxton*. Villiform teeth are absent on the palatine of *Apogon* (*Brephamia*), *Cercamia*, *Fowleria*, *Neamia*, and *Pterapogon* (*Pterapogon*). Species in the genus *Foa* have a wide band, narrow band, or a single row of villiform teeth on the palatine. Species in *Cheilodipterus* and *Lachneratus* have either a narrow band or single row of villiform teeth on the palatine. When villiform teeth are present on the palatine in *Apogon* (*Pristiapogon*) and *Apogonichthys* they are in a single row. *Rhabdamia* (*Rhabdamia*) and *Rhabdamia* (*Verulux*) have few to no villiform teeth on the palatine. A reduction in the presence of villiform teeth has been treated as derived among the Apogonidae (Fraser, 1972). For the analysis of the genus *Apogon* this character was coded as present or absent.

Ectopterygoid teeth (*B.13*, *C.13*). – (0) present; (1) absent. Wide bands of villiform teeth can be found on the ectopterygoid and endopterygoid of beryciforms (Patterson, 1964).

A small number of percoid families have ectopterygoid and endopterygoid teeth (Fraser, 1972). No apogonid genus has endopterygoid teeth. A reduction in the presence of villiform teeth on the ectopterygoid has been treated as derived among the Apogonidae (Fraser, 1972). *Apogonichthys ocellatus*, *Glossamia*, *Pseudamia*, and *Pseudamiops* are the only apogonids that possess ectopterygoid teeth.

Preopercular ridge (*A.9*, *B.14*, *C.14*). – (0) smooth; (1) weakly serrate; (2) serrate; (3) spinous. The spinous and serrate condition of the preopercle and opercle in beryciforms and other percoids suggests that a spiny condition may be ancestral (Fraser, 1972). This implies that the smooth condition may be derived and the serrate condition may be intermediate between the two. The preopercular ridge is serrate in *Apogon* (*Pristiapogon*) and *Apogon* (*Pristicon*) and weakly serrate in *Apogon* (*Jaydia*). *Cercamia* has a spine at the angle of the preopercle. The ridge of the preopercle is smooth in all other apogonids.

Preopercular edge (*A.10*, *B.15*, *C.15*). – (0) smooth; (1) weakly serrate; (2) serrate. The preopercular edge in apogonids varies from smooth to serrate. The spinous and serrate condition of preopercle and opercle in beryciforms suggests that a spiny condition may be ancestral (Fraser, 1972). This implies that the smooth condition may be derived and the serrate condition may be intermediate between the two. The preopercular edge is smooth in *Apogonichthys*, *Archamia*, *Astrapogon*, *Cercamia*, *Foa*, *Fowleria*, *Glossamia*, *Lachneratus*, *Neamia*, *Phaeoptyx*, *Rhabdamia* (*Bentuviaichthys*), *Rhabdamia* (*Rhabdamia*), *Rhabdamia* (*Verulux*), and the pseudamine genera *Gymnapogon*, *Pseudamia*, and *Pseudamiops*. All of the *Apogon* subgenera, with the exception of *Apogon* (*Jaydia*), have serrate preopercular edges. The preopercular edge is weakly serrate in *Apogon* (*Jaydia*). *Coranthus*, *Holapogon*, *Pterapogon (Pterapogon)*, *Pterapogon (Quinca)*, *Siphamia*, *Sphaeramia*, and *Vincentia* have a serrate preopercular edge. The preopercular edge of *Cheilodipterus* is either weakly serrate or serrate, depending on the species. The preopercle of *Paxton* is covered by skin and therefore this character is not applicable to that species.

Ossification of preopercular edge (*A.11*, *B.16*, *C.16*). – (0) unossified; (1) partially ossified; (2) ossified. The ventral preopercular edge is unossified in *Apogon* (*Apogon*) and *Apogon* (*Zapogon*) and is partially unossified in *Apogon* (*Paroncheilus*) and *Phaeoptyx*. The ventral preopercular edge is ossified in the remaining apogonid taxa. The preopercula of *Gymnapogon* and *Paxton* are covered by skin and therefore this character is not applicable to these species.

Spine on preopercular edge (*B.17*, *C.17*). – (0) absent; (1) one spine; (2) more than one spine. *Paxton* and *Gymnapogon* have a single large spine extending from the posterior edge of the preopercle, and although they are differently shaped (the spine of *Gymnapogon* is larger and more pointed) they occur in the same relative position on the preopercle and are suggested as being homologous (Baldwin and Johnson, 1999). *Cercamia* has two to five short spines on the preopercular margin. *Lachneratus* has three spines on the preopercular edge.

Preopercle obscured by skin (*B.18*, *C.18*). – (0) not obscured; (1) partially obscured; (2) completely obscured. Both *Gymnapogon* and *Paxton* have their preopercula obscured by skin. The preopercle of *Paxton* is completely obscured, but only the ventral flange is obscured in *Gymnapogon* (Baldwin and Johnson, 1999).

Preopercle with a fleshy flap (*A.10*, *B.19*, *C.19*). – (0) flap absent; (1) flap present. *Phaeoptyx* and the pseudamine genera *Gymnapogon* and *Paxton* have a fleshy flap extending posteriodorsally from the ventral surface of their preopercula. The only other apogonids known to have this character are *Apogon* (*Apogon*) *deetsie* Randall, 1998 and a new *Apogon* (*Apogon*) sp. (being described by Greenfield).

Lower Hyoid Arch

Ceratohyal (*A.12*, *B.20*, *C.20*). – (0) perforated; (1) notched/deeply notched; (2) weakly notched; (3) smoothly concave. The ceratohyal functions as the principal site of attachment for the branchiostegal rays. Beryciforms and primitive percoids have a perforated ceratohyal (McAllister, 1968; Fraser, 1972). The only apogonid to retain a perforated ceratohyal is *Holapogon maximus*. The dorsal surface of the ceratohyal in the remaining apogonid species ranges from deeply notched, a presumed remnant of the perforated condition, to smooth (Fraser, 1972).

Ceratohyal – epihyal junction (*B.21*, *C.21*). – (0) dentate; (1) smooth. The typical morphology is for the ceratohyal and epihyal to interdigitate in order to strengthen the connection between the two bones (Gregory, 1933). These bony struts thus formed give the suture a dentate appearance. Beryciforms do not have a dentate suture joining the ceratohyal and epihyal (Patterson, 1964; McAllister, 1968). The nature of the suture between the ceratohyal and epihyal varies among the apogonids. The dentate morphology is found in *Glossamia*, *Paxton*, and in some *Cheilodipterus* species. The suture between the epihyal and ceratohyal is smooth in all other apogonids. Fraser (1972) hypothesized that the dentate condition was primitive.

Gill Arches

First pharyngobranchial (B.22, C.22). – (0) present; (1) developing within tip of epibranchial; (2) absent. The typical condition of the first pharyngobranchial (Fraser's suspensory pharyngeal) in the Apogonidae is to be well-developed and ossified. Fraser (1972) suggested that the suspensory pharyngeal was unossified in *Gymnapogon* and absent in *Apogonichthys*, *Astrapogon*, and *Fowleria.* Baldwin and Johnston's (1999) examination of cleared and stained specimens revealed, however, that the suspensory pharyngeal is present and ossified in *Astrapogon*, and specimens of *Apogonichthys* and *Fowleria* show evidence that the pharyngobranchial is ossifying within the first epibranchial. The first pharyngobranchial is absent only in *Gymnapogon* and *Paxton.*

Pharyngeal tooth plates (B.23, C.23). – (0) 5 tooth plates; (1) 4 tooth plates; (2) 3 tooth plates resulting from the loss/fusion of tooth plate on the second epibranchial; (3) 3 tooth plates resulting from the loss of the tooth plate on the third pharyngobranchial. Only a few apogonids have five upper pharyngeal tooth plates. Most have four tooth plates resulting from either loss of the second epibranchial tooth plate or its fusion to the tooth plate on the second pharyngobranchial (Fraser, 1972). One species each of *Cheilodipterus* and *Apogonichthys* have lost the tooth plates on both the second epibranchial and second pharyngobranchial and have only three pharyngeal tooth plates. *Paxton* also has three pharyngobranchial tooth plates, however, this morphology has evolved via a different pathway. *Paxton* retains the second pharyngobranchial tooth plate but has lost the tooth plate on the third epibranchial. *Paxton* is unique among apogonids in lacking a tooth plate on the third epibranchial (Baldwin and Johnson, 1999).

Gill-rakers (*B.24*, *C.24*). – (0) present only on the first arch; (1) present on the first and second arches. Among apogonids, *Archamia*, *Astrapogon*, *Cercamia*, *Gymnapogon*, and *Paxton* have gill-rakers on both the first and second arches; the remainder has them only. on the first arch (Baldwin and Johnson, 1999).

Post axial skeleton

Number of vertebrae (*B.25*, *C.25*). – (0) 10 + 15; (1) 10 + 14; (2) 9 + 15. The ancestral number of vertebrae in percoids is 24-25 (10 + 14-15) (Gosline, 1968, 1971; Johnson, 1984). The number of vertebrae is relatively constant in the Apogonidae (Fraser, 1972). There are two exceptions to the typical 10 pre-caudal and 14 caudal apogonid vertebral count: *Vincentia* has 10 + 15 vertebrae and *Cercamia* has 9 + 15 vertebrae.

Epipleural ribs (*A.13*, *B.26*, *C.26*). – (0) 10 epipleurals; (1) 9 epipleurals; (2) 8 epipleurals; (3) 7 epipleurals; (4) 6 epipleurals; (5) 5 epipleurals; (6) 4 epipleurals; (7) 3 epipleurals; (8) 2 epipleurals. Only *Neamia* has epipleural ribs on all 10 pre-caudal vertebrae. The tenth epipleural is absent in all other genera; the eighth and ninth epipleurals are also frequently absent. *Apogon* (*Lepidamia*), *Apogon* (*Pristicon*), *Apogon* (*Yarica*), *Glossamia*, and *Vincentia* have 9 epipleural ribs. Eight epipleural ribs are present in *Apogon* (*Brephamia*), *Apogon* (*Paroncheilus*), *Apogon* (*Pristiapogon*), *Apogon* (*Ostorhinchus*), *Apogon* (*Zapogon*), *Apogonichthys*, *Archamia*, *Astrapogon*, *Foa*, *Fowleria*, *Holapogon*, *Phaeoptyx*, *Siphamia*, *Sphaeramia*, and the pseudamine genus *Paxton*. *Coranthus*, *Rhabdamia* (*Bentuviaichthys*), and *Rhabdamia* (*Rhabdamia*) have 7 epipleural ribs. The pseudamine genus *Gymnapogon* has 6 epipleural ribs. Depending on the species, *Pseudamia* has 5 or 6 epipleural ribs. *Lachneratus* has three epipleural ribs and *Cercamia* and *Pseudamiops* have only two epipleural ribs. Depending on the species, *Apogon* (*Apogon*) has 8 or 9 epipleural ribs. Also depending on the species, *Cheilodipterus* has 7 or 8 epipleural ribs. The monotypic *Rhabdamia* (*Verulux*) exhibits variation in this character, with individuals having either 5 or 6 epipleural ribs. Because x-ray images were used to examine the osteological characters, instead of cleared and stained specimens, it was not possible to determine how many epipleural ribs were present in *Pterapogon* (*Pterapogon*) and *Pterapogon* (*Quinca*). Epipleurals are present on at least the first six pleural ribs in *Pterapogon* (*Pterapogon*) and on at least the first two vertebrae and five pleural ribs in *Pterapogon* (*Quinca*) (Fraser, 1972). Because it was impossible to determine if epipleurals were present on additional vertebrae and pleural ribs, this character was coded as uncertain for these taxa.

Median Fins

Predorsals (*A.14*, *B.27*, *C.27*). – (0) 3 predorsals; (1) 2 predorsals; (2) 1 predorsals; (3) 0 predorsals. Smith and Bailey (1961) suggested that predorsal bones are derived from pterygiophores that once bore either spines or rays. Fraser (1972) has argued that they are supraneurals. The true identity of these structures has yet to be determined. The presence of three predorsals is common among percoids and has therefore, been considered the primitive condition (Johnson, 1984; Baldwin and Johnson, 1999). Loss of one or more predorsals is common in the Apogonidae (Fraser, 1972). Predorsals are absent in *Cercamia* (Randall and Smith, 1988; Hayashi, 1991) and *Lachneratus* (Fraser and Struhsaker, 1991) and in two pseudamine genera, *Gymnapogon* and *Paxton* (Baldwin and Johnson, 1999).

First pterygiophore (*A.15*, *B.28*, *C.28*). – (0) two spines on first pterygiophore; (1) one spine on first pterygiophore. Apogonids with eight or nine visible first dorsal-fin spines always have two spines on the first pterygiophore. Species with seven visible first dorsal-fin spines always have one spine on the first pterygiophore (Fraser, 1972). The latter condition has been treated as derived within the Apogonidae (Fraser, 1972).

Eighth dorsal-fin spine (*A.16*, *B.29*, *C.29*). – (0) visible externally; (1) reduced or hidden; (2) absent. There is a trend for the reduction and loss of the eighth dorsal-fin spine within the Apogonidae. This reduction is accompanied by a series of changes in the structures of the supporting pterygiophores, pterygiophores eight and nine, that lead to the complete division of the dorsal fins. Evidence from the examination of living and fossil beryciforms suggests that the spinous elements of the dorsal fin are continuous with the rayed elements (Patterson, 1964, 1967). In kurtids, pempherids, and several other lower percoids, the dorsal fin is deeply notched (Fraser, 1972). Over the course of evolution, the loss of the eighth fin spine and its supporting elements has resulted in two separate dorsal fins. Because the dorsal fin morphology of apogonids varies from deeply notched to widely separate, all conditions, except those with an externally visible eighth dorsal-fin spine and well-developed support elements, were treated as derived among the Apogonidae by Fraser (1972). The eighth spine is absent in most apogonids. The spine is much reduced, and may be hidden by skin and scales, in species of *Apogon* (*Apogon*), *Apogonichthys*, *Astrapogon*, *Fowleria*, *Holapogon*, and *Vincentia.* It is, however, fully developed and visible in species of *Neamia.* Notably in apogonids the first two dorsal-fin spines lack supporting pterygiophores. The third spine is serially supported by a pterygiophore and the first two spines are supported metamerically by that same pterygiophore (Fraser, 1972; Gon, 1996). Thus, the literature describes this character as either the eighth dorsal-fin spine (Fraser, 1972; Gon, 1996) or the fin spine associated with the sixth dorsal pterygiophore (Baldwin and Johnson, 1999).

Pectoral Girdle

Posttemporal (*A.17*, *B.30*, *C.30*). – (0) smooth; (1) weakly serrate; (2) serrate; (3) with spine. The condition of the posterior margin of the posttemporal bone varies from smooth to serrate in apogonids. *Apogon* (*Brephamia*), *Apogon* (*Paroncheilus*), *Apogon* (*Yarica*), *Apogon* (*Zapogon*), *Apogon* (*Zoramia*), *Apogonichthys*, *Astrapogon*, *Cheilodipterus*, *Foa*, *Fowleria*, *Glossamia*, *Neamia*, *Phaeoptyx*, *Rhabdamia*

(*Bentuviaichthys*), *Rhabdamia* (*Rhabdamia*), *Rhabdamia* (*Verulux*), *Vincentia* and the four pseudamine genera have a smooth margin on the posttemporal bone. The posttemporal margin in *Apogon* (*Apogon*) and *Apogon* (*Jaydia*) is weakly serrate. The posttemporal margin is smooth to weakly serrate in *Apogon* (*Pristicon*) and *Siphamia*. *Apogon* (*Lepidamia*), *Archamia* and *Sphaeramia* have a serrate posterior posttemporal edge. *Cercamia*, *Coranthus*, and *Holapogon* have one or more spines emanating from the posterior margin of the posttemporal.

Postcleithrum (*B.31*, *C.31*). – (0) 2 postcleithra; (1) 1 postcleithrum. Among the apogonids only *Gymnapogon* and *Paxton* possess only one postcleithrum (Baldwin and Johnson, 1999). All other apogonids have two postcleithra (Fraser, 1972).

Caudal Skeleton

Autogenous haemal spines (*B.32*, *C.32*). – (0) 2 pairs; (1) 1 pair; (2) absent. Beryciforms have at least two autogenous haemal spines. Gosline (1960, 1961) considered that the evolution of the caudal skeleton in teleosts is mainly a progressive simplification resulting from the fusion of parts. And thus, the fusion of the spines to their respective neural arches has been treated as derived within the Apogonidae. Fusion occurs first with pre-ural centrum 2 and then with pre-ural centrum 1 (Fraser, 1972). Autogenous haemal spines are absent in *Cercamia, Lachneratus, Paxton, Pseudamia, Rhabdamia* (*Bentuviaichthys*), *Rhabdamia* (*Rhabdamia*), and *Rhabdamia* (*Verulux*). There are 0 to 1 autogenous haemal spines in *Siphamia* and *Gymnapogon*. All other apogonids have 2 autogenous haemal spines (Fraser, 1973; Baldwin and Johnson, 1999).

Epurals (*B.33*, *C.33*). – (0) 3 epurals; (1) third epural reduced; (2) 2 epurals. Beryciforms possess three epurals. Johnson (1984) considered that three epurals seemed to be primitive in the percoids. In several apogonid genera, the number of epurals is reduced. Patterson (1968) found that in some lower percoids the reduction of the number of epurals occurred because the first epural fused with the second pre-ural neural arch. This does not appear to be the mechanism responsible for the reduction in the number of these bones in the Apogonidae. Fraser (1972) considered that the shape of the pre-ural neural arch does not indicate fusion with another bone. Instead, he proposed that the reduction in the number of epurals in apogonids occurs because of the reduction and loss of the third epural bone. The number of epurals is reduced to two in *Gymnapogon*, *Paxton*, *Pseudamia*, *Pseudamiops*, *Rhabdamia* (*Verulux*), and some species of *Siphamia* by the reduction and/or loss of the third bone. All other apogonids have three epurals.

Uroneurals (*A.18*, *B.34*, *C.34*). – (0) 2 pairs; (1) 1 pair; (2) 1 reduced pair; (3) absent. The beryciform caudal skeleton has two pairs of uroneurals. These bones undergo reduction and loss in the Apogonidae. The most primitive (i.e. most similar to the beryciform structure) perciform caudal skeleton is found in *Kuhlia sandvicensis* (Steindachner, 1876). The principal difference between the caudal skeleton of a beryciform and that of *K. sandvicensis* is a reduction in the number of branched caudal rays and the presence of a single urostylar ossification in *K. sandvicensis* (Gosline, 1961). The caudal skeletons of serranids are similarly complex and they are therefore considered to be fairly primitive perciforms. The significant difference between these caudal skeletons is that the two pairs of uroneurals that are present in *K. sanvicensis* are fused in serranids. Gosline (1961) compared the uroneurals of a serranid species of the genus *Epinephelus* Bloch, 1793 with *Apogon snyderi* Bleeker, 1856[a] and found that in comparison to the fused uroneurals of a serranid, those of *A. snyderi* were reduced to two rudimentary ossicles embedded in the flesh dorsal of the urostyle. Through these comparisons Gosline showed that the posterior-most pair of uroneurals is lost first. Fusion with the ural centrum does not occur but, in those fishes known to have reduced numbers of uroneurals, the second pair is thin and its fusion with the first pair cannot be ruled out. The first pair, being also small, disappears after the posterior-most pair. Within the Apogonidae, only *Coranthus* and *Holapogon* have two pairs of uroneurals. One pair of uroneurals is present in *Apogon* (*Lepidamia*), *Apogon* (*Pristicon*), *Apogon* (*Yarica*), *Apogon* (*Zapogon*), *Apogon* (*Zoramia*,) *Apogonichthys*, *Archamia*, *Cheilodipterus*, *Fowleria*, *Glossamia*, *Pterapogon* (*Pterapogon*), and *Pterapogon* (*Quinca*). *Ostorhinchus*, *Foa*, *Neamia*, *Rhabdamia* (*Bentuviaichthys*), *Sphaeramia*, *Vincentia*, and *Pseudamia* all have one reduced pair of uroneurals. Uroneurals are absent in *Apogon* (*Apogon*), *Apogon* (*Brephamia*), *Apogon* (*Paroncheilus*), *Apogon* (*Pristiapogon*), *Astrapogon*, *Cercamia*, *Gymnapogon*, *Lachneratus*, *Paxton*, *Phaeoptyx*, *Pseudamiops*, *Rhabdamia* (*Rhabdamia*), *Rhabdamia* (*Verulux*), and *Siphamia*. The uroneurals in species of *Apogon* (*Jaydia*) occur as either a single, reduced pair or are absent.

Parhypural (*B.35*, *C.35*). – (0) free; (1) fused. Beryciforms have a free parhypural. This bone is fused to the lower hypural plate in *Gymnapogon* and *Paxton*, but is free in all other apogonids

Hypurals (*B.36*, *C.36*). – (0) 5 hypurals; (1) 4 hypurals; (2) 3 hypurals; (3) 2 hypurals. The beryciform caudal skeleton is characterized by 6 hypurals. The most primitive percoid caudal skeleton includes 5 hypurals. In the Apogonidae the most common number of hypurals is 5. The number of hypurals is reduced in some species by the fusion of adjacent hypurals into plates (Fraser, 1972). Hypurals 1 and 2 fuse forming a lower plate and hypurals 3 and 4 fuse forming an upper plate. Those species with a fused upper plate also have a fused lower hypural plate suggesting that hypurals 1 and 2 tend to fuse first over the course of evolution. This morphology is present in *Astrapogon*, *Cercamia*, *Neamia*, *Phaeoptyx*, *Pterapogon* (*Pterapogon*), and *Siphamia*. *Paxton* is unique among the Apogonidae as its fifth hypural is also fused to the plate formed from the fusion of hypurals 3 and 4 (Baldwin and Johnson, 1999). In all other apogonids, hypural 5 is free. In *Lachneratus*, *Rhabdamia* (*Bentuviaichthys*), *Rhabdamia* (*Rhabdamia*), and *Rhabdamia* (*Verulux*) hypurals 1, 2, 3, and 4 are fused into one large fan-shaped plate.

Fusion of hypural plate to ural centrum (*B.37*, *C.37*). – (0) not fused to centrum; (1) upper plate/hypural 4 fused to centrum; (2) lower plate fused to centrum; (3) both plates fused to centrum. Fusions can occur between hypural 4 and the ural centrum, or between the plate formed from the fusion of hypurals 3 and 4 and the ural centrum (Fraser, 1972). Hypural 4 is fused to the ural centrum in *Apogonichthys*. The upper hypural plate, formed from hypurals 3 and 4 (and 5 in the case of *Paxton*), is fused to the ural centrum in *Astrapogon*, *Gymnapogon*, *Neamia*, *Paxton*, *Pseudamiops*, and *Siphamia*. Both plates are fused to the ural centrum in *Cercamia*, *Rhabdamia* (*Bentuviaichthys*), *Rhabdamia* (*Rhabdamia*), and *Rhabdamia* (*Verulux*).

Secondary caudal rays (*B.38*, *C.38*). – (0) segmented; (1) fused. In beryciforms, the secondary rays in the caudal fin are true spines (Patterson, 1968). In perciforms, the secondary caudal rays are typically segmented with separate right and left halves (Fraser, 1972). These usually segmented rays are fused in *Cercamia*, *Pterapogon* (*Pterapogon*), *Pterapogon* (*Quinca*), and *Sphaeramia*. When fused, the rays are indistinguishable from spines.

Caudal fin shape (*A.19*, *B.39*, *C.39*). – (0) forked; (1) truncate; (2) rounded. The principal caudal rays of apogonids generally form a forked shape, but may also be truncate or rounded (Fraser, 1972). Gon (1996) cited the rounded morphology as a synapomorphy within *Apogon* for the *Apogon* (*Jaydia*) species. Some *Ostorhinchus* and *Glossamia* species, and all *Apogonichthys*, *Astrapogon*, *Foa*, *Fowleria*, *Neamia*, *Pseudamia*, and *Pseudamiops* have rounded caudal fins. Some species of *Cheilodipterus*, *Apogon* (*Yarica*), *Coranthus*, *Holapogon*, *Paxton*, and *Vincentia* have truncate caudal fins. All other apogonids have forked caudal fins.

Squamation

Scale type (*B.40*, *C.40*). – (0) ctenoid; (1) weakly ctenoid; (2) cycloid; (3) absent. Because beryciform fishes have ctenoid scales, Fraser (1972) considered ctenoid scales to be the primitive condition in the Apogonidae. He considered weakly ctenoid and cycloid scales to be more derived. Scanning electron micrographs have revealed that all scales traditionally classified as ctenoid are not the same (Johnson, 1984). The ctenii of beryciforms and of many percoids are structurally different and most likely formed via different mechanisms, and are therefore not homologous (Johnson, 1984). *Cercamia*, *Rhabdamia* (*Bentuviaichthys*), *Rhabdamia* (*Rhabdamia*), *Rhabdamia* (*Verulux*), and *Siphamia* have weakly ctenoid to cycloid scales. *Apogon* (*Paroncheilus*), *Astrapogon*, *Lachneratus*, *Pseudamia*, and *Pseudamiops* have cycloid scales. *Gymnapogon* and *Paxton* lack scales. All other apogonids have ctenoid scales.

Deciduousness of scales (*B.41*, *C.41*). – (0) not deciduous; (1) deciduous. Deciduous scales are rare among apogonids and for that reason have been considered a derived state (Baldwin and Johnson, 1999; Fraser, 1972). *Cercamia*, *Lachneratus*, and *Pseudamia* have deciduous scales.

Scale size (*A.20*, *B.42*, *C.42*). – (0) large scales (9-12); (1) medium-sized scales (22-28); (2) small scales (25-50). The relative size of scales is inferred from the number of scales in the complete lateral line. *Pseudamiops* has large scales. *Apogon* (*Lepidamia*), *Apogon* (*Zapogon*), *Glossamia*, and *Pseudamia* have small scales. The remaining apogonids have medium-sized scales. For those species with an incomplete lateral line, the scale size is scored as medium unless otherwise observed or referenced in the literature.

Lateral line

Lateral line (*B.43*, *C.43*). – (0) complete; (1) incomplete; (2) absent. Most apogonids have complete lateral lines with pored scales extending onto the base of the caudal fin. *Apogon* (*Brephamia*), *Foa*, and *Pseudamia* have incomplete lateral lines. Some species of *Fowleria* have complete lateral lines but others have incomplete lateral lines. This taxon was therefore coded as both complete and incomplete. The lateral line is absent in *Cercamia*, *Gymnapogon*, *Paxton*, and *Pseudamiops*. In *Vincentia*, the lateral-line scales on the caudal fin are fused into one large scale with numerous pores. Although this is an interesting autapomorphy of this species it was not included in the analysis.

Bioluminescence

Bioluminous organs (*B.44*, *C.44*). – (0) absent; (1) bacterial; (2) enzymatic. Several apogonid species possess light organs; however, the light-producing mechanisms differ among them. The bioluminescent organs of *Siphamia* are bacterial whereas those of a number of the (*Apogon*) *Jaydia* species are based on a luciferin-luciferase enzymatic mechanism. All species of *Siphamia* possess bioluminescent organs; this character is considered synapomorphic for the group (Iwai, 1958, 1959; Fraser, 1972). Gon's (1996) phylogenetic analysis of the *Jaydia* subgenus suggested that the group's most primitive species all possess bioluminescent organs, whereas the most advanced species do not. The most parsimonious explanation for this character distribution is a secondary loss of the light producing ability; therefore, the subgenus is coded as if all species possess this organ.

Assessment of Relationships Within *Apogon*

Cladistic analysis yielded 23 most parsimonious cladograms. The most parsimonious cladogram was 55 steps long. A strict consensus of these cladograms is given in Figure 40. For the sake of clarity, only subgeneric names will be used to label the termini of the clades presented in this dissertation. This cladogram has a consistency index of 0.6545, retention index of 0.5366, and a rescaled consistency index of 0.3512.

Cladistic Analysis of the Apogonidae

Cladistic analysis yielded 866 most parsimonious cladograms. The most parsimonious cladogram was 209 steps long. A strict consensus of these cladograms is given in Figure 41. This cladogram has a consistency index of 0.4689, retention index of 0.6186, and a rescaled consistency index of 0.2900. The strict consensus and semi-strict consensus cladograms are topologically identical. A 75% majority-rule consensus cladogram is given in Figure 42.

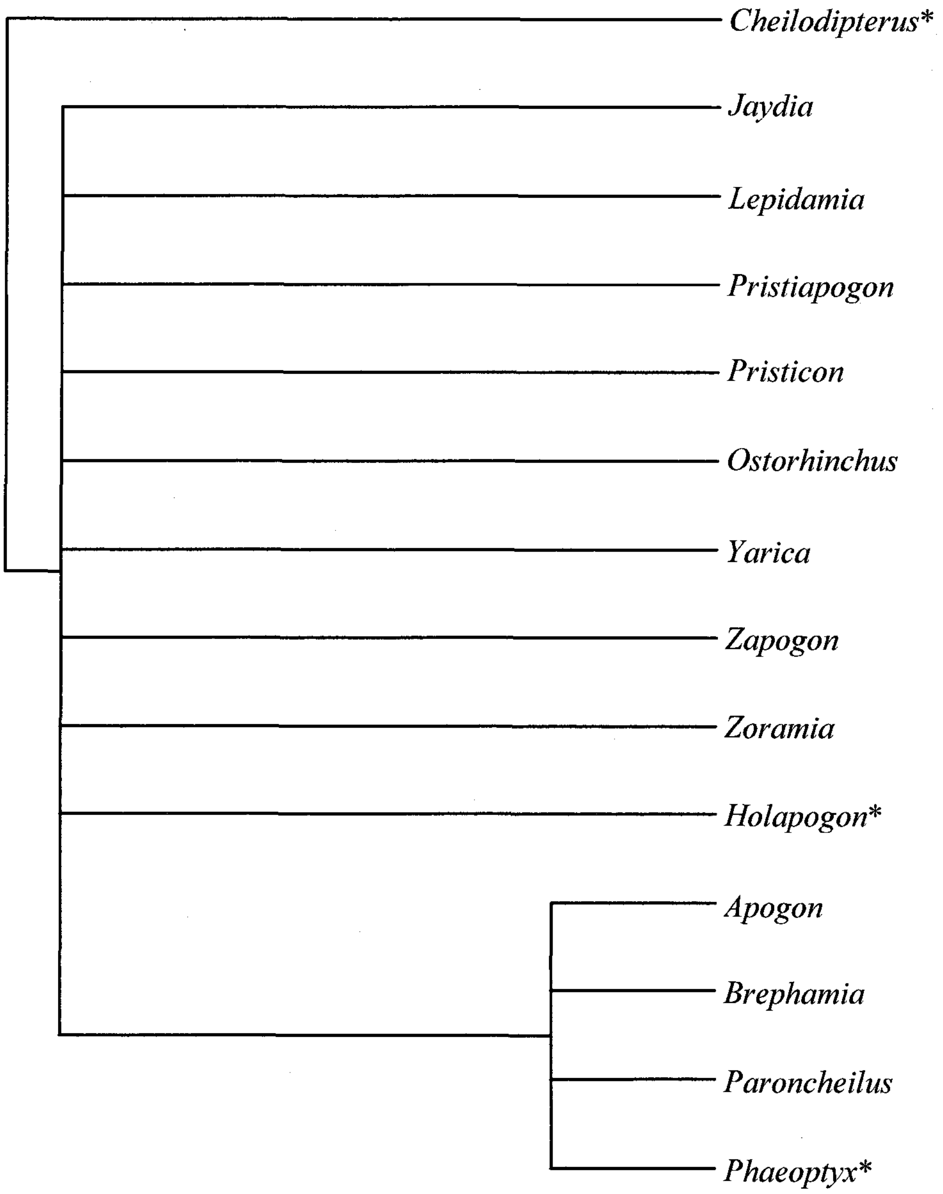


Figure 40. Strict consensus of 23 cladograms generated by parsimony analysis of 20 osteological and morphological characters for 11 *Apogon* subgeneric ingroup taxa and three putative outgroup apogonid taxa (indicated by an asterisk).

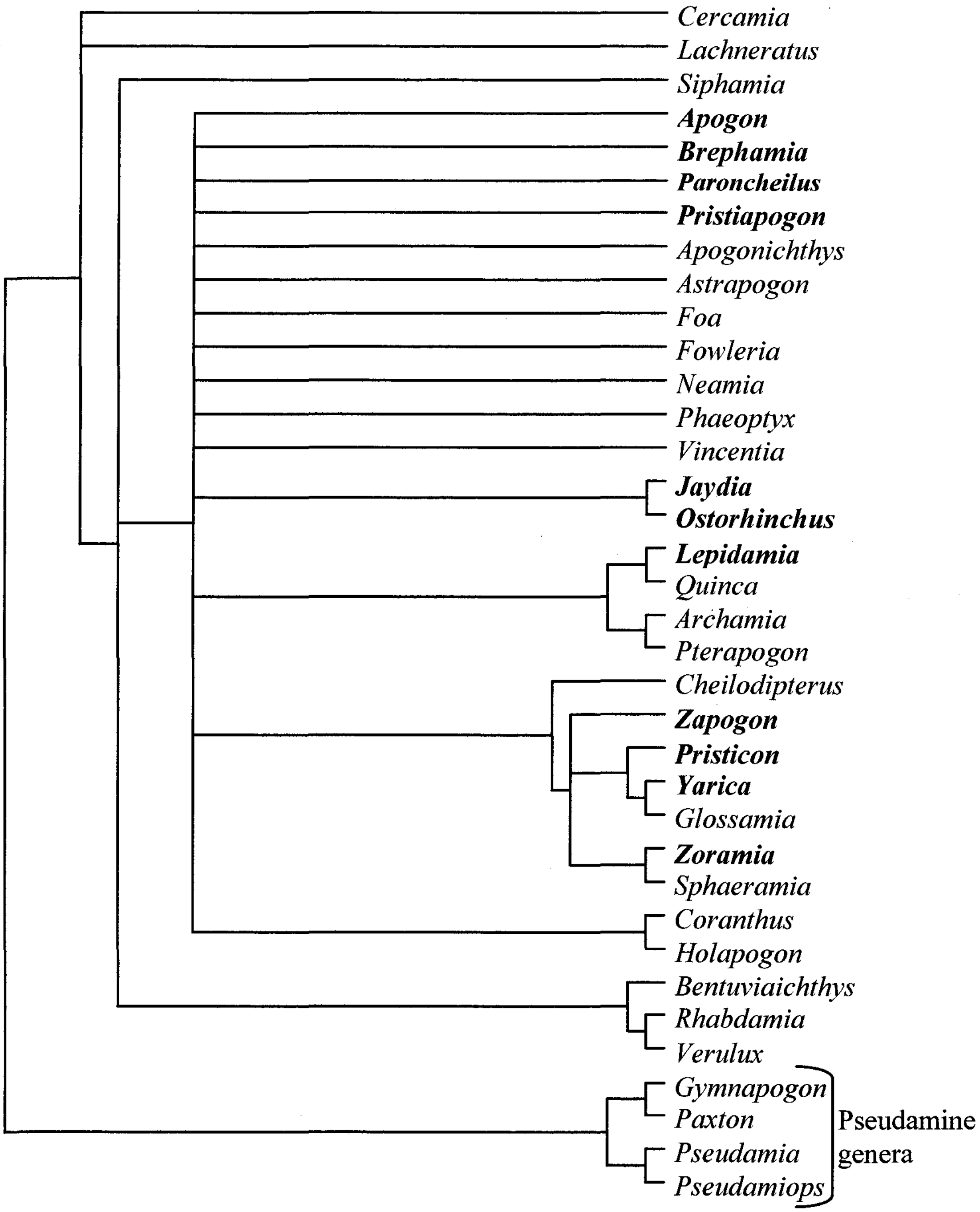


Figure 41. Strict consensus of 866 most parsimonious cladograms generated by parsimony analysis of 44 osteological and morphological characters for 36 apogonine ingroup taxa and four pseudamine outgroups taxa. The names of the *Apogon* subgenera are in bold.

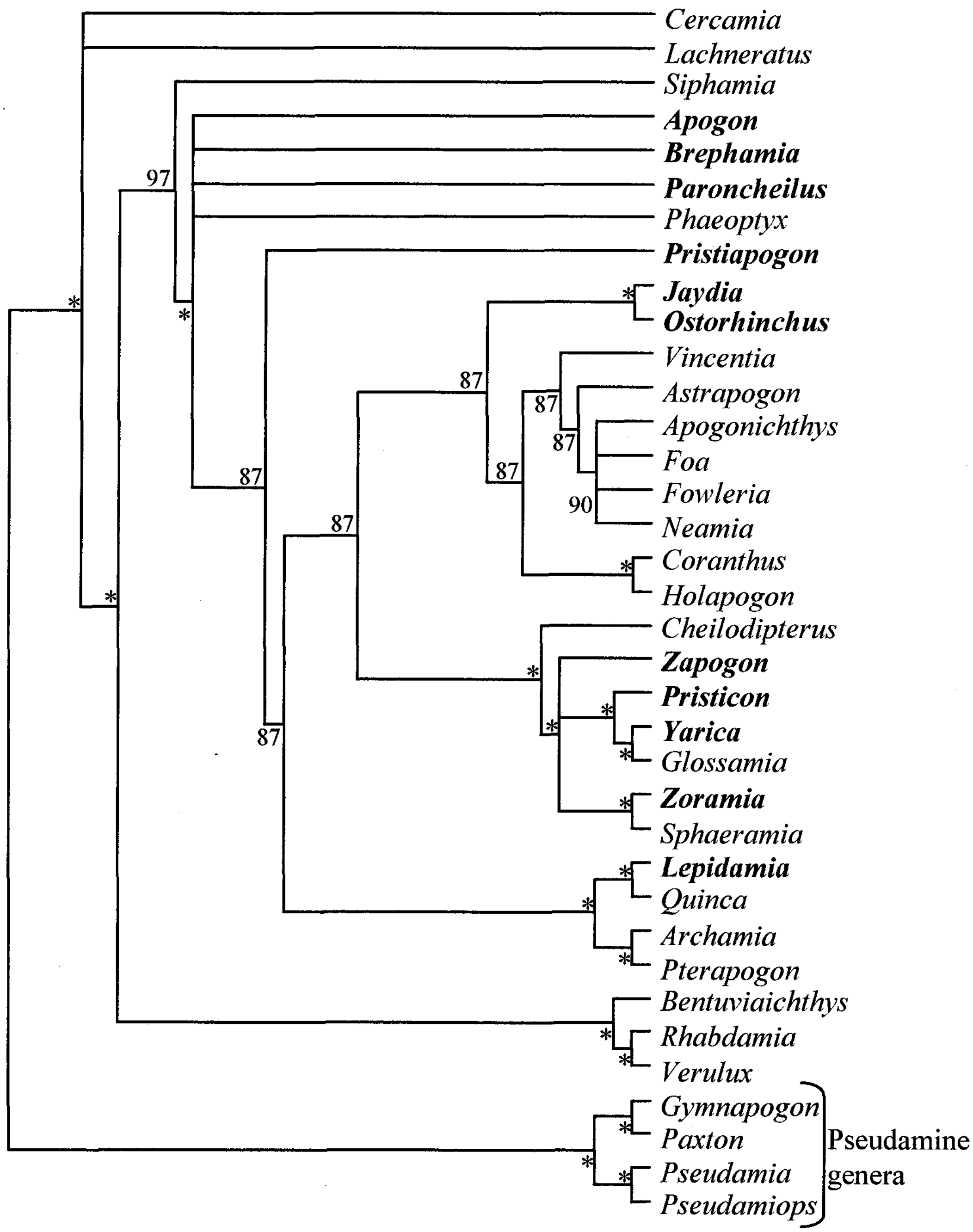


Figure 42. 75 % majority rule consensus tree generated by parsimony analysis of 44 osteological and morphological characters for 36 apogonine ingroup taxa and four pseudamine outgroup taxa. The names of the *Apogon* subgenera are in bold. Asterisks indicate nodes resolved in 100 % of the cladograms. The numbers alongside the nodes equate to the percentage of cladograms in which the node was resolved.

Discussion

Assessment of the Relationships Within *Apogon*

Cladistic analysis resulted in 23 most parsimonious cladograms. All of the cladograms suggest that the genus *Apogon* is not monophyletic as it is currently defined. Two of the three outgroups consistently nest within the ingroup. In all cladograms, *Phaeoptyx* nested within a clade containing *Apogon* (*Apogon*), *Apogon* (*Brephamia*), and *Apogon* (*Paroncheilus*). *Holapogon* was also positioned within *Apogon*, as a member of the clade containing the remaining *Apogon* subgenera.

The terminal branches of each of the alternate topologies are marked by more numerous character state transformations (39 of the 55 character state changes) than are the branches leading to the cladograms' internal nodes (Figure 43). This is to be expected, as the analysis must join the provided taxa, even in situations where the ingroup taxon is not monophyletic. Given that *Apogon* may represent an unnatural taxon and therefore, several of the closest relatives of the ingroup taxa may be absent, one could predict that many changes would be required along each terminal branch in order to allow for the cladograms' internal topology.

Of importance to this argument is the fact that the subgenera of *Apogon* are distinguished among and defined by the same characteristics used to diagnose the different apogonid genera. And thus, fairly relaxed and most likely plesiomorphic characters define the genus. This analysis failed to reveal any characters that could be considered synapomorphies of *Apogon* sensu lato. There is no viable argument to uphold the taxon's monophyly; it is quite likely that future research will reveal that it is phylogenetically more accurate to treat some or all of the *Apogon* subgenera as genera.

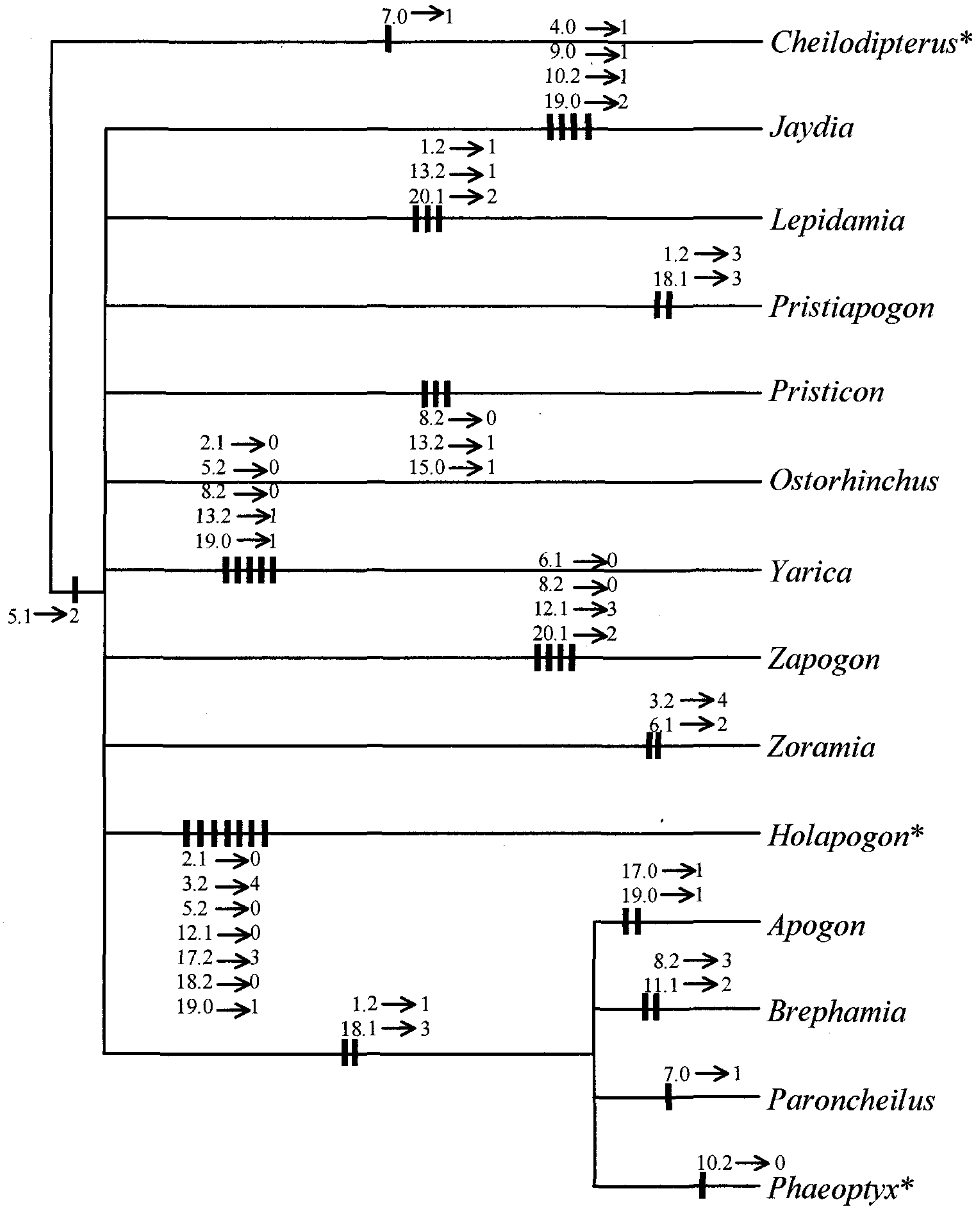


Figure 43. Strict consensus of 23 cladograms generated by parsimony analysis of 20 osteological and morphological characters for 11 *Apogon* subgeneric ingroup taxa and three putative outgroup apogonid taxa (indicated by an asterisk). Selected character state changes are indicated on the branches.

Cladistic Analysis of Fraser's Data for the Entire Family

The consistency and retention indices indicate high levels of homoplasy in the data set. Only 44 characters, distilled from Fraser's data set, were used for the analysis of a 32 taxon ingroup. The relatively small number of characters, combined with the high levels of homoplasy, resulted in a large number of weakly supported cladograms. In spite of these weaknesses, many nodes remain resolved in the consensus trees. The phylogenetic hypotheses obtained in this study support the monophyly of the Apogoninae and the monophyly of the Pseudaminae.

It is accepted that some of the relationships cannot be satisfactorily resolved at this time, and so, the discussion will focus on those aspects of the cladograms that are consistently revealed among the most parsimonious trees. Clades are arbitrarily named by assigning each (with the exception of the Apogoninae and Pseudaminae subfamilies) a two-part name consisting of the names of the first and last taxon in the clade. The numbers of the characters, corresponding to the numbering in the data matrix (Appendix B), are given in parentheses.

Apogoninae. – Monophyly of this subfamily is supported by the cladistic analysis. Four character state changes occur along the branch leading to the group: intercalary facet included on the otic bulla (B.5; reverses two times within the Apogoninae), band of villiform teeth on the palatine reduced to a single row (B.12; character state changes numerous times within Apogoninae), fusion of hypural plates 1 and 2 (B.36; character state changes numerous times within the Apogoninae), and medium-sized scales (B.42; small scales in *Apogon* (*Lepidamia*), *Glossamia*, and *Apogon* (*Zapogon*)) (Figure 44).

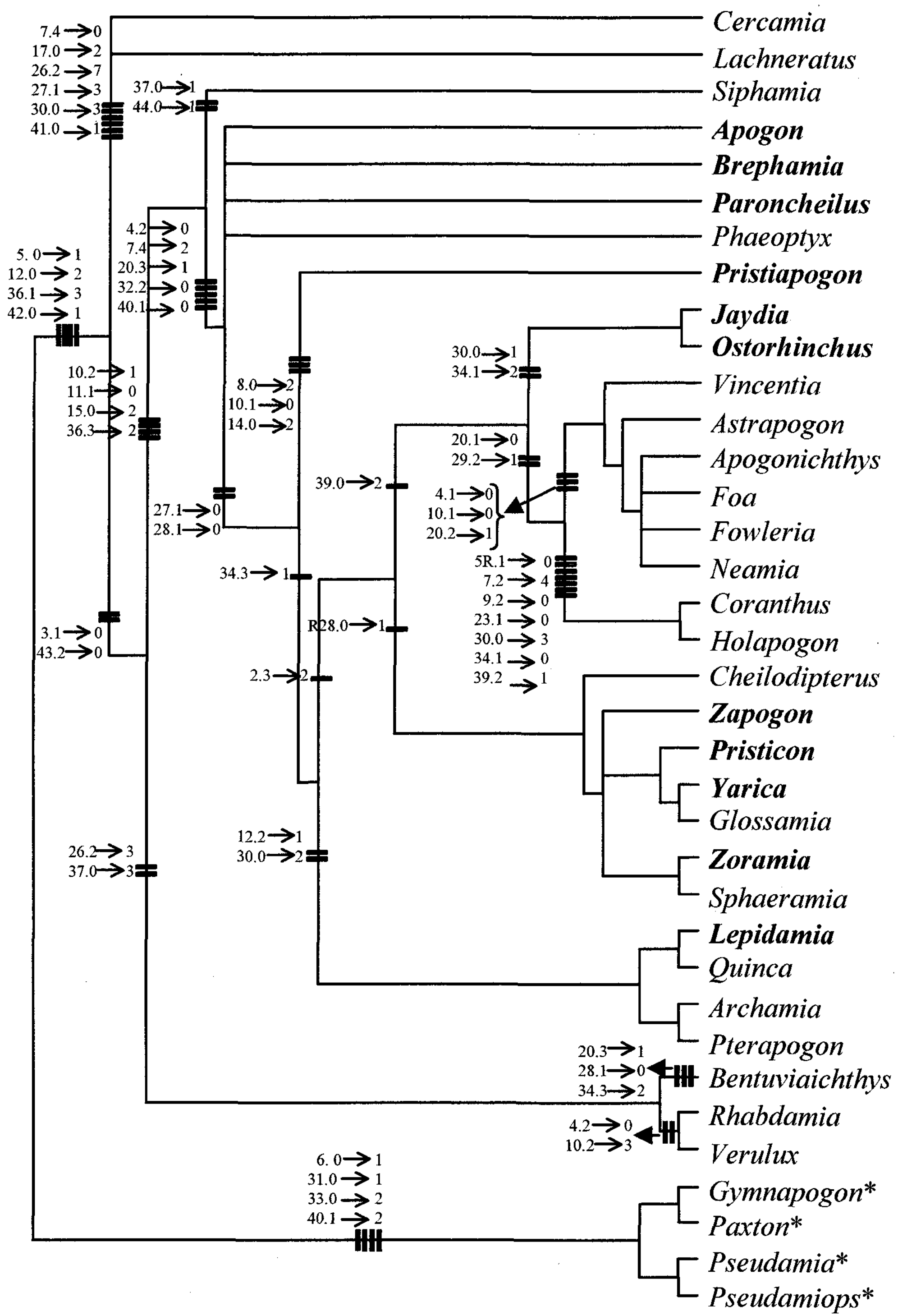


Figure 44. 75% majority-rule consensus cladogram of 866 trees for 32 apogonine ingroup taxa and four pseudamine apogonid taxa. Selected character state changes are indicated on the branches. Reversed characters are indicated with an "R" after the character number, and homoplasious changes are indicated by open rather than solid bars.

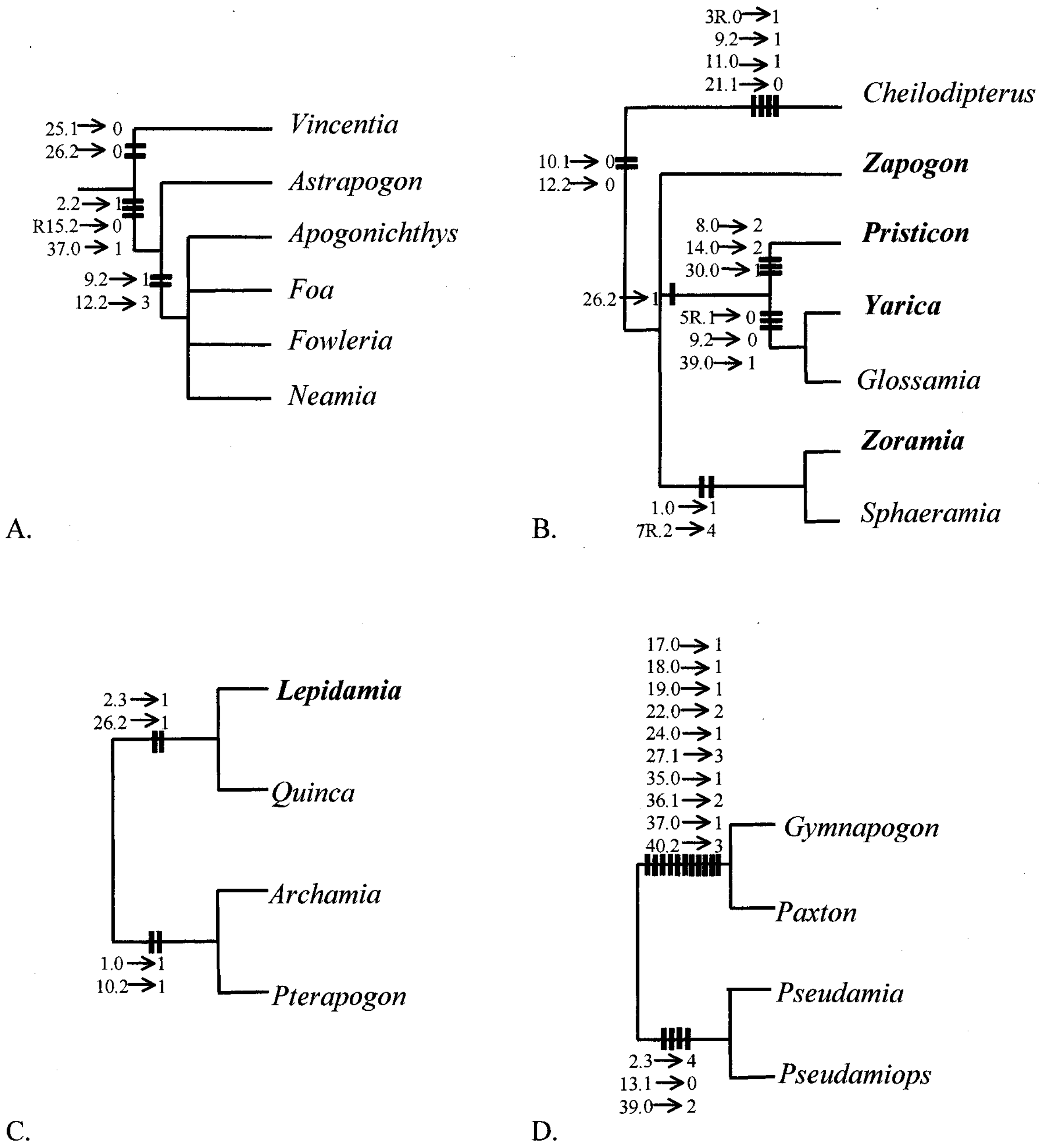


Figure 45. Selected clades from 75% majority-rule consensus cladogram with character states changes labeled on the branches. A. *Vincentia—Neamia* clade, B. *Cheilodipterus—Sphaeramia* clade, C. *Lepidamia—Pterapogon* clade, D. *Gymnapogon—Pseudamiops* clade. Reversed characters are indicated with an "R" after the character number, and homoplasious changes are indicated by open rather than solid bars.

Cercamia – Lachneratus clade. – The analysis resulted in *Cercamia* and *Lachneratus* forming an unresolved clade that is sister to the remaining apogonine taxa. Six character state changes occur along the branch leading to this group: shelf present on all infraorbitals (B.7; character states changes several times within the Apogoninae), spines present on the edge of the preopercle (B.17), 3 epipleural ribs (B.26), no predorsals (B.27), posttemporal with a spine (B.30), and the presence of highly deciduous scales (B.41) (Figure 44). *Cercamia* is distinguished from *Lachneratus* by the presence of a single row of villiform teeth on the vomer and jaws (B.2, B.10), absence of canines on the jaws (B.11), absence of villiform teeth on the palatine (B.12), presence of gill-rakers on the first and second gill arch (B.24), 9 + 15 vertebrae (B.25), two epipleural ribs (B.26), fused secondary caudal rays (B.38), and the presence of weakly ctenoid scales (B.40; versus cycloid scales in *Lachneratus*). It has been proposed that a close evolutionary relationship exists between *Cercamia* and the *Rhabdamia* subgenera (Fraser and Struhsaker, 1991; Hayashi, 1991). Fraser and Struhsaker (1991) suggested that *Lachneratus*i s more closely related to *Cercamia* than to the *Rhabdamia* subgenera. The results of this research indicate that *Lachneratus*is more closely related to *Cercamia* than either genus is to the *Rhabdamia* subgenera.

Siphamia – Verulux clade. – Two character state changes occur on the branch leading to this clade: the absence of canines on the vomer (B.3; character reverses in *Coranthus* and *Cheilodipterus*) and a complete lateral line (B.43; character reverses in *Apogon* (*Brephamia*), *Foa*, and *Fowleria*) (Figure 44). In contrast to *Cercamia*, *Lachneratus*, and the pseudamine genera, members of this clade also lack a spine on the preopercular edge (B.18) and have fixed scales (B.42).

Rhabdamia – Verulux clade. – The cladograms generated in this analysis support the monophyly of the *Rhabdamia* genus as it is currently defined. The cladograms also suggest that structure exists within the genus, and give support to its division into three subgenera. Two character state changes occur along the branch leading to this clade: the presence of seven epipleural ribs (B.26) and the fusion of the first four hypurals into an upper and lower hypural plate (B.37) (Figure 44). *Rhabdamia* (*Bentuviaichthys*) is distinguished from *R.* (*Rhabdamia*) and *R.* (*Verulux*) by the presence of a deeply notched ceratohyal (B.20), two spines on the first pterygiophore (B.28), and one reduced pair of uroneurals (B.34) (Figure 44). Two characters support the *R.* (*Bentuviaichthys*) and *R.* (*Verulux*) clade: the presence of a basisphenoid (B.4) and a single row of villiform teeth on the jaws (B.10) (Figure 44). *Rhabdamia* (*Rhabdamia*) is distinguished from *R.* (*Verulux*) by the presence of a shelf on the third infraorbital (B.7), presence of two predorsals (B.27; versus one predorsal in *R.* (*Verulux*)), and the presence of three epurals (B.33; the number of epurals is reduced to two in *R.* (*Verulux*)).

Siphamia – Pterapogon clade. – Four character state changes occur on the branch leading to the group: the presence of a band of villiform teeth in jaws (B.10, character state changes several times within clade), absence of canines on the jaws (B.11; character undergoes homoplastic changes, as canines are present in some *Apogon* (*Paroncheilus*) species, *Coranthus*, and *Cheilodipterus*), a serrate preopercular edge (B.15; character reverses on branch leading to *Astrapogon* – *Neamia* clade) (Figure 45A), and three hypurals (B.36; character state changes several times within clade) (Figure 44). This clade is also characterized by an increase in the number of epipleurals from the maximum number of seven present in some *Rhabdamia* taxa (B.26) and a complete lateral line (B.43; the lateral line is either incomplete or absent in members of the *Rhabdamia* clade, *Cercamia*, *Lepidamia*, and the pseudamine genera). *Siphamia* is distinguished from the remainder of the clade by the fusion of the upper hypural plate to the ural centrum (B.37) and the presence of bacterial bioluminescent organs (B.44).

Apogon – *Pterapogon clade*. – This 26 taxon clade is characterized by five characters: the presence of a developed basisphenoid (B.4; reduced in the *Vincentia* – *Neamia* clade), a shelf on the third infraorbital (B.7; shelf on the third, fourth, and fifth infraorbitals in *Fowleria*, shelf absent in *Apogon* (*Zoramia*) and *Sphaeramia*), a notched ceratohyal (B.20), two autogenous haemal spines (B.32), and the presence of ctenoid scales (B.40; cycloid scales are present in *Astrapogon* and *Apogon* (*Paroncheilus*)) (Figure 44). In contrast to *Cercamia*, *Lachneratus*, the *Rhabdamia* clade, and the pseudamine genera, members of this clade lack fusion among the hypurals (B.36; character changes in *Astrapogon*, *Neamia*, *Pterapogon* (*Pterapogon*)). The relationship between *Phaeoptyx* and the rest of the clade is unresolved in the consensus cladograms; however, in a number of the most parsimonious trees *Phaeoptyx* was positioned as basal to the remainder of the clade. Fusion of the hypurals supports this topology (B.36). In *Phaeoptyx* the upper and lower hypurals are fused into two hypural plates, resulting in three total hypurals. In the remaining taxa of the *Apogon* – *Pterapogon* clade the common morphology (*Astrapogon*, *Neamia*, and *Pterapogon* (*Pterapogon*) also have the fused three-hypural morphology) is the unfused condition, or five hypurals.

Pristiapogon – Pterapogon clade. –Two spines on the first pterygiophore (B.28; reverses in the *Cheilodipterus – Sphaeramia* clade; *Astrapogon* and *Archamia* also have one spine on the first pterygiophore) and the retention of three predorsals (B.27; *Astrapogon*, *Zapogon*, and *Pterapogon* have two predorsals) support this node (Figure 44). The other genera in the *Apogon – Pterapogon* clade have two predorsals. Species of *Rhabdamia* (*Rhabdamia*) have either one or two predorsals. *Cercamia* and *Lachneratus* have lost all of the predorsal bones. The Pseudaminae have taxa that express all character states, but it is most common for them to have a reduced number of predorsal bones, i.e. fewer than three. *Apogon* (*Pristiapogon*), *Apogon* (*Jaydia*), and *Apogon* (*Pristicon*) all have infraorbitals with serrate edges, representing three independent origins of this character on the cladogram (B.8) (Figure 44 and Figure 45B). These three taxa also possess a serrate preopercular ridge (B.14) (Figure 44 and Figure 45B). *Apogon* (*Pristiapogon*) is further distinguished from the remainder of the clade by the presence of a wide band of villiform teeth on the jaws (B.10). *Cheilodipterus* and the taxa in the *Vincentia — Neamia* clade, with the exception of *Neamia*, also share this condition. *Neamia* species have a medium-width band of villiform teeth on the jaws.

Jaydia – Pterapogon clade. – This clade is characterized by the presence of a single uroneural (B34; uroneural is reduced in *Apogon* (*Jaydia*), *Apogon* (*Ostorhinchus*), *Foa*, and *Apogon* (*Lepidamia*), and is absent in *Astrapogon*; *Coranthus* and *Holapogon* have two uroneurals) (Figure 44).

Jaydia – Sphaeramia clade. – This clade is characterized by the presence of a narrow band of villiform teeth on the vomer (B.2; character state changes on branch leading to *Astrapogon – Neamia* clade, the *Astrapogon – Neamia* clade is characterized by a medium-width band of villiform teeth on the vomer) (Figure 44).

Jaydia – Holapogon clade. – One character state change occurs on the branch leading to this clade: the shape of the caudal fins changes from forked to rounded (B.39; *Coranthus* and *Holapogon* have truncate caudal fins) (Figure 44).

Jaydia – Ostorhinchus clade. –The presence of a reduced pair of uroneurals (B.34) and a weakly serrate posterior posttemporal margin (B.30) diagnose this clade (Figure 44). *Apogon* (*Jaydia*) is distinguished from *Apogon* (*Ostorhinchus*) by six characters: weakly serrate edges on the infraorbitals (B.8), an absence of canines on jaws (B.11), a narrow band of villiform teeth on palatine (B.12), weakly serrate preopercular ridge and edge (B.14, B.15), and the presence of enzymatic bioluminescent organs (B.44).

Vincentia – Holapogon clade. – Two character state changes occur on the branch leading to this clade: the ceratohyal is notched (B.20; condition changes and a deeply notched ceratohyal characterizes the *Vincentia – Neamia* clade) and the eighth dorsal-fin spine is retained, although it is reduced and may be covered by skin (B.29; spine is lost in *Vincentia* and *Foa* and fully visible in *Neamia*) (Figure 44).

Vincentia – Neamia clade. – The genera in this clade share a reduction and/or absence of the basisphenoid (B.4; reduced in *Apogonichthys* and *Foa* and absent in the other taxa in the clade), a wide band of villiform teeth on the jaws (B.10; *Neamia* has a medium-width band of villiform teeth on jaws), and a weakly notched ceratohyal (B.20) (Figure 44). *Vincentia* is distinguished from the remainder of the clade in possessing 10 + 15 vertebrae (B.25) and ten epipleural ribs (B.26) (Figure 45A).

Astrapogon – Neamia clade. – This clade is diagnosed by three characters: a medium-width band of villiform teeth on the vomer (B.2), a smooth vertical edge of the preopercle (B.15), and fusion of the upper hypural plate to the ural centrum (B.37; the fourth hypural is fused in *Apogonichthys*, no hypurals are fused in *Foa* and *Fowleria*) (Figure 45A). The uroneurals are reduced and or lost in this clade (B.35). They are reduced in *Foa* and some *Neamia* species and are lost in *Astrapogon*. *Astrapogon* may be distinguished from the remainder of the clade by the presence of gill-rakers on the first and second gill arch (B.24), a single predorsal bone (B.27), one spine on the first pterygiophore (B.28), no uroneurals (B.34), and cycloid scales (B.40).

Apogonichthys – Neamia clade. – Members of the *Apogonichthys – Neamia* clade share the presence of a reduced supramaxilla (B.9) and the absence of villiform teeth on the palatine (B.12) (Figure 45A). The analysis was unable to resolve the relationships among these genera, and they appear as an unresolved clade in the 75% majority-rule consensus cladogram. Several characters are shared among different subsets of these genera. The ceratohyal is notched in *Neamia*, weakly notched in *Fowleria*, and smooth in *Apogonichthys* and *Foa* (B.20). A separate first pharyngobranchial is absent in *Apogonichthys* and *Fowleria*, but is present as a stainable ossification within a cartilaginous extension of the tip of the first epibranchial (B. 23). The first pharyngobranchial is absent in the other two members of the clade. The hypurals in *Fowleria* and *Foa* are not fused to the ural centrum (B.37) and both taxa possess incomplete lateral lines (B. 44). *Apogonichthys* and *Foa* both retain a basisphenoid, albeit in a reduced form; this bone is absent in the other two taxa (B.4).

Coranthus – Holapogon clade. – This clade is diagnosed by seven characters: intercalary facet not included on otic bulla (B.5), absence of a shelf on the infraorbital bones (B.7), presence of a large supramaxilla (B.9), five pharyngeal tooth plates (B.23), a spine on the posttemporal (B.30), two pairs of uroneurals (B.34), and a truncate caudal fin (B39) (Figure 44). *Holapogon* is distinguished from *Coranthus* by the presence of a medium-width band of villiform teeth on the palatine (B.12). *Coranthus* is further distinguished from *Holapogon* by the presence of canines on the vomer and jaws (B.3, B.11) and seven epipleural ribs (B.26). *Holapogon* is distinguished from all apogonids by the presence of a perforated ceratohyal (B.20; condition of this character is unknown in *Coranthus*).

Cheilodipterus – Sphaeramia clade. – The presence of one spine on the first pterygiophore diagnoses this clade (B.28) (Figure 44). *Cheilodipterus* is separated from the *Zapogon – Sphaeramia* clade by the presence of canines on the vomer (B.3), a reduced supramaxilla (B.9), canines on the jaws (B.11), and a dentate suture between the epihyal and ceratohyal (B.21) (Figure 45B).

Zapogon – Sphaeramia clade. – These six taxa share the presence of villiform teeth on jaws (B.10) and a band of villiform teeth on the palatine (B.12; reduced to a single row in *Apogon* (*Zoramia*)) (Figure 45B). *Apogon* (*Zapogon*) is distinguished from the remainder of the clade by having an unossified ventral edge of preopercle (B.16), a smoothly concave ceratohyal (B.20), two predorsals (B.27), and small scales (B.42).

Pristicon – Glossamia clade. – This clade is diagonised by the presence of 9 epipleural ribs (B.26) (Figure 45B). *Apogon* (*Pristicon*) is distinguished from the remainder of the clade by the presence of serrate edges on the infraorbital bones (B.8), a serrate preopercular ridge (B.14), and a weakly serrate posterior posttemporal margin (B.30). The sister group relationship between *Apogon* (*Yarica*) and *Glossamia* is supported by the exclusion of the intercalary facet from the otic bulla (B.5), presence of a large supramaxilla (B.9), and a truncate caudal fin morphology (B.40; rounded in some *Glossamia* species) (Figure 45B). *Glossamia* is distinguished from *Apogon* (*Yarica*) by the absence of a basisphenoid (B.4), the presence of ectopterygoid teeth (B.13), a smooth vertical preopercular edge (B.15), a dentate suture between the epihyal and ceratohyal (B.20), five pharyngeal tooth plates (B. 23), and small scales (B.42).

Zoramia – Sphaeramia clade. – Two characters diagnose this clade: a crest on the supraoccipital (B.1) and the absence of a shelf on the third infraorbital bone (B.7; character reversal) (Figure 45B). *Apogon* (*Zoramia*) may be distinguished from *Sphaeramia* by the presence of a narrow band of villiform teeth on the jaws (B.10) and a single row of villiform teeth on the palatine (B.12). *Sphaeramia* is further distinguished from *Apogon* (*Zoramia*) by the presence of a reduced eighth dorsal-fin spine (B.29), a serrate posterior posttemporal margin (B.30), and the development of the secondary caudal rays into spinous elements (B.38).

Lepidamia – Pterapogon clade. – These taxa all exhibit an increase in the number of villiform teeth on the palatine from a single row to a narrow band (B.12; villiform teeth on the palatine are absent in *Pterapogon* (*Pterapogon*)) and a serrate posterior posttemporal margin (B.30) (Figure 44). *Pterapogon* (*Quinca*) and *Pterapogon* (*Pterapogon*) both possess spinous secondary caudal-fin rays (B.39)

Lepidamia – Quinca clade. –The presence of a medium-width band of villiform teeth on the vomer (B.2) and nine epipleural ribs (B.26) characterize this clade (Figure 45C). *Apogon* (*Lepidamia*) is distinguished from *Pterapogon* (*Quinca*) by the retention of the eighth dorsal-fin spine (B.29), a reduced pair of uroneurals (B.34), small scales (B.42), and segmented secondary caudal-fin rays (B.39; secondary caudal-fin rays of*Pterapogon* (*Quinca*) are spinous).

Archamia – Pterapogon clade. – These two taxa share a crest on the supraoccipital (B.1) and a narrow band of villiform teeth on the jaws (B.10) (Figure 45C). *Archamia* is distinguished from *Pterapogon* (*Pterapogon*) by having a smooth vertical preopercular edge (B.14), gill-rakers on the first and second gill arch (B.24), one spine on the first pterygiophore (B.28), and a smooth posterior posttemporal margin (B.30; *Pterapogon* (*Pterapogon*) has a serrate edge on the posttemporal). *Pterapogon* (*Pterapogon*) is further distinguished from *Archamia* by the absence of villiform teeth on palatine (B.12), two predorsals (B.27), fused upper and lower hypural plates (B.36), and spinous secondary caudal-fin rays (B.38).

Pseudaminae. – Four character state changes occur on the branch leading to the pseudamine subfamily: absence of the prootic extension that separates the parasphenoids and pterosphenoids (B.6), a single postcleithrum (B.31), two epurals (B.33), and medium-sized scales (B.40) (Figure 44). The pseudamine genera share a number of other characters: absence of the basisphenoid (B.4), absence of a shelf on any of the infraorbital bones (B.7), narrow bands of villiform teeth on both jaws (B.10), presence of canines on the jaws (B.11), smooth preopercular edges (B.16), and six or fewer epipleural ribs (B.27). Baldwin and Johnson (1999) also included the vomer flattened on its dorsal side and an elongate neurocranium among their diagnostic characters for the Pseudaminae.

Gymnapogon – Paxton clade. – *Gymnapogon* and *Paxton* share eleven characters: a single spine on preopercular edge (B. 17), preopercle obscured by skin (B.18), a fleshy flap on the preopercle (B.19), absence of the first pharyngobranchial (B.22), gill-rakers present on the first and second gill arch (B.24), no predorsal bones (B.27), a fused parhypural (B.35), three hypurals (B.36), fusion of the upper hypural plate to the ural centrum (B.37), an absence of scales (B.40), and no lateral line (B.43) (Figure 45D). The preopercle is obscured by skin to some degree in *Gymnapogon* and *Paxton* (B.18). It is fully obscured in *Paxton*, whereas only the ventral flange of the preopercle is covered by skin in *Gymnapogon*. *Gymnapogon* is distinguished from the remainder of the Pseudaminae by possessing a single autogenous haemal spine (B.33). The remaining pseudamine genera have lost all autogenous haemal spines. *Gymnapogon* is distinguished from *Paxton* by the presence of a reduced shelf on the third infraorbital (B.7), three pharyngeal tooth plates (B.23), and the presence of six epipleural ribs (B.26). *Paxton* is distinct in having the fifth hypural fused to the plate formed from the fusion of hypurals 1, 2, 3, and 4 (B.37). *Paxton* is further distinguished from *Gymnapogon* by having a single row of villiform teeth on the palatine (B.12), dentate suture between the epihyal and ceratohyal (B.20), and a truncate caudal-fin (B.39).

Pseudamia – Pseudamiops clade. – *Pseudamia* and *Pseudamiops* are diagnosed as sister taxa on the basis of three characters: absence of villiform teeth on the vomer (B.2), presence of ectopterygoid teeth (B.13), and a round caudal fin (B.39) (Figure 45D). Additional shared characters include a spine on preopercular edge (B.17), two predorsals (B.27; included by Baldwin and Johnson (1999) as a synapomorphy for the subfamily), four hypurals (B.36), cycloid scales (B.40), and reduction of the lateral line (B.43; absent in *Pseudamiops* and incomplete in *Pseudamia*) (Figure 45D). *Pseudamiops* is distinguished from *Pseudamia* in possessing a smooth ceratohyal (B.20; versus notched in *Pseudamia*), two epipleural ribs (B.26; epipleural ribs absent in *Pseudamia*), no uroneurals (B.34; one reduced pair present in *Pseudamia*), the lower hypural plate fused to the ural centrum (B.37), fixed scales (B.41; Pseudamia has deciduous scales), and in lacking a lateral line (B.43; lateral line is present in *Pseudamia*). *Pseudamia* also has small scales (B.42)

Implications for the classification of the family

The data support the monophyly of both apogonid subfamilies, although no conclusions can be drawn in regards to the monophyly of the family for no group outside of the family was analyzed. Four characters support the monophyly of the Apogoninae: inclusion of the intercalary facet on the otic bulla (B.5), reduction of the number of villiform teeth on the palatine to a single row (B.12), fusion of hypural plates 1 and 2 (B.36), and the presence of medium-sized scales (B.42; small scales in *Apogon* (*Lepidamia*), *Glossamia*, and *Apogon* (*Zapogon*)) (Figure 44). The condition of villiform teeth on the palatine and the degree of fusion among the hypural plates changes several times within the subfamily. None of the characters can accurately be termed synapomorphies for the subfamily.

The data demonstrate that *Apogon* sensu lato as historically conceived is polyphyletic. Several of the *Apogon* subgenera are more closely related to other genera than they are to one another. Therefore, the current classification of family is not consistent with the group's evolutionary history.

Because the relationships among *Apogon* (*Apogon*), *Apogon* (*Brephamia*), *Apogon* (*Paroncheilus*) and *Phaeoptyx* are unresolved in the consensus cladograms a clade comprised of only these taxa cannot be ruled out. Thesetaxa are, however, distinguished from one another by several character state changes that occur on their terminal branches. *Apogon* (*Pristiapogon*) is sister to the clade containing, but not consisting exclusively of, the remaining *Apogon* subgenera.

Apogon (Jaydia) and *Apogon* (Ostorhinchus) form a clade in all of the cladograms. Fraser (2000) had questioned the validity of *Jaydia* Gon, 1996, stating that all of the group's diagnostic, "synapomorphic" characters grade into those of other *Apogon* subgenera, particularly the subgenus *Ostorhinchus*. In the current analysis six character state changes distinguish *Apogon* (*Jaydia*) from *Apogon* (*Ostorhinchus*): the presence of weakly serrate edges on the infraorbital bones in *Apogon* (*Jaydia*) (B.8), an absence of canines on the jaws in *Apogon* (*Jaydia*) (B.11), a narrow band of villiform teeth on the palatine in *Apogon* (*Jaydia*) (B.12), a weakly serrate preopercular ridge and edge in *Apogon* (*Jaydia*) (B.14, B.15), and the presence of enzymatic bioluminescent organs in *Apogon* (*Jaydia*) (B.44). Only one of these, the presence of enzymatic bioluminescent organs (B.44), is included on Gon's (1996) original list of synapomorphies of *Apogon* (*Jaydia*). The results of this analysis concur with Fraser (2000) that *Apogon* (Jaydia) and *Apogon* (*Ostorhinchus*) are closely related. The cladograms suggest that although they form a clade, there is sufficient structure within it to continue to consider the two groups as separate taxa. Whether or not these two groups should be treated as separated genera or as subgenera of one another remains to be seen. In order to examine this question, and to test the monophyly of the two groups, a cladistic analysis should be run with individual species of the two taxa.

The cladograms show that *Apogon* (*Yarica*) is more closely related to the genus *Glossamia* than any of the *Apogon* subgenera. The *Apogon* (*Yarica*) – *Glossamia* clade is supported by the exclusion of the intercalary facet from the otic bulla (B.5), presence of a large supramaxilla (B.9), and a truncate caudal-fin morphology (B.40; rounded in some *Glossamia* species) (Figure 45B). *Glossamia* is distinguished from *Apogon* (*Yarica*) by the absence of a basisphenoid (B.4), the presence of ectopterygoid teeth (B.13), a smooth vertical preopercular edge (B.15), a dentate suture between the epihyal and ceratohyal (B.20), five pharyngeal tooth plates (B. 23), and small scales (B.42). Fraser (1973) considered *Apogon* (*Yarica*) and *Glossamia*, in addition to *Coranthus* and *Holapogon*, to be among the most primitive of apogonids. These four taxa did not group together on any of the cladograms, although *Coranthus* and *Holapogon* also form a monophyletic clade. Species of *Glossamia* and *Apogon* (*Yarica*) occur in fresh and brackish water and overlap in their range. *Apogon* (*Pristicon*) is sister to the *Apogon* (*Yarica*) – *Glossamia* clade. This relationship is supported by the presence of nine epipleural ribs (B.26) (Figure 45B).

Apogon (*Zoramia*) is more closely related to *Sphaeramia* than to any of the other *Apogon* subgenera. This clade is supported by two characters: a crest on the supraoccipital (B.1) and the absence of a shelf on the third infraorbital (B.7) (Figure 45B). The *Apogon* (*Zoramia*) – *Sphaeramia* clade comprises a monophyletic clade along with the *Apogon* (*Pristicon*) – *Glossamia* clade and *Apogon* (*Zapogon*). This clade is most closely related to *Cheilodipterus*.

Apogon (*Lepidamia*) is more closely related to *Pterapogon* (*Quinca*) than to any of the *Apogon* subgenera. The presence of a medium-width band of villiform teeth on the vomer (B.2) and nine epipleural ribs (B.26) support this relationship (Figure 45C). *Quinca* is currently considered a subgenus of *Pterapogon* although the results of this analysis suggest that *Pterapogon*, as it is currently defined, is not monophyletic. *Pterapogon* is more closely related to *Archamia* than to *Quinca*. These two taxa share a crest on the supraoccipital (B.1) and a narrow band of villiform teeth on the jaws (B.10) (Figure 45C). Together the *Apogon* (*Lepidamia*) – *Quinca* clade and the *Pterapogon* – *Archamia* clade form a monophyletic group. This group is diagnosed by an increase in the number of villiform teeth on the palatine from a single row to a narrow band (B.12; villiform teeth on the palatine are absent in *Pterapogon* (*Pterapogon*)) and a serrate posterior posttemporal margin (B.30) (Figure 44). *Pterapogon*, including *Quinca*, can be considered monophyletic only if its limits are expanded to include *Apogon* (*Lepidamia*) and *Archamia*. Another possible strategy would be to treat both *Pterapogon* and *Quinca* as separate genera.

Apogonichthys, *Foa*, *Fowleria*, and *Neamia* have been suggested to be related (Fraser, 1972; Fraser and Allen, 2001). The results of this research support a close relationship among these taxa, but the data was unable to resolve the individual relationships. Members of the *Apogonichthys* – *Neamia* clade share the presence of a reduced supramaxilla (B.9) and the absence of villiform teeth on the palatine (B.12) (Figure 45A). Fraser and Allen (2001) present six additional characters shared by these taxa: smooth preopercle ridge and edges (B.14, B.15), low number of well developed gill-rakers (5-9) (character not included in present analysis), a smooth posterior posttemporal margin (B.30), one pair of uroneurals (B.34), and round caudal fins (B.39).

The data support the monophyly of the *Rhabdamia* genus as it is currently defined. The three *Rhabdamia* subgenera form a monophyletic clade and the cladograms suggest that enough structure exists within the group to support its division into three subgenera: *Rhabdamia* (*Rhabdamia*), *Rhabdamia* (*Bentuviaichthys*), and *Rhabdamia* (*Verulux*).

Cercamia and *Lachneratus* form an unresolved clade that is sister to the remaining apogonine genera. Six characters support a close relationship between the two taxa: shelf present on all infraorbitals (B.7), presence of spines on the edge of the preopercle (B.17), 3 epipleural ribs (B.26), no predorsals (B.27), posttemporal with a spine (B.30), and the presence of highly deciduous scales (B.41) (Figure 44). A close evolutionary relationship has been suggested between *Cercamia* and the *Rhabdamia* subgenera (Fraser and Struhsaker, 1991; Hayashi, 1991). Fraser and Struhsaker (1991) further suggested that *Lachneratus* is more closely related to *Cercamia* than to the *Rhabdamia* subgenera, as is supported by the present analysis.

The results of this research support the monophyly of the Pseudaminae. Four characters support the clade: the absence of the extension of the prootic that separates the parasphenoids and pterosphenoids in apogonine taxa (B.6), a single postcleithrum (B.31), two epurals (B.33), and medium-sized scales (B.40). The pseudamine genera share a number of other characters: no basisphenoid (B.4), no shelf the infraorbital bones (B.7), narrow bands of villiform teeth on both jaws (B.10), canines on the jaws (B.11), smooth preopercular edges (B.16), and six or fewer epipleural ribs (B.27). Baldwin and Johnson (1999) also included the vomer flattened on its dorsal side and an elongate neurocranium among their diagnostic characters for the Pseudaminae. The results of this research also suggest that *Pseudamia* and *Pseudamiops* and *Gymnapogon* and *Paxton* are most closely related to one another. Baldwin and Johnson (1999) proposed a number of characters that unite *Gymnapogon* and *Paxton* in a sister group relationship. Few of these characters were included in the present analysis and thus, this analysis serves as an independent corroboration of this relationship.

This research has resulted in the first cladistically derived hypothesis of the evolutionary history of the Apogonidae. The most significant aspect of which is that the two of the apogonid genera, *Apogon* and *Pterapogon*, are not monophyletic as they are currently defined. The genus *Apogon* can be considered monophyletic only if its limits are expanded to include the entire *Apogon – Pterapogon* clade. The significance of this is underscored by the fact that *Apogon* sensu lato currently encompasses more than one-third of the family's species. If its boundaries were expanded to include all descendents of the genus' (as it is currently defined) common ancestor then nearly all of the family's species would fall within its boundaries. This strategy would mask almost all knowledge of the group's evolutionary history. And, since one of the major purposes of any classification is to convey information about a group's phylogeny, this is not a viable strategy. An alternative strategy would be to elevate the current *Apogon* subgenera to the generic level. This may be a reasonable solution, given that the *Apogon* subgenera are based upon the very same characters and character states that are used to define family's genera. However, decisions of this magnitude must be based upon strongly supported phylogenies, and the low consistency indices of the cladograms presented here, indicate that a more robust hypothesis should be found before such revisionary action is taken.

CHAPTER 4. EVOLUTION OF THE APOGONID CEPHALIC LATERALIS

This chapter, a synergy of the two previous chapters, has the dual purpose of describing the evolution of the cephalic lateralis system in apogonids and also investigating the potential of the system as an evolutionarily informative data set. There are two main opinions regarding the use of cephalic lateralis characters in phylogenetic reconstruction. One view supports the utilization of the characters as a highly diverse and phylogentically informative data set (Hoese, 1983; Takagi, 1989; Pezold, 1993, 2004). Miller and Wongrat (1979) contend that for diverse taxa, their phylogenetic relationships are best revealed by equally diverse data sets, such as those that include both the simple characters of osteological fusion and reduction and the more complex cephalic lateralis characters.

The opposing view rejects the inclusion of these characters on account of their presumably homoplastic nature (Coombs et al., 1988). It has been suggested that characters based on the morphology of any sensory system are of no utility in systematic studies because of the strong likelihood of parallel evolution and convergence upon an optimal, but not homologous, functional morphology (Quicke, 1993). This hypothesized homoplasy is tested by optimization of the cephalic lateralis characters onto the 75% majority rule consensus cladogram generated in Chapter 3 from Fraser's (1972) morphological and osteological data. Conclusions about the evolution of the cephalic lateralis in apogonids are based upon the number of separate occasions specific characters evolved within the family. The greater the number of independent lineages that evolved a given character, the more likely it is the character evolved as a result of selection pressure, rather than common ancestry.

The second vein of inquiry is an investigation into the utility of the cephalic lateralis as an evolutionary informative data set. This entails cladistic analysis of a data matrix composed of both Fraser's (1972) morphological and osteological characters and the cephalic lateralis characters (here forth referred to as the combined data set). Thus, the characters will be analyzed for their potential to elucidate the systematic relationships among the apogonid genera.

Methods for the Cladistic Analysis of the Combined Data Set

Eight characters from the cephalic lateralis system were combined with the 44 characters compiled from Fraser's (1972) osteological and morphological data set to create a matrix of 52 characters. Forty-eight of these characters were parsimony informative at the family level. The data matrix was analyzed with PAUP (Swofford, 1998) using 100 replicates of a heuristic search. Thirty-five of the 52 characters were multi-state (characters 2, 4, 7-10, 12, 14-18, 20, 22-23, 25-27, 29-30, 32-34, 36-37, 39-40, 42-44, 46-48, 50-51). Multi-state characters were run unordered per reasons given in the previous chapter. The remaining characters were binary. A "?" in the matrix is used to represent missing data and a "-" in the data matrix is used when that character or character state is inappropriate for, or inapplicable to, a given taxon. Missing data indicate that the character state could not accurately be determined due to problems stemming from compilation of the data matrix from a pre-existing data set, and not from the specimens themselves. Inappropriate or inapplicable data most frequently indicate the absence of a character, and thus, coding the condition of that character was impossible, e.g., absence of scales and scale type. The consistency and retention indices were generated for the phylogeny as a whole.

Results

Characters Compiled from the Descriptions of the Cephalic Lateralis System

Shared Characters

There are four significant cephalic lateralis characters shared by all apogonids. Whether or not these characters are apomorphic cannot be determined, for the sister group to the Apogonidae is unknown. These characters are listed below and are briefly described. The first two characters are specific to the infraorbital canal and the last two characters are specific to the mandibular portion of the preoperculomandibular canal. The characters are listed beginning with anterior-most region of each canal system.

Terminal infraorbital pore. – The infraorbital canal of all apogonids terminates in an obvious pore (Figure 46A). The location of the pore varies slightly, being either posterior of the internarial space or posterior of the anterior nostril. The shape and sized of the pore varies, but it is frequently slit-shaped and is usually one of the larger pores in the fishes' cephalic lateralis system.

Ventral lachrymal pores. – Two long pores characteristically perforate the distal margin of the suborbital portion of the infraorbital canal along the ventral edge of the lachrymal (Figure 46A). Although the shape and relative size of these pores varies among apogonine genera, all possess two lachrymal pores. In contrast, three pseudamine genera, *Gymnapogon*, *Paxton*, and *Pseudamiops*, possess only one lachrymal pore.

Dentary pores. -- In all apogonids, the mandibular portion of the preoperculomandibular canal terminates anteriorly in a pair of pores that perforate the dentary (Figure 46A). These pores vary among the taxa in size and shape, but their presence is consistent.

Mental pores. -- In all apogonids, just posterior of the dentary and on each side of the basihyal, the mandibular canal is perforated by a mental pore (Figure 46B). The size and shape of these pores varies from small and round to relatively large and sub-triangular. But, as with the dentary pores, their presence does not vary within the Apogonidae.

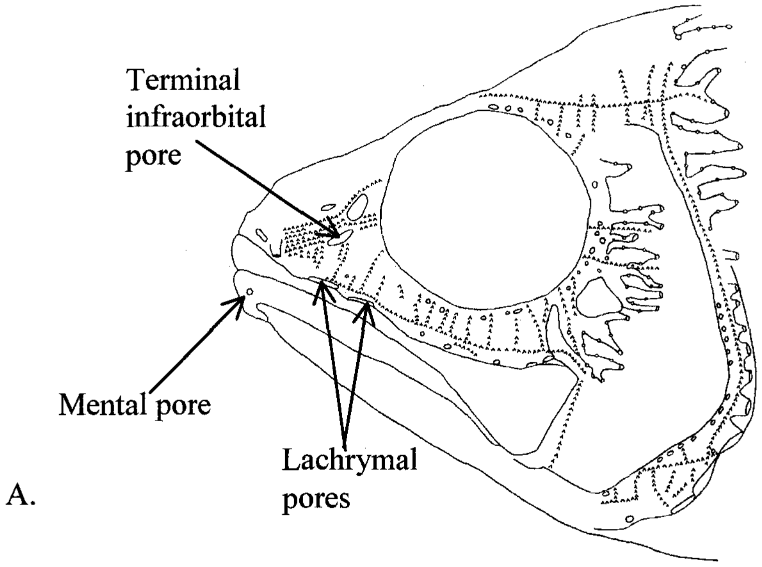


Figure 46. Illustration showing the four cephalic lateralis characters shared by all apogonids. A. Shows the location of the terminal infraorbital pore, the lachrymal pores, and the mental pores.

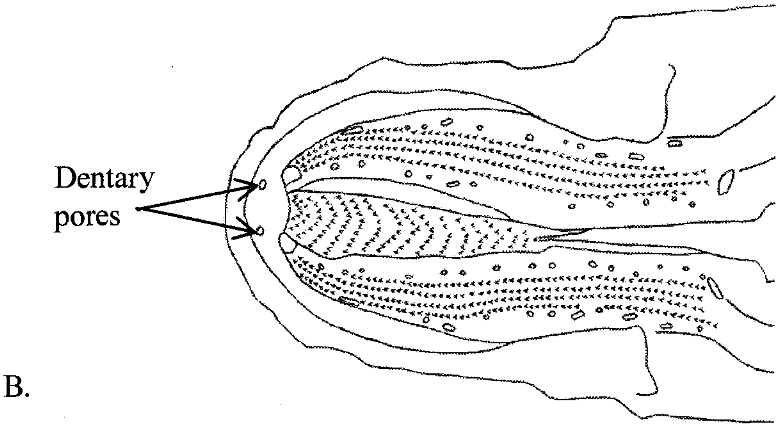


Figure 46 continued. Illustration showing the four cephalic lateralis characters shared by all apogonids. B. Shows the location of the dentary pores.

Variable Characters

The descriptions of the cephalic lateralis systems were used to compile a set of eight characters. Although a tremendous amount of variation exists among the cephalic lateralis systems of apogonids, only eight characters were consistent at the level necessary for cladistic analysis of intergeneric relationships. The cephalic lateralis characters are listed below (descriptions of the morphological and osteological characters are located in Chapter 3), according to their order of occurrence in Chapter 2, and are numbered (in parentheses following the character name) in correspondence with the numbering in the data matrix (Appendices C). The Appendix is referenced first, followed by the number to which the character corresponds in that matrix. All descriptions begin with the anterior-most portion of each canal system. For each character, the character states are described and illustrated when applicable.

Supraorbital Canal

Nasal Portion

Terminal pore at tip of snout – (*C.45*). (0) pore not at tip of snout (Figure 47A); (1) pore at tip of snout (Figure 47B). The supraorbital canal of all apogonid species terminates anteriorly in a pore near the anterior nostril. The degree of canal extension varies among the taxa. Each generic or subgeneric taxon is characterized by one of two morphologies: the canal either extends to the end of the snout such that the terminal pore is located at the tip of the snout, under a flap of skin along the premaxilla (Figure 47B); or the canal terminates posterior of the tip of the snout with the pore located just medial to and anterior of the anterior nostril (Figure 47A). Termination of the supraorbital canal prior to the tip of the snout is the more common morphology in apogonids. The canal extends to the tip in only nine of the thirty-six taxa examined: *Apogon* (*Apogon*), *Apogon* (*Lepidamia*), *Apogon* (*Ostorhinchus*), *Apogon* (*Pristiapogon*), *Apogon* (*Zapogon*), *Apogonichthys*, *Neamia*, *Pterapogon* (*Quinca*), and *Vincentia.* In *Apogon* (*Apogon*) the morphology of the flap of skin covering the terminal pore varies such that a group of species can be diagnosed as possessing a smooth flap and a second species group can be diagnosed as having a flap with its lateral edge formed into a cleft (Greenfield, 2001). In either instance, the supraorbital canal extends the full length of the snout, terminating just superior of the premaxilla.

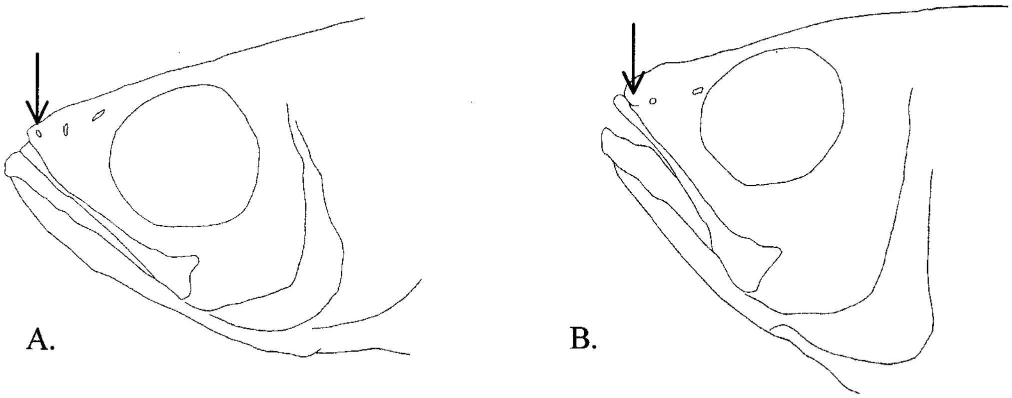


Figure 47. Alternate positions of the terminal supraorbital pore. A. At the tip of the snout, B. Posterior of the tip of the snout.

Lateral margin of the supraorbital canal adjacent to posterior nostril – (C.46). (0) lateral margin not perforated; (1) lateral margin perforated by a single, large pore (Figure 48A); (2) lateral margin developed into multiple pore-ended projections (Figure 48B). The lateral supraorbital margin is perforated adjacent to the posterior nostril in all apogonid taxa except *Pseudamia.* In *Pseudamia* several small pores perforate the median adjacent to the posterior nostril, but the lateral margin is un-perforated. In the remaining apogonid taxa, the morphology of the lateral supraorbital margin adjacent to the posterior nostril may be divided into two general categories: either perforated by a single, large pore (Figure 48A) or developed into multiple projections that extend laterally and terminate in small pores (Figure 48B). The morphology characterized by a single pore is more common among apogonids. The lateral margin is developed into projection in only four apogonid taxa: *Apogon* (*Ostorhinchus*), *Cheilodipterus*, *Coranthus*, and *Holapogon.* The lateral margin of *Holapogon maximus* is unique in that the lateral margin is developed into a few short, pore-ended projections adjacent to the anterior nostril.

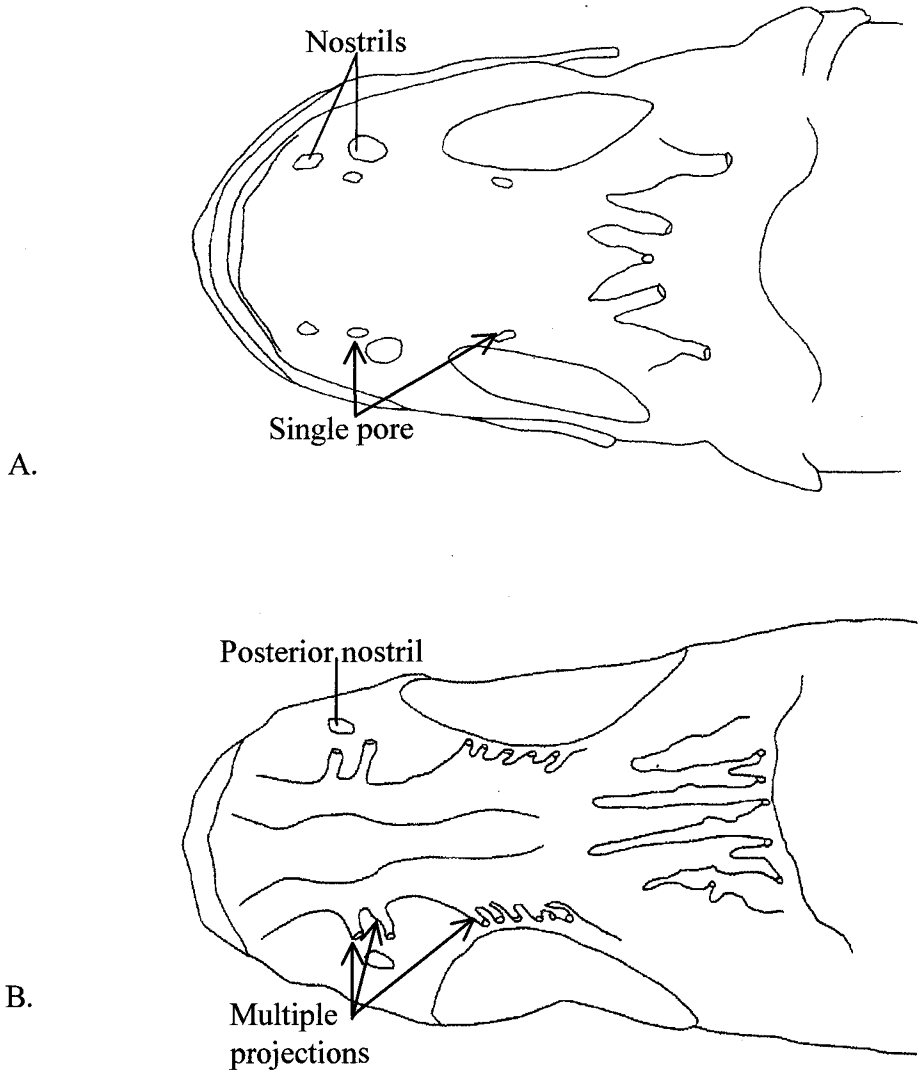


Figure 48. Alternate morphologies of the supraorbital lateral margin. A. Lateral margin adjacent to posterior nostril and in mid-interorbital space perforated by single large pores, B. Margin adjacent to the posterior nostril and in the mid-interorbital space developed into pore-ended projections that extend laterally toward the posterior nostril and orbit, respectively.

Interorbital Portion

Lateral margin of supraorbital canal near longitudinal mid-point of interorbital space -- (*C.47*). (0) lateral margin not perforated; (1) lateral margin perforated by a single, large pore (Figure 48A); (2) lateral margin developed into multiple pore-ended projections (Figure 48B). The lateral interorbital margin is not perforated in *Pseudamia* however, a few small pores perforate the median in the interorbital space. The alternate morphologies of the perforated lateral interorbital margin are similar to the morphological variants of the lateral margin adjacent to the posterior nostril. The margin is either perforated by a single large pore (Figure 48A) or is formed into pore-ended projections that extend toward the orbit (Figure 48B). Although these two morphologies are quite similar, they do not co-vary. The morphology characterized by a single, large pore is more common among the apogonid taxa. Ten apogonid taxa have the morphology characterized by the presence of pore-ended projections:*Apogon* (*Apogon*), *Apogon* (*Lepidamia*), *Apogon* (*Pristicon*), *Apogon* (*Yarica*), *Coranthus*, *Holapogon*, *Pterapogon* (*Quinca*), *Rhabdamia* (*Bentuviaichthys*), *Rhabdamia* (*Rhabdamia*), and *Rhabdamia* (*Verulux*). Depending on the species, *Archamia* and *Cheilodipterus* display both perforated morphologies.

Postorbital Portion

Postorbital secondary development -- (*C.48*). (0) postorbital secondary projections absent; (1) developed into a few, relatively simple secondary projections (Figure 49A); (2) developed into numerous, branching projections (Figure 49B). The postorbital portion of the supraorbital canal is not developed into secondary projections in the pseudamine species. In no apogonine taxon are the postorbital projections absent; they are, however, developed to a variable degree. *Cercamia* and *Lachneratus* display a rudimentary level of development, with the medial margin formed into only two short, pore-ended projections that extend toward the midline of the body. *Apogon* (*Zapogon*) *evermanni* is also characterized by a comparatively simple postorbital canal structure. The species has narrow canals that are located a distance from the orbits and a single projection projecting medially from the dorsoposterior margin of the orbit. This morphology is distinct from that of *Cercamia* and *Lachneratus*as broad canals whose lateral margins lie along the rim of the orbit characterize these species. The remaining apogonine taxa possess several postorbital projections but the structure of these projections ranges from un-branched and simple (Figure 49A) to highly branched and densely perforated, extending posteriorly to nearly meet, if not fuse with, the supratemporal canal (Figure 49B). *Holapogon maximus* and *Coranthus polyacanthus* have a unique morphology characterized by the presence of an exceptionally broad medial postorbital projection that is confluent with the supratemporal canal. *Vincentia* and *Archamia* species are also characterized by postorbital secondary projections that extend to join the supratemporal canal although in these species, the projections are very narrow and appear to fuse with projections of the anterior margin of the supratemporal canal.

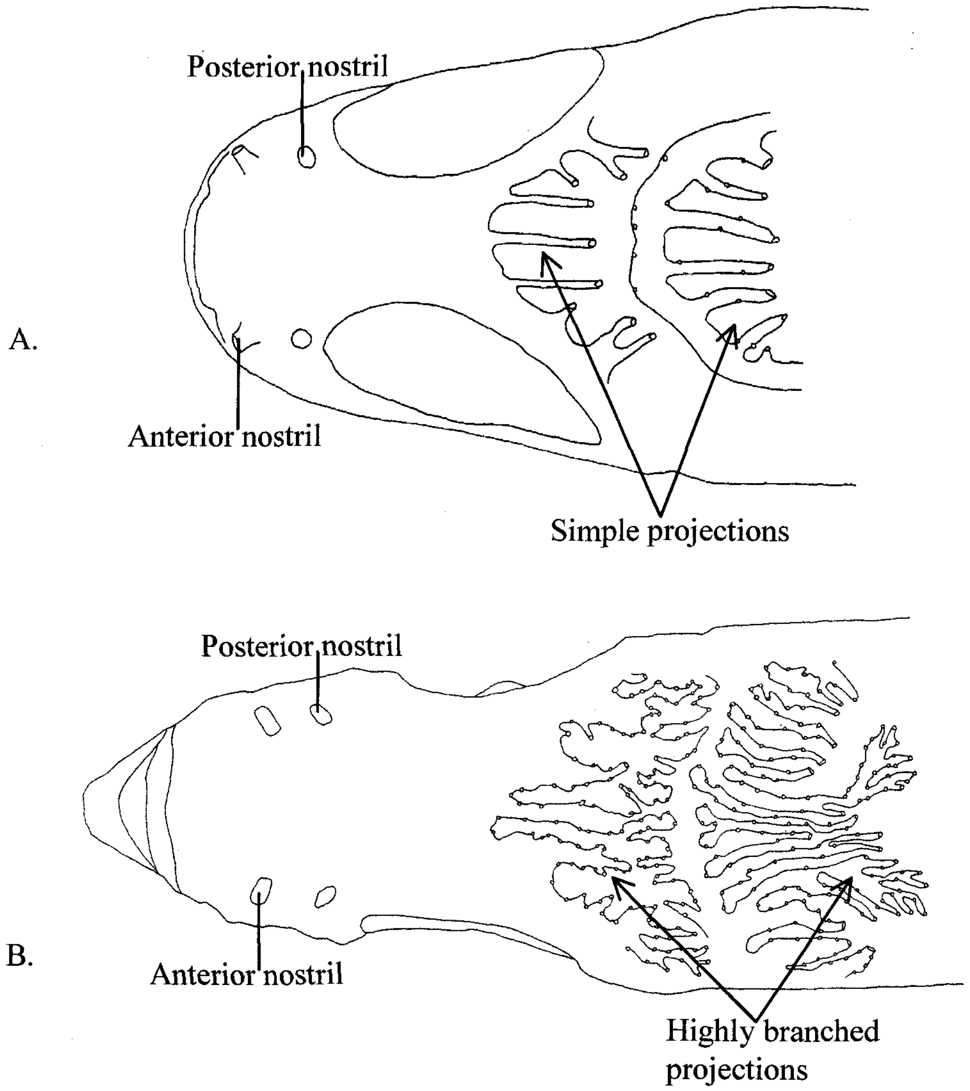


Figure 49. Illustration representing the two extremes of secondary postorbital and supratemporal canal development. A. Postorbital secondary canal development minimum; anterior margin of supratemporal canal not developed into projections; and posterior supratemporal margin developed into few, simple projections, B. Postorbital secondary projections highly branched, extending posteriorly to the supratemporal canal; anterior margin of supratemporal canal developed into projections; posterior margin of supratemporal canal highly branched into many long projections.

Supratemporal Canal

Anterior margin – (C.49). (0) anterior margin not developed into projections (Figure 49A); (1) anterior margin developed into projections (Figure 49B). The typical apogonid morphology is a smooth anterior margin, perforated by small pores but not developed into projections. The anterior margin of *Fowleria aurita* and *Neamia octospina* is not smooth, having two small bulges along its length, but is not considered developed into projections. A single median projection characterizes the anterior supratemporal margin of *Apogon* (*Brephamia*) *parvulus*. The anterior supratemporal margins of *Rhabdamia* (*Bentuviaichthys*), *Rhabdamia* (*Verulux*), and S*iphamia tubifer* are all developed into a number of anteriorly projecting extensions. The anterior margin of *Archamia* is also developed into projections, although these projections are significantly shorter than those of the aforementioned taxa.

Posterior margin – (C.50). (0) posterior margin not developed into projections; (1) posterior margin developed into few projections (Figure 49A); (2) posterior margin developed into numerous, long projections (Figure 49B). The pseudamine species possess a structurally simple supratemporal canal. The canal itself is not visible in *Pseudamia* or *Paxton*, although a few small pores perforate the skin in the general area. A few moderately sized pores perforate the posterior margin in *Gymnapogon*, but the margin is not developed into projections. The posterior margin in *Apogon* (*Zapogon*) *evermanni*, *Glossamia*, and *Lachneratus* is similar in structure to that of *Gymnapogon*, being perforated and not developed into projections. The posterior margin of *Cercamia* is relatively undeveloped with a single, median pore-ended projection. The posterior supratemporal margin is developed into numerous pore-ended projections in the remaining apogonid species (Figure 49A). These projections vary in length and may branch multiple times to form sequentially finer divisions (Figure 49B).

Preoperculomandibular Canal

Mandibular Portion

Morphology of the lateral margin -- (*C.51*). (0) lateral margin not perforated; (1) lateral margin perforated but not developed into projections, pores often large relative to the surrounding pores (Figure 50A); (2) lateral margin formed into bulges or short projections near first and second pores (Figure 50B); (3) pores located at the ends of prominent projections (Figure 50C). Apogonids display a diversity of mandibular canal morphologies. A reoccurring pattern among apogonids is the presence of pores one-quarter, one-half, and often three-quarters of the way along the length of the mandibular canal portion. These pores are typically larger than the other pores perforating the same expanse of canal and may occur at the ends of projections. The only apogonid taxon to possess an un-perforated lateral mandibular margin is *Paxton*. The lateral mandibular margin of *Lachneratus* is characterized by a relatively large pore one-quarter of the way along the length of the canal portion. *Apogon* (*Jaydia*) and *Apogon* (*Zoramia*) are both characterized by the presence of a large pore one-half way along the length of the canal portion. *Astrapogon*, *Apogon* (*Brephamia*), *Pseudamiops*, and *Pterapogon* (*Pterapogon*), are characterized by a lateral margin perforated by relatively large pores one-quarter and one-half way along the length of the canal. *Apogon* (*Zapogon*), *Foa*, *Fowleria*, *Glossamia*, *Neamia*, *Siphamia*, and *Sphaeramia* are characterized by a lateral margin that is perforated one-quarter, one-half, and three-quarters of the way along the length of the canal (Figure 50A). *Apogon* (*Paroncheilus*), and *Apogon* (*Pristiapogon*) have similar perforation patterns to *Astrapogon*, etc., but the canal is formed into bulges in the proximity of these two enlarged pores. The situation is the same for *Apogon* (*Yarica*) in that the canal bulges near each of the three pores. The lateral margin of *Pseudamia* is formed into a very small projection near the midpoint of the maxilla. In several taxa the canal is expanded such that the pore perforating the canal one-quarter of the way along its length, is located at the jaw's periphery while the second and third enlarged pores are located at the ends of a short projections (Figure 50B). Such is the case in *Apogon* (*Apogon*), *Apogon* (*Lepidamia*), *Apogon* (*Pristicon*), *Pterapogon* (*Quinca*), *Rhabdamia* (*Rhabdamia*), *Rhabdamia* (*Verulux*), and *Vincentia.* This morphology is mirrored in *Holapogon* with the addition of numerous shorter projections formed in the lateral margin along the canal's length, from the halfway point posteriorly to the terminus of the maxilla. The pores perforating the lateral mandibular margin of *Apogon* (*Ostorhinchus*), *Coranthus*, and *Rhabdamia* (*Bentuviaichthys*) one-quarter, two-quarters, and three-quarters of the way along the length of the canal's expanse are all located at the ends of projections (Figure 50C). The lateral margin in *Cheilodipterus* is typically developed into projections, the exception being *C. singapurensis* whose margin is perforated but not developed into projections *Archamia* species exhibit both morphologies: the expanded canal near the first enlarged pore characterizes *A. bleekeri* whereas; *A. macroptera* is characterized by the presence of pore-ended projections one-quarter, two-quarters, and three-quarters of the way along the length of the canal.

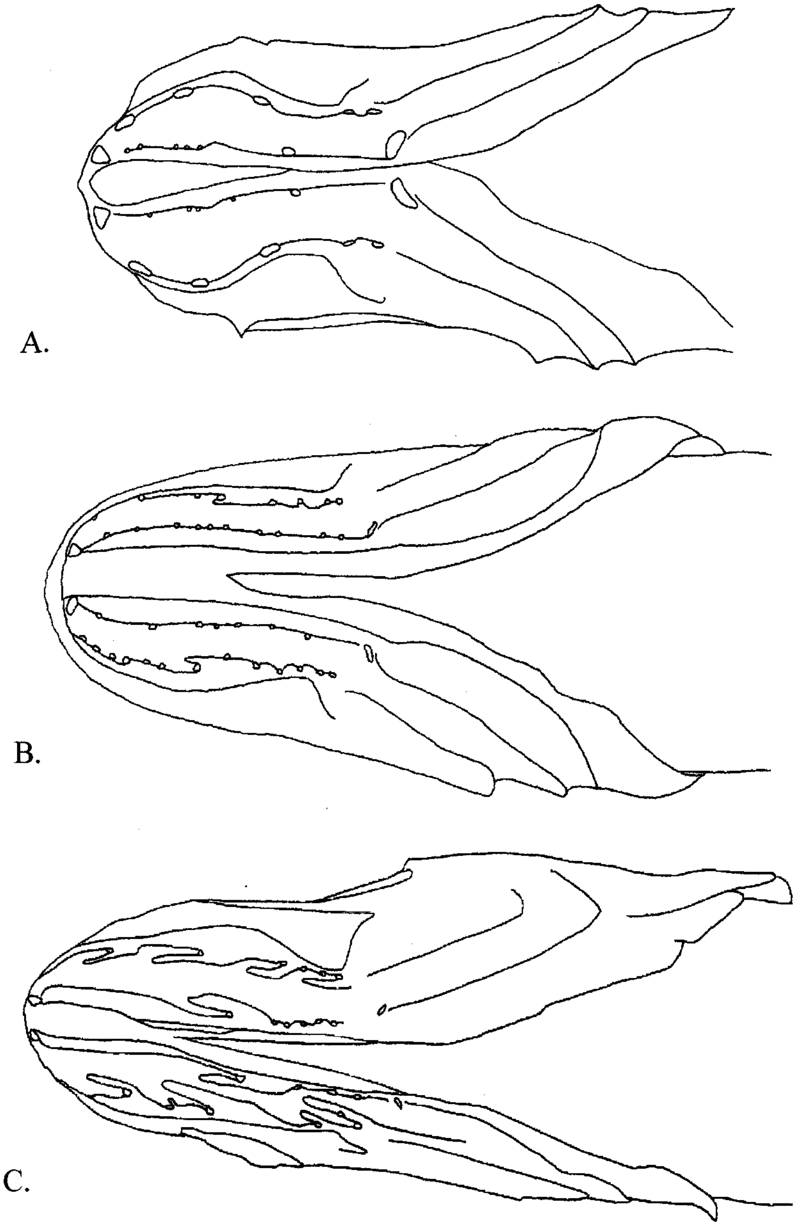


Figure 50. Alternate morphologies of the mandibular margin in apogonids. A. Lateral margin perforated but not developed into bulges or projections, B. Lateral margin developed into a short, pore-ended projection half-way along the canal's length, C. Lateral margin developed into pore-ended projections one-quarter, two-quarters, and three-quarters of the way along the length of the mandibular canal.

Terminal mandibular pore – (*C.52*). (0) present (Figure 51A); (1) absent (Figure 51B). In many apogonid taxa a pore, the terminal mandibular pore, perforates the medial margin near the arbitrary boundary between the mandibular and preopercular portions of the preoperculomandibular canal. This pore is absent in *Apogon* (*Apogon*), *Paxton*, *Pseudamia*, *Rhabdamia* (*Bentuviaichthys*), *Rhabdamia* (*Rhabdamia*), and *Rhabdamia* (*Verulux*). The pore is present in some species of *Archamia* and is absent in other *Archamia* species. A small pore is present in this relative position in *Cercamia* and *Cheilodipterus* but is not significantly larger than those surrounding it. The pore is present in the remaining apogonid taxa. In most of these taxa the pore is larger than those surrounding it, but not large enough to disrupt the confluence of the two canal portions. *Pseudamiops* is the exception to this generalization having a large, centrally positioned pore that creates a break between the mandibular and preopercular canal portion.

A.

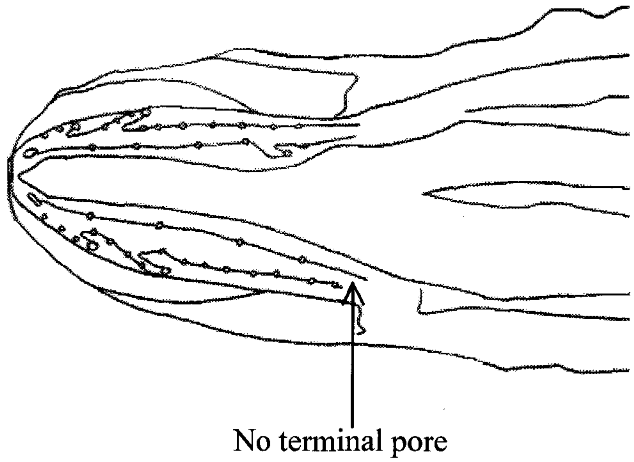


Figure 51. Illustration showing the absence and presence of the terminal mandibular pore. A. Terminal mandibular pore absent.

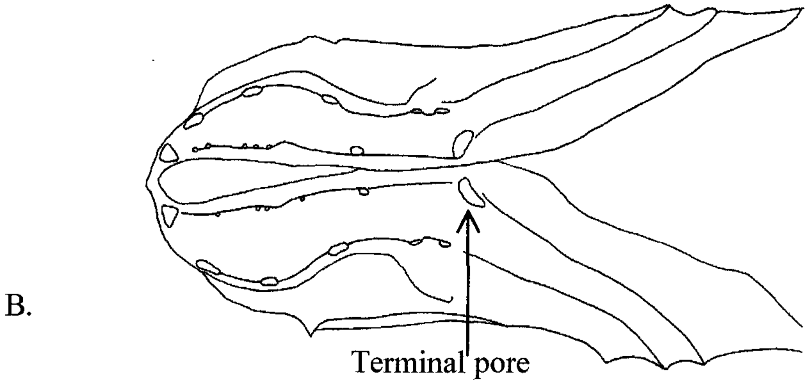


Figure 51 continued. Illustration showing the absence and presence of the terminal mandibular pore. B. terminal mandibular pore present.

Cladistic Analysis of the Combined Data Set

Cladistic analysis yielded 905 most parsimonious cladograms. A strict consensus of these cladograms is given in Figure 52. This cladogram is 245 steps long and has a consistency index of 0.4735, retention index of 0.6172, and a rescaled consistency index of 0.0.2922. The strict consensus and semi-strict consensus cladograms are topologically identical. A 75% majority-rule consensus cladogram is presented in Figure 53.

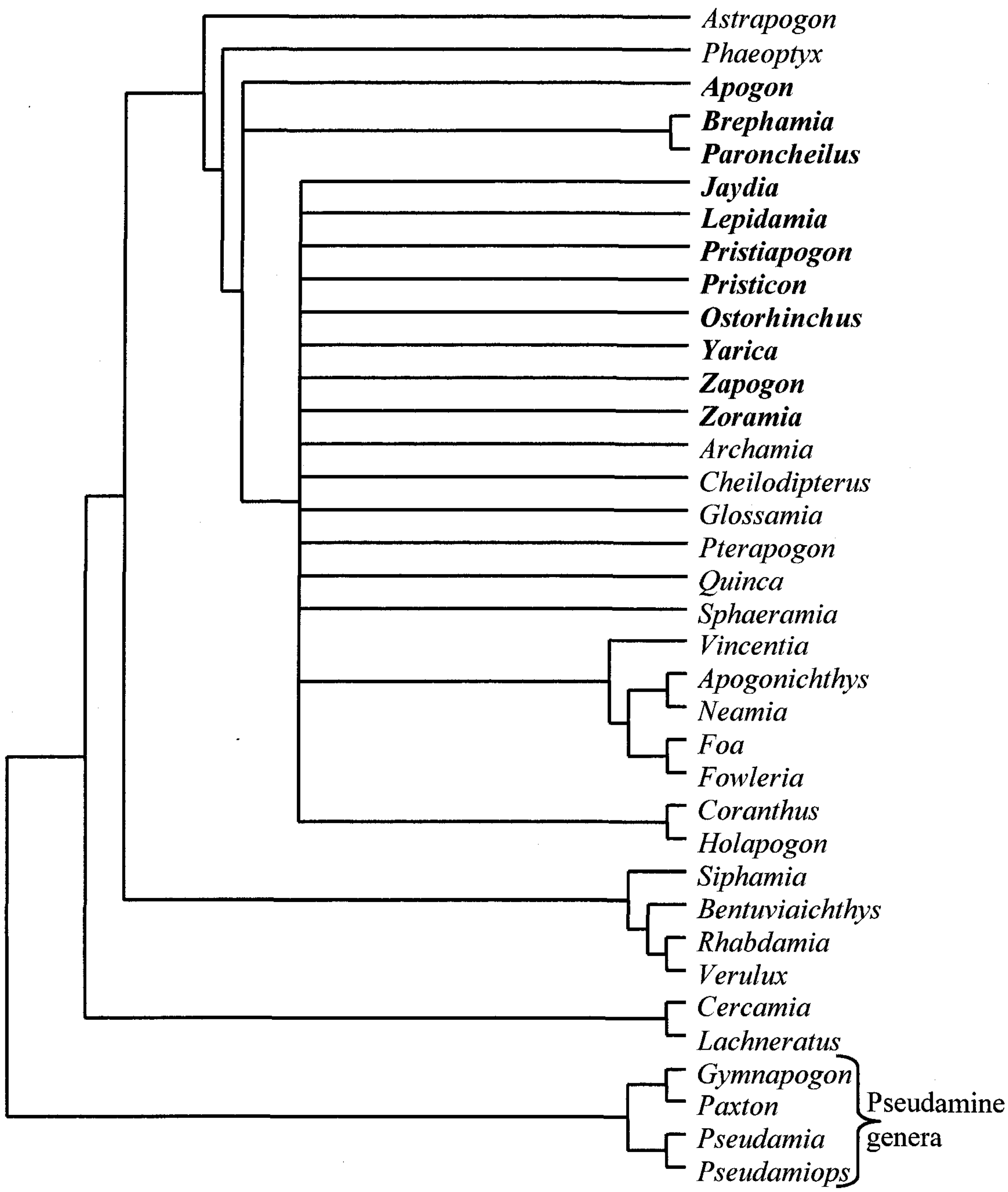


Figure 52. Strict consensus cladogram of the 905 most parsimonious cladograms generated from the cladistic analysis of the combined data set for 36 apogonine ingroup taxa and four pseudamine outgroups taxa. The names of the *Apogon* subgenera are in bold. .

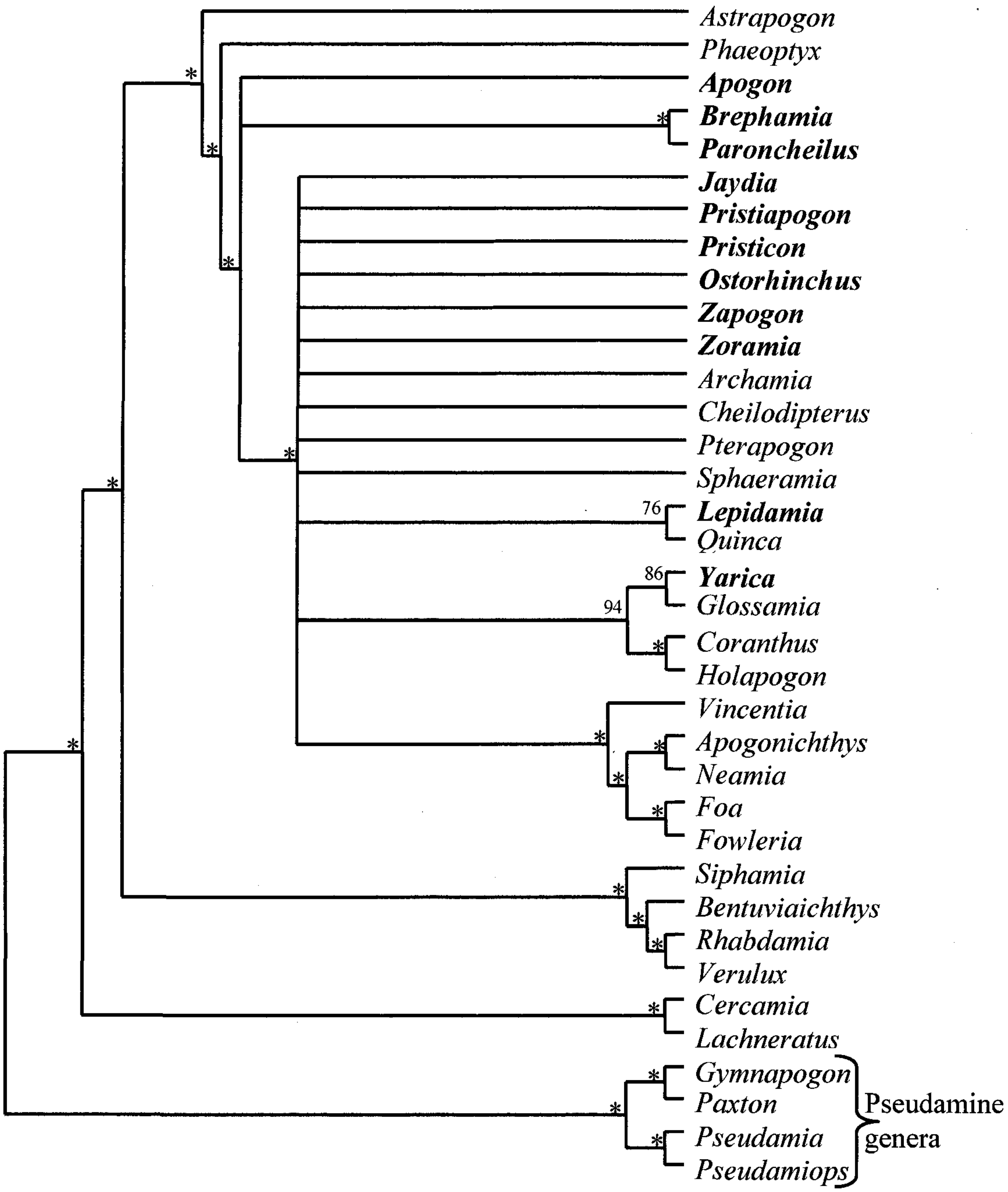


Figure 53. 75% majority-rule consensus cladogram of 905 most parsimonious cladograms generated from the analysis of the combined data set for36 apogonine ingroup taxa and four pseudamine outgroups taxa. The names of the *Apogon* subgenera are in bold.

Discussion

Comments on the Usefulness of Cephalic Lateralis Characters in the Cladistic Analysis of the Apogonidae

The eight cephalic lateralis characters here selected for inclusion in the combined data set are but a small subset of the diversity in this system exhibited by the species in the Apogonidae. These characters were selected because, in general, they did not vary within each genus. And yet, variation among these characters did exist within a few taxa, specifically *Archamia* and *Cheilodipterus*. It was found, however, that the variation observed in these taxa may parallel supra-specific group boundaries as defined by other characteristics. For example, the species in *Cheilodipterus* can be divided into two groups upon the basis of the presence or absence of a tooth patch on the second epibranchial and a notched, versus a smooth, ceratohyal (Fraser, 1972; Gon, 1993). *Cheilodipterus macrodon*, the type species of the genus, possesses a notched ceratohyal, a dentate suture between the epihyal and ceratohyal, and pore-ended projections near the posterior nostril and in the interorbital space. In comparison, *C. singapurensis* has a smooth ceratohyal, a smooth junction between the epihyal and ceratohyal, and a cephalic lateralis characterized the presence of large, singular pores perforating the lateral supraorbital margin adjacent to the posterior nostril and in the interorbital space. Other cheilodipterids display the singular nasal pore as well (in combination with interorbital pore-ended projections in *C. quinquelineatus*), but the osteology of these species is unknown. And so, it is possible that there exist definable supraspecific groups within these larger generic taxa and it is within these smaller groups that the cephalic lateralis characters will be constant.

The greatest intra-generic variation can be attributed to the combined variation of perforation density and sensory papillae patterns. Unfortunately, due to their great densities, it was impossible to quantify the number of pores perforating certain portions of the fishes' cephalic lateralis system. Thus, it was necessary to refer to the perforation density in a relative sense. And because these small pores typically perforate thin and delicate tissues it was, at times, difficult to diagnose them as real, and not artifacts of previous desiccation and/or damage to the specimen. Because it was impossible to attain more accurate data for these characters, they were not included, in spite of their great potential as a highly variable data set, in the systematic analysis.

Another set of highly variable characters is the sensory papillae patterns. Johnson (1993) cited the presence of vertical and horizontal rows of sensory papillae on the head and body of apogonids as a synapomorphy for the family. But, this character has since come into question, as these free neuromasts are more common in teleosts than was once thought (Baldwin and Johnson, 1999).

The homology of the sensory papillae is also questionable. From a merely visual perspective, the sensory neuromasts forming the characteristic rows of the pseudamine taxa appear very different from those on the canal surfaces of the apogonine taxa. The sensory papillae are significantly larger in the Pseudaminae and are arranged into a fairly regular grid pattern across the surface of the head and anterior portion of the trunk. In contrast, the sensory papillae of the apogonine genera are generally confined to the membranes covering the canal surfaces, are much smaller, and occur in more dense and variable patterns. Although the pattern in some genera can be referred to as "crosshatch", it is still qualitatively different than the grid-like pattern of the pseudamine genera.

An in-depth investigation into the microstructure of these papillae and their differences is beyond the scope of this research. However, there are a few possible explanations that should be mentioned. Superficial neuromasts arise via a number of developmental processes. During embryonic development superficial neuromasts may develop from epidermal thickenings, termed placodes, whereas; others develop during the larval and juvenile stages, either by budding off of canal neuromasts or by arising directly, and in place, from the basal layer of the epidermis (Coombs, et al., 1988). And thus, without observation of the ontogeny of the cephalic lateralis system in apogonids, it is impossible to determine the homology of the various superficial neuromasts, further precluding their utilization in this, or any, phylogenetic analysis.

Evolution of the Cephalic Lateralis System in the Apogonidae

Optimization of the cephalic lateralis characters onto the 75% majority-rule consensus cladogram (generated from the cladistic analysis of Fraser's (1972) osteological and morphological data set) resulted in a pattern of character state changes was complex and replete with homoplasy (Figure 54). The inability to detect definite trends in the evolution of the cephalic lateralis system in apogonids is due to a number of factors, including the possibility that the cladogram used was not an accurate hypothesis of the family's evolutionary history and / or the variation observed in the cephalic lateralis system is a product of convergent evolution, rather than common ancestry. Although the character state changes were not easily mapped onto the cladogram, it was possible to identify a number of changes that were shared by members of several clades.

The overall evolutionary trend in the cephalic lateralis system in the Apogonidae is one of increasing complexity. Simple, sparsely perforated canals characterize the cephalic lateralis system of the Pseudaminae. The supraorbital canal does not extend to the tip of the snout in these taxa (C.45). The lateral supraorbital margin adjacent to posterior nostril is perforated in three of the genera, *Gymnapogon*, *Paxton*, and *Pseudamiops*, but not developed into projections (C.46). The postorbital portion of the supraorbital canal and the supratemporal canal are also not developed into projections in these taxa (C.47, C.48). The lateral mandibular margin is perforated in Gymnapogon and *Pseudamiops*, but is not developed into projections in any of the pseudamine taxa (C.51). The terminal mandibular pore is present only in *Paxton* and *Pseudamia* (C.52). The pseudamine genera are further characterized by the presence of sensory papillae on all planes of the head. The papillae are organized into a regular crosshatch pattern in *Gymnapogon*, *Paxton*, and *Pseudamiops* (Figures 35, 36, 38). The papillae of*Pseudamia* are arranged into a much denser pattern, so dense that the term crosshatch does not accurately describe their arrangement (Figure 37).

The branch leading to the Apogoninae is marked by the development of the postorbital portion of the supraorbital canal and the posterior margin of the supratemporal canal into a few projections (C.48, C.50). Among the apogonine taxa the cephalic lateralis systems of *Cercamia* and *Lachneratus* are the most similar to the patterns exhibited by the pseudamine genera (Figures 17, 24). *Cercamia* and *Lachneratus* are both characterized by a rudimentary level of development of the postorbital portion of the supraorbital canal and the posterior margin of the supratemporal canal (C.47, C.50). The posterior margin of the supratemporal canal of *Cercamia* is developed into one, short projection but the margins of the supratemporal canal in *Lachneratus*are entirely undeveloped. The postorbital portion of the supraorbital canal of both taxa is characterized by the presence of two, short projections that extend medially and terminate in pores. A few rows of sensory papillae traverse the dorsal surface of the head from posterior of the posterior nostril to the mid-interorbital space in both genera.

Two character state changes occur on the branch leading to the clade containing the remaining apogonine genera: the development of the postorbital portion of the supraorbital canal into numerous projections (C.48; character reverses numerous times within the clade) and the development of the anterior supratemporal margin into projections (C.49; character reverses several times within the Apogoninae).

The *Rhabdamia* clade, consisting of *Rhabdamia* (*Bentuviaichthys*), *Rhabdamia* (*Rhabdamia*), and *Rhabdamia* (*Verulux*), is characterized by a highly branched cephalic lateralis system (Figures 29, 30, 31). The lateral supraorbital margin near the longitudinal midpoint of the interorbital space (C.47), postorbital portion of the supraoribtal canal (C.48), posterior margin of the supratemporal canal (C.50), and the lateral mandibular margin (C.51) are all developed into a number of projections in these taxa. This clade is further characterized by the absence of the terminal mandibular pore. This character undergoes homoplastic changes, as it is present in *Gymnapogon*, *Pseudamiops*, *Lachneratus*, and all other apogonids except, *Apogon* (*Apogon*), *Cheilodipterus*, and some species of *Archamia*.

The lateral margin of the supraorbital canal adjacent to the posterior nostril and in the mid-interorbital space is perforated in all members of the *Astrapogon* – *Neamia* clade (C.46, C.47). A terminal mandibular pore is also present in these taxa (C.52). The supratemporal canal extends to the tip of the snout in both *Apogonichthys* and *Vincentia* (Figures 14, 34). This may represent a convergence upon this morphology, as the two taxa do not share a most recent common ancestor. Some degree of development of the postorbital portion of the supraorbital canal exists in all five taxa (C.48). The anterior margin of the supratemporal canal in *Vincentia* is modified into a projection that is confluent with one of the supraorbital projections extending posteriorly from the postorbital space. The lateral mandibular margin is perforated in *Apogonichthys*, *Foa*, and *Neamia* (Figures 14, 20, 25). In contrast, the lateral mandibular margin is developed into projections in the remaining taxa of the clade (Figures 16, 21). Although numerous taxa from this group share different cephalic lateralis characters, there is no observable trend in the evolution of the canal branching patterns or patterns of perforation within this clade. There does, however, appear to be a trend in the degree of sensory papillae covering in these species. *Vincentia* and *Astrapogon* have dense papillae patterns in the suborbital, supraorbital, and mandibular regions of the canal system. In contrast, *Apogonichthys* and *Neamia* are nearly free of sensory papillae, the only exception being the anterior-most portion of the basihyal in *Apogonichthys*. The density of papillae on *Foa* and *Fowleria* is intermediate between these two extremes. This variation is suggestive of an evolutionary trend that cannot be tested with the current data, as the morphological and osteological data was unable to resolve the relationships among these taxa.

The overall structure of the cephalic lateralis systems of *Coranthus* and *Holapogon* are very similar although *Coranthus* exhibits a more extensive branching pattern (Figures 19, 23). The only significant difference between the two canal systems is that the supraorbital canals extends to the tip of the snout in *Holapogon.* These two taxa share a morphology that is unique among the Apogonidae. The supraorbital and supratemporal canals are connected by a wide projection along the midline of the dorsal surface of the head. Although there are other apogonid taxa that have long postorbital projections that extend posteriorly to meet the supratemporal canal, these are the only two taxa in which the two canal portions are confluent.

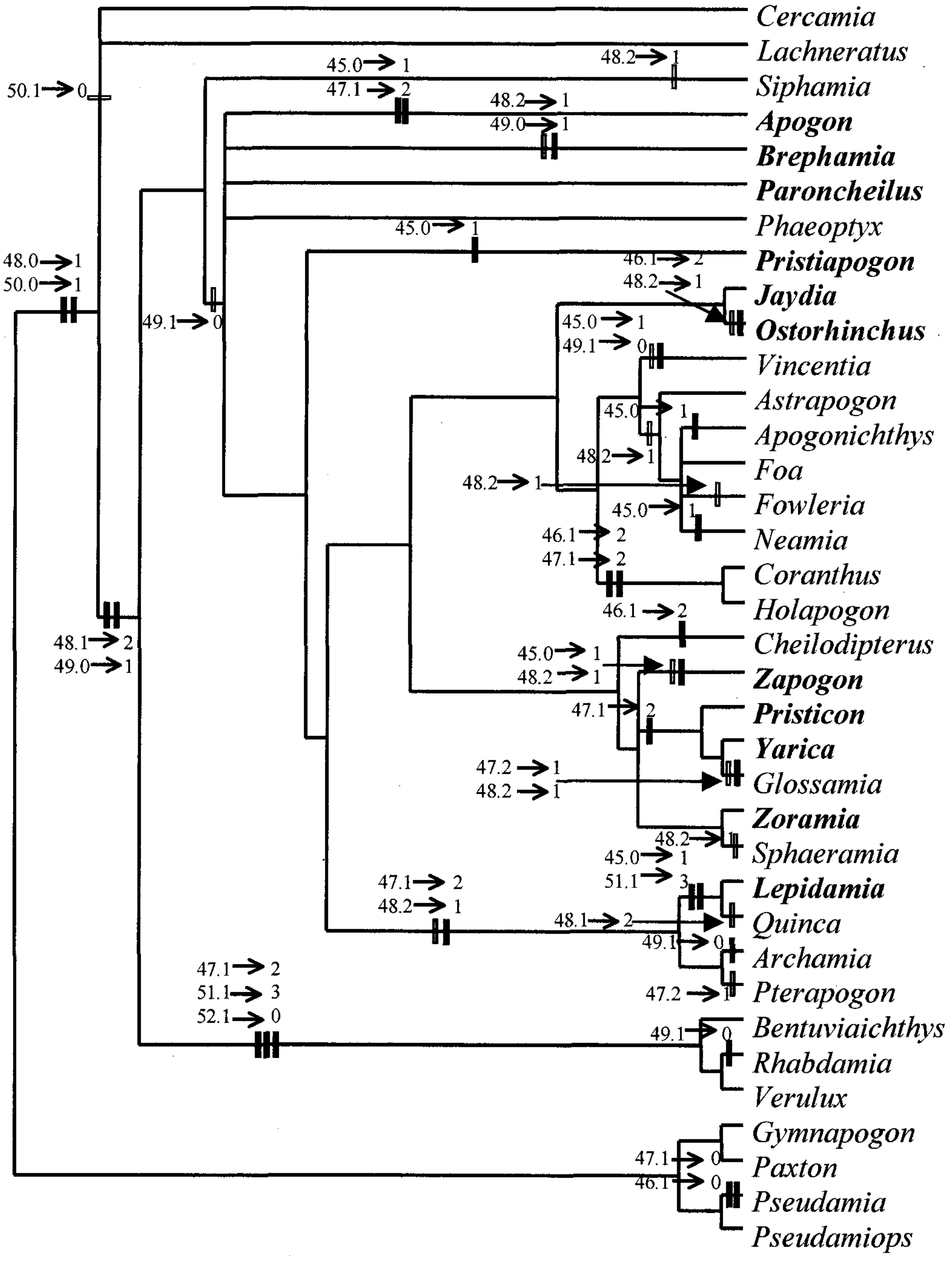


Figure 54. Optimization of selected cephalic lateralis characters onto the 75% majority-rule consensus cladogram generated from the cladistic analysis of 44 morphological and osteological characters for a 32 apogonine ingroup taxa and a 4 pseudamine outgroup taxa. The names of the *Apogon* subgenera are in bold. Homoplasious changes are indicated by open rather than solid bars.

Cladistic Analysis of the Combined Data Set

The consistency and retention indices indicate high levels of homoplasy in the data set. Only 52 characters were used for the analysis of a 32 taxon ingroup. The relatively small number of characters, combined with the high levels of homoplasy, resulted in a large number of weakly supported cladograms. In spite of these weaknesses, many nodes remain resolved in the consensus trees.

The topology of the 75% majority-rule consensus cladogram generated from the analysis of the combined data set differs from the topology of the 75% majority-rule consensus cladogram generated from the analysis of Fraser's (1972) morphological and osteological data set (presented in Chapter 3). Both phylogenetic hypotheses support the monophyly of the Apogoninae and the monophyly of the Pseudaminae, but some of the cladograms' internal clades differ substantially. A discussion of the cladogram generated from the analysis of the combined data set follows, with special emphasis placed on the aspects of the cladogram that differ from cladogram based on the morphological and osteological data.

Clades are arbitrarily named by assigning each (with the exception of the Apogoninae and Pseudaminae subfamilies) a two-part name consisting of the names of the first and last taxon in the group. The numbers of the characters, corresponding to the numbering in the data matrix (Appendix C), are given in parentheses.

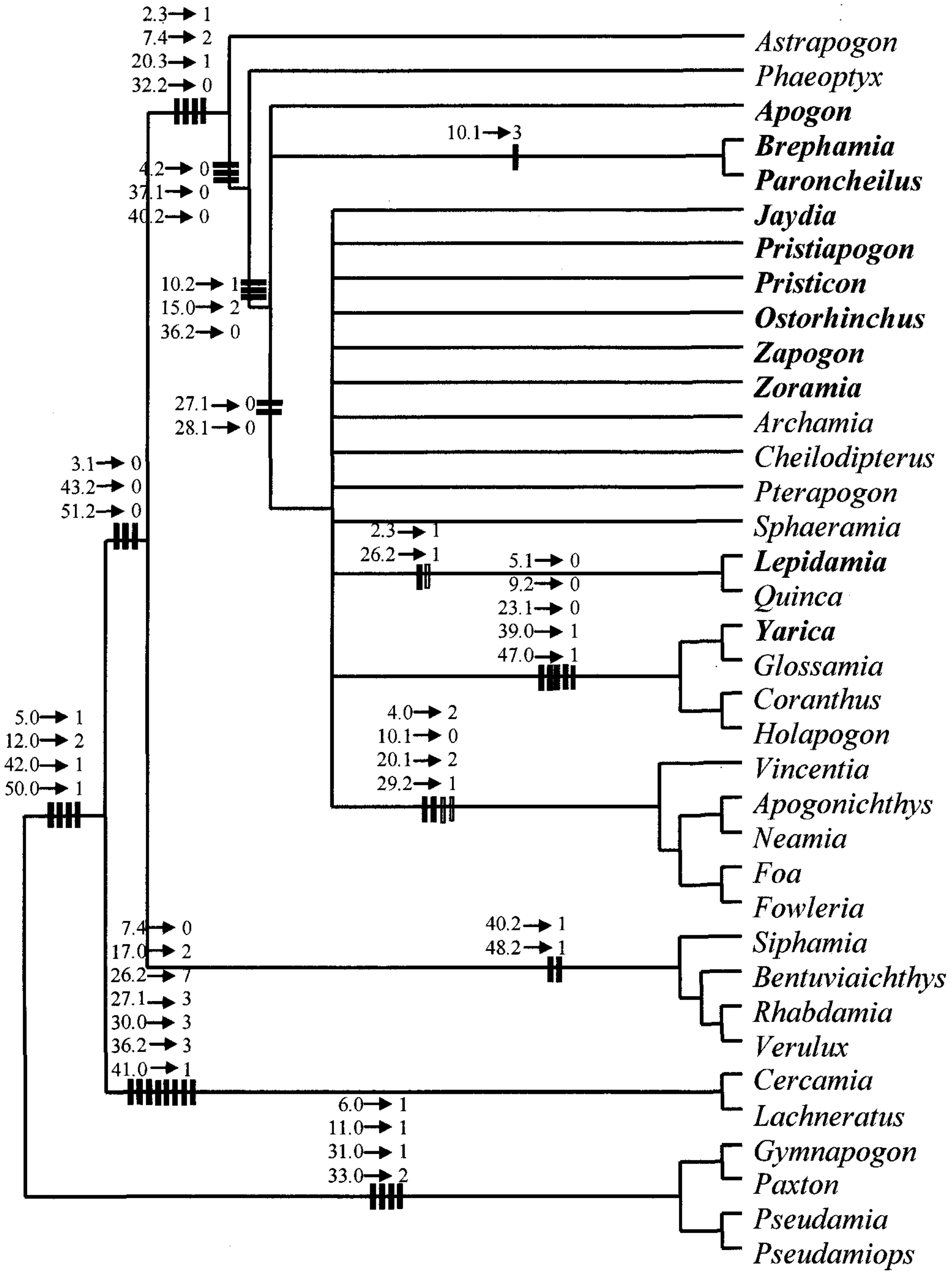


Figure 55. 75% majority-rule consensus cladogram of 905 trees for 32 apogonine ingroup taxa and four pseudamine apogonid taxa. Selected character state changes are indicated on the branches. The names of the *Apogon* subgenera are in bold. Homoplasious changes are indicated by open rather than solid bars.

Apogoninae. – Monophyly of this subfamily is supported by the cladistic analysis. Four character state changes occur along the branch leading to the group: intercalary facet included on the otic bulla (C.5; reverses just basal of the *Apogon* (*Yarica*) – *Holapogon* clade), band of villiform teeth on the palatine reduced to a single row (C.12; character state changes numerous times within Apogoninae), medium-sized scales (C.42; small scales in *Apogon* (*Lepidamia*), *Glossamia*, and *Apogon* (*Zapogon*)), and posterior supratemporal margin that is developed into a few projections (C.50) (Figure 55). In comparison to the previous cladistic analysis, the fusion of the hypural plates (C.36) was not included as a character state change on this branch.

Cercamia – Lachneratus clade. – The clade composed of *Cercamia* and *Lachneratus* is sister to the remaining apogonine taxa. Eight character state changes support this clade: infraorbital shelf present on all infraorbitals (C.7), presence of spines on the edge of the preopercle (C.17), three epipleural ribs (C.26), no predorsals (C.27), posttemporal with a spine (C.30), two hypurals (C.36), highly deciduous scales (C.41), and an undeveloped anterior margin of the supratemporal canal (C.50) (Figure 55). The last character, that of the cephalic lateralis system, was not included in the analysis described in Chapter 3. Its inclusion, along with the hypural character (C.36), resulted in the resolution of the clade. The relationship between these two taxa was unresolved in the previous analysis. The results of this analysis support for the hypothesis presented by Fraser and Struhsaker (1991) that *Lachneratus* is more closely related to *Cercamia* than to the *Rhabdamia* subgenera.

Astrapogon –Verulux clade. – Three characters diagnose this group: absence of canines on the vomer (C.3), a complete lateral line (C.43; reversed in *Apogon* (*Brephamia*), *Foa*, and some *Fowleria* species), and an un-perforated lateral mandibular margin (C.51; changes multiple times within clade) (Figure 55). The previous analysis also contained a clade composed of these same taxa, but in a slightly different configuration. The characters supporting the clade, with the exception of the cephalic lateralis character (C.43), were identical to those presented here.

Astrapogon – Fowleria clade. – Four character state changes occur on the branch leading to this clade: medium-width band of villiform teeth on the vomer (C.2), shelf only on the third infraorbital bone (C.7), notched ceratohyal (C.20), and two pairs of autogenous haemal spines (C.32). *Astrapogon* is distinguished from the remainder of the clade by seven characters: a wide band of villiform teeth on the jaws (C.10), a weakly notched ceratohyal (C.20), gill-rakers present on the first and second arch (C.24), a single predorsal bone (C.27), the presence of the eighth dorsal fin spine, although hidden by skin and scales (C.29), round caudal fin (C.39), and the presence of a single, large pore perforating the lateral margin of the supraorbital canal in the mid-interorbital space (C.47).

Phaeoptyx – Fowleria clade. – Three characters diagnose this group: the presence of the basisphenoid (C.4; character reverses on the branch leading to the *Apogonichthys – Vincentia* clade), hypurals not fused to the ural centrum (C.37), and ctenoid scales (C.40; *Apogon* (*Paroncheilus*) has cycloid scales) (Figure 55). *Phaeoptyx* is distinguished from the remainder of the clade by the presence of a partially ossified ventral preopercular edge (C.16; also present in *Apogon* (*Paroncheilus*)) and the presence of a fleshy flap extending from the preopercle (C.19; also occurs in some *Apogon* (*Apogon*) species).

Apogon – Fowleria clade. – Three character state changes occur along the branch leading to this clade: an increase in the number of villiform teeth on the jaws from a narrow band to a band of medium width (C.10), serrate preopercular edge (C.15), and an increase in the number of hypurals from three to five (C.36) (Figure 55). The presence of an unossified ventral edge on the preopercle (C.16), a weakly serrate posterior posttemporal margin (C.30), and a truncate caudal fin (C.36) distinguish *Apogon* (*Apogon*) from the remainder of the clade.

Brephamia – Paroncheilus clade. – These two taxa share a medium-width band of villiform teeth on the jaws (C.10) (Figure 55). *Apogon* (*Brephamia*) may be distinguished from *Apogon* (*Paroncheilus*) by the absence of villiform teeth on the palatine (C.12), lateral mandibular margin that is perforated but not developed into projections (C.51; the lateral mandibular margin of*Apogon* (*Paroncheilus*) is formed into numerous short projections), absence of canines on jaws (C.11; present in *Apogon* (*Paroncheilus*)), ossified ventral preopercular edge (C.16; unossified in *Apogon* (*Paroncheilus*)), ctenoid scales (C.40; versus cycloid in *Apogon* (*Paroncheilus*)), and the presence of a few, simple postorbital projections (C.48; versus numerous long and branching postorbital projections in *Apogon* (*Paroncheilus*)).

Jaydia – Fowleria clade. – This group of twenty-one taxa shares three predorsal bones (C.27) and two spines on the first pterygiophore (C.28; condition changes a number of times within clade) (Figure 55).

Lepidamia – Quinca clade. – These two taxa share a medium-width band of villiform teeth on the vomer (C.2) and nine epipleural ribs (C.26).

Yarica – Holapogon clade. – Four characters diagnose this group: exclusion of the intercalary facet from the otic bulla (C.5; character reversal), presence of supramaxilla (C.9), five pharyngeal tooth plates (C.23), truncate caudal fin (C.39; some *Glossamia* species have round caudal fins), and a single large pore perforating the lateral margin of the supraorbital canal in the mid-interorbital space (C.47) (Figure 55). The *Apogon* (*Yarica*) – *Holapogon* clade is composed of two, two taxon clades: the *Apogon* (*Yarica*) – *Glossamia* clade and the *Coranthus – Holapogon* clade. The *Apogon* (*Yarica*) – *Glossamia* clade is characterized by the presence of nine epipleural ribs (C.26) (Figure 56A). *Coranthus* and *Holapogon* share seven characters: no shelf on the infraorbital bones (C.7), a narrow band of villiform teeth on the palatine (C.12), perforated ceratohyal (C.20), two spines on the first pterygiophore (C.28), no eighth dorsal-fin spine (C.29), spine on the posttemporal (C.30), and two pairs of uroneurals (C.34). The*Apogon* (*Yarica*) – *Holapogon* clade was not present in the cladograms generated from the cladistic analysis of Fraser's (1972) data set. It had previously been proposed that these four taxa are closely related (Fraser, 1973). This cladogram is the first cladistically derived piece of evidence supporting this hypothesis.

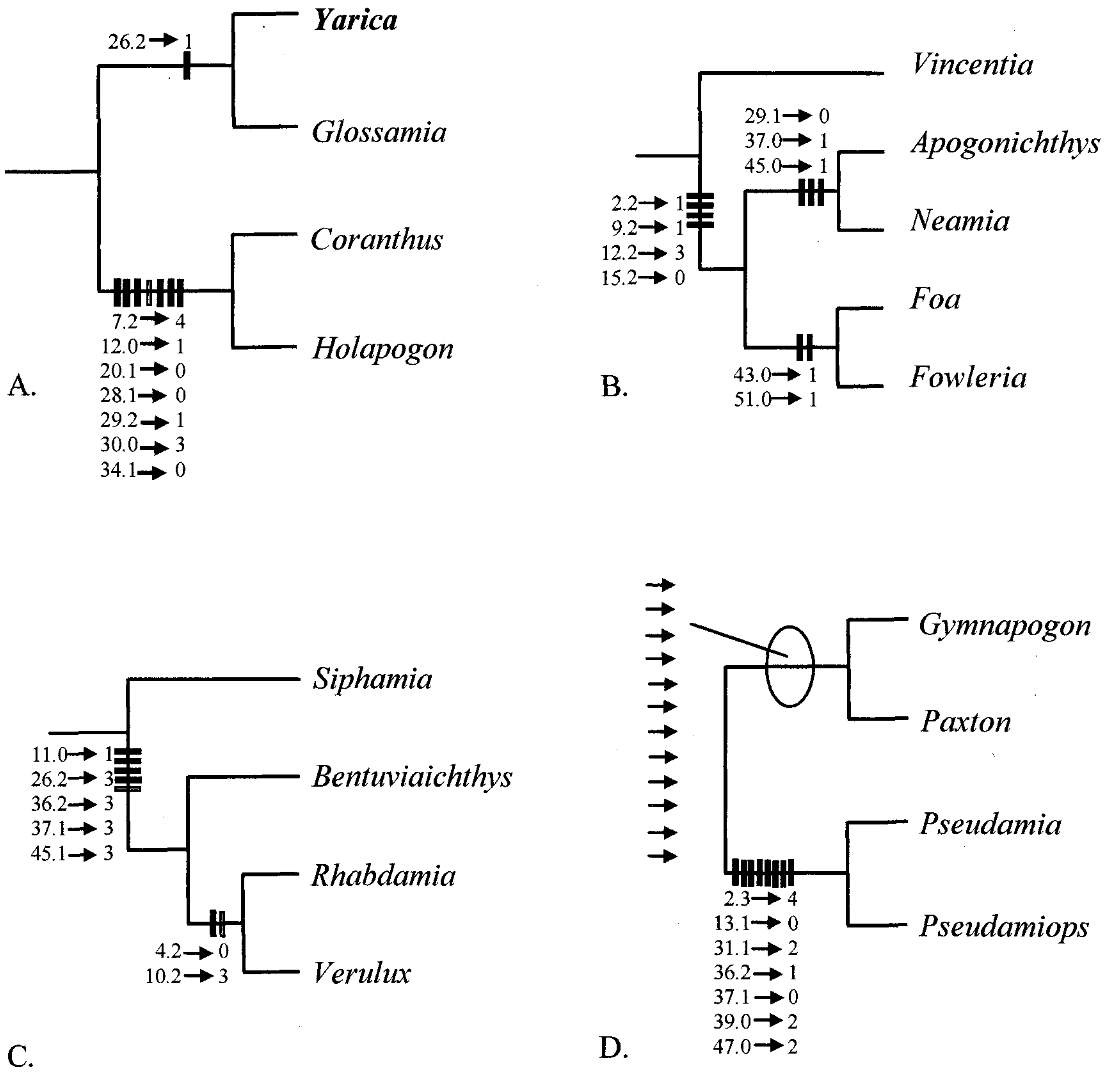


Figure 56. Selected clades from 75% majority-rule consensus tree with selected character state changes labeled on the branches. A. *Apogon* (*Yarica*)—*Holapogon* clade, B. *Vincentia—Fowleria* clade, C. *Siphamia—Rhabdamia* (*Verulux*) clade, D. *Gymnapogon—Pseudamiops* clade. The names of the *Apogon* subgenera are in bold. Homoplasious changes are indicated by open rather than solid bars.

Vincentia – Fowleria clade. – This five taxon group shares four characters: no basisphenoid (C.4), a wide band of villiform teeth on the jaws (C.10), a weakly notched ceratohyal (C.20), a reduced or hidden eighth dorsal-fin spine (C.29) (Figure 55). *Vincentia* is distinguished from the remainder of this clade in having 10 + 15 vertebrae (C.25), ten epipleural ribs (C.26), and the lateral margin of the supraorbital canal near the longitudinal mid-point of the interorbital space perforated by a single, large pore (C.47). *Apogonichthys*, *Neamia*, *Foa*, and *Fowleria* form a monophyletic group within the larger clade. This group is diagnosable by the presence of a medium-width band of villiform teeth on the vomer (C.2), a reduced supramaxilla (C.9), no villiform teeth on the palatine (C.12), and a smooth preopercular edge (C.15) (Figure 56B). Prior to the inclusion of the cephalic lateralis data, the morphological and osteological data was unable to resolve the relationships among the genera of the *Apogonichthys – Fowleria* clade. The results of the current analysis suggest that *Apogonichthys* and *Neamia* form a monophyletic group and *Foa* and *Fowleria* form a second monophyletic group, and together, these two groups form a clade that is sister to *Vincentia* (Figure 55). Two characters support the sister relationship between *Apogonichthys* and *Neamia*: the presence of an eighth dorsal-fin spine that is either visible or hidden by skin (C.29) and the fusion of the upper hypural plate to the ural centrum (C.37) (Figure 56B). The sister relationship between *Foa* and *Fowleria* is also supported by two characters: an incomplete lateral line (C.43) and a lateral mandibular margin that is perforated by is not developed into projections (C.51) (Figure 56B).

Siphamia – Verulux clade. – The four taxa in this clade share weakly ctenoid scales (C.40) and the development of the postorbital portion of the supraorbital canal into a few, relatively simple secondary projections (C.48). The 75% majority-rule cladogram supports the monophyly of the *Rhabdamia* genus as it is currently defined, for *Rhabdamia* (*Bentuviaichthys*), *R.* (*Rhabdamia*), and *R.* (*Verulux*) form a monophyletic clade within the *Siphamia – Verulux* clade (Figure 55). The *Rhabdamia* clade is diagnosed by three characters: the presence of canines on the jaws (C.11), seven epipleural ribs (C.26), two hypurals (C.36), and the upper and lower hypural plates fused to the ural centrum (C.37) (Figure 56C). The cladogram also suggests that structure exists within the genus, and provides support to its division into subgenera. *Rhabdamia* (*Bentuviaichthys*) is distinguished from *R.* (*Rhabdamia*) and *R.* (*Verulux*) by the presence of a deeply notched ceratohyal (C.20), two spines on the pterygiophore (C.28), and one reduced pair of uroneurals (C.34). *Rhabdamia* (*Bentuviaichthys*) and *R.* (*Bentuviaichthys*) share the presence of a basisphenoid (C.4) and a single row of villiform teeth on the jaws (C.10) (Figure 56C). *Rhabdamia* (*Rhabdamia*) is distinguished from *R.* (*Verulux*) by the presence of a shelf on the third infraorbital (C.7), two predorsals (C.27; versus one predorsal in *R.* (*Verulux*)), and three epurals (C.33; the number of epurals is reduced to two in *R.* (*Verulux*)). *Siphamia* is distinguished from the *Rhabdamia* clade by a medium-width band of villiform teeth on the jaws (C.10), serrate preopercular edge (C.15), presence of a bioluminescent organ (C.44), and the presence of a terminal mandibular pore (C.52) (Figure 56C).

Pseudaminae. – This group is diagnosed by four characters: the parasphenoid and pterosphenoid are not separated by an extension of the prootic (C.6), presence of canines on the jaws (C.11), a single postcleithrum (C.31; *Pseudamia* and *Pseudamiops* possess two postcleithra), and two epurals (C.33) (Figure 55). This clade is topologically identical to the pseudamine clade generated by the cladistic analysis of the morphological and osteological data set, only the character state changes that occur on the branch leading to the clade are different. The previous results included the presence of medium-sized scales (B.40) among the characters diagnosing the Pseudaminae. The current results do not include this character, and include one additional character, the presence of canines on the jaws (C.11), among those diagnosing the clade. Both analyses resulted in a sister group relationship between *Gymnapogon* and *Paxton.* The characters diagnosing this clade were identical except the analysis of the combined data set also included three cephalic lateralis characters: absence of postorbital projections (C.48) and the anterior and posterior supratemporal margins not developed into projections (C.49, C.50) (Figure 56D).

The cladograms generated from the cladistic analysis of the combined data set were topologically different than those generated from the analysis of the morphological and osteological data alone. Analysis of the combined data set yielded cladograms with more topological variance, as indicated by the reduced resolution of the various consensus trees. The strict consensus and 75% majority-rule consensus cladograms were topologically identical except for the resolved relationship between *Apogon* (*Lepidamia*) and *Pterapogon* (*Quinca*) in the 75% majority-rule consensus cladogram. Over half of the *Apogon* subgenera were members of an unresolved clade. The remaining *Apogon* subgenera were more closely related to non-*Apogon* taxa then they were to one another. The results of the cladistic analysis of the combined data set corroborate the previous findings of the polyphyletic nature of the *Apogon* and *Pterapogon* genera as they are currently defined.

Although the conclusion that *Apogon* sensu lato and *Pterapogon* sensu lato represent unnatural taxa is significant, it represents only a small subset of the potential information that can be obtained from a cladistic analysis. There are significant limitations on the conclusions that can be drawn from the current analyses, and neither one of the data sets was better than the other in terms of resolving the relationships among the apogonid taxa. Perhaps, this is not a fair criticism of the cephalic lateralis characters, as only eight (out of a total of 52) characters were added to Fraser's (1972) morphological and osteological characters to create the combined data set. The results of that analysis were still heavily biased toward the topologies driven by the morphological and osteological character state changes.

The low character to taxon ratio was a factor that may have contributed to the lack of resolution in the consensus cladograms. The character to taxon ration was less than 1:2 for both analyses. Low character to taxon ratios result in each node being supported by only a few character state changes. The higher the character to taxon ratio, the better the analysis, as there are more characters and character state changes available to diagnose the clades.

A lack of resolution, however, is not the most significant problem with the current analysis. The most significant weakness is the high level of homoplasy in the data set.

High levels of homoplasy in the data mean that even resolved relationships may not be based on homologous character state changes. The cladograms' low consistency indices are indicative of a large number of homoplastic character state changes. The low consistency indices do not affect the conclusion that *Apogon* sensu lato and *Pterapogon* sensu lato are unnatural taxa. Every cladogram generated in these analyses showed that the subgenera of these two taxa were more closely related to other genera, than they were to one another. And so, the conclusions that these two taxa are not monophyletic and that the family's current classification is not consistent with its evolutionary history are sound. But, the weakly supported phylogenies provide very little information upon which to make the necessary taxonomic revisions. Additional research is needed that focuses on the relationships within, rather than among, the Apogonidae's supra-specific taxa. Because the limits of most apogonid genera and subgenera have not been cladistically tested, it is quite likely that many of the larger supra-specific taxa represent non-monophyletic groups. This made identifying appropriately stable cephalic lateralis characters difficult, and it certainly increased the level of homoplasy seen in the cladograms. And so, to paraphrase Fraser (1972), the more we know about the systematic relationships among the apogonid species the easier it will be to understand how the supra-specific taxa are related.

CHAPTER 5. SUMMARY OF CONCLUSIONS

The family Apogonidae, with more than 250 species in 21 genera, is the eighth most speciose family in the Perciformes. Members of this family are found on every coral reef in all tropical and subtropical waters worldwide and yet, despite this apparent ubiquity, the systematic relationships of its species are poorly understood. Few studies have attempted to address the question of the family's evolutionary history and, as a result, little is known about the evolution of this major group of coral reef fish. This dissertation addresses this shortcoming by using data derived from the cephalic lateralis system, in conjunction with preexisting morphological and osteological data (Fraser, 1972), to produce a cladistically derived hypothesis of the evolutionary relationships among the genera and subgenera of the family.

Chapter 2 presents detailed descriptions of the cephalic lateralis system of each genus and subgenus in the family. The cephalic lateralis of apogonids is a highly diverse system; much variation exists within and among the family's genera and subgenera. In spite of the system's diversity, four cephalic lateralis characters are shared by all apogonids: the infraorbital canal terminates in a pore, two long pores perforate the distal margin of the suborbital portion of the infraorbital canal along the ventral edge of the lachrymal, the mandibular portion of the preoperculomandibular canal terminates anteriorly in a pair of pores that perforate the dentary, and the mandibular canal is perforated by a mental pore just posterior of the dentary. Whether or not these characters are apomorphic cannot be determined, for the sister group to the Apogonidae is unknown. Only eight cephalic lateralis characters were consistent at the level necessary for cladistic analysis of intergeneric relationships: the position of the terminal pore of the supraorbital canal, the development and perforation of the lateral supraorbital canal margin adjacent to the posterior nostril, the development and perforation of the supraorbital canal near the longitudinal mid-point of the interorbital space, the degree of development of the supratemporal canal in the postorbital space, the development of the anterior supratemporal margin, the development of the posterior supratemporal margin, the morphology of the lateral mandibular margin, and the presence or absence of the terminal mandibular pore.

Optimization of the cephalic lateralis characters onto the 75% majority-rule consensus cladogram (generated from the cladistic analysis of Fraser's (1972) osteological and morphological data set) resulted in a pattern of character state changes was complex and replete with homoplasy. Although the character state changes were not easily mapped onto the cladogram, it was possible to identify a number of changes that were shared by members of several clades. The overall evolutionary trend in the cephalic lateralis system in the Apogonidae is one of increasing complexity from the simple, sparsely perforated canals that characterize the cephalic lateralis system of the Pseudaminae to the highly branched and densely perforated canals characteristic of most apogonine taxa.

Chapters 3 and 4 attempt to fill the gap in our knowledge of the evolution of the Apogonidae by presenting a hypotheses of the family's evolutionary history based on two cladistic analyses. The first was an analysis of Fraser's (1972) morphological and osteological data and the second, an analysis of a data set composed of cephalic lateralis characters and Fraser's (1972) morphological and osteological characters. These analyses resulted in a number of well-resolved, but not well-supported (as indicated by the consistency and retention indices), equally parsimonious cladograms. Homoplasies aside, all of the cladograms suggest that the apogonid genera *Apogon* sensu lato and *Pterapogon* sensu lato are not monophyletic as they are currently defined. The results of this research indicate that the current classification of the Apogonidae, one of the world's most speciose coral reef fish families, is in need of revision, as it does not inaccurately portray the group's evolutionary history.

Although the conclusion that *Apogon* sensu lato and *Pterapogon* sensu lato represent unnatural taxa is significant, it represents only a small subset of the potential information that can be obtained from a cladistic analysis. There are significant limitations on the conclusions that can be drawn from the current analyses.
The low character to taxon ratio was a factor that may have contributed to the lack of resolution in the consensus cladograms. The character to taxon ration was less than 1:2 for both analyses. Low character to taxon ratios result in each node being supported by only a few character state changes. The higher the character to taxon ratio, the better the analysis, as there are more characters and character state changes available to diagnose the clades.

A lack of resolution, however, is not the most significant problem with the current analysis. The most significant weakness is the high level of homoplasy in the data set. High levels of homoplasy in the data mean that even resolved relationships may not be based on homologous character state changes. The cladograms' low consistency indices are indicative of a large number of homoplastic character state changes. The low consistency indices do not affect the conclusion that *Apogon* sensu lato and *Pterapogon* sensu lato are unnatural taxa. Every cladogram generated in these analyses showed that the subgenera of these two taxa were more closely related to other genera, than they were to one another. And so, the conclusions that these two taxa are not monophyletic and that the family's current classification is not consistent with its evolutionary history are sound. But, the weakly supported phylogenies provide very little information upon which to make the necessary taxonomic revisions.

The results of this research highlight the fact that much remains unknown about the phylogenetic history of the Apogonidae. They also function to identify specific areas in need of attention before significant progress can be made toward understanding the evolutionary history of the family as a whole. Future research must focus on the relationships within, rather than among, the family's supra-specific taxa. The limits of most apogonid genera and subgenera have not been cladistically tested and it is likely that many of the more speciose supra-specific taxa are not monophyletic. Cladistic analyses need to be completed on each supra-specific taxon, and the cladograms presented in this dissertation can provide guidance for outgroup selection in these investigations.

APPENDIX A.

Taxon by Character Matrix for *Apogon* Subgenera and Outgroups

Taxon	Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Apogon	0	1	1	0	2	0	0	2	1	2	1	$^{0}_{1}{}^{2}$	1	1	1	3	0	1
Brephamia	2	1	1	0	2	2	0	3	0	2	1	2	1	1	0	3	0	1
Jaydia	1	1	?	1	2	0	0	1	2	1	1	$^{0}_{1}$	0	1	0	$^{2}_{3}$	2	1
Lepidamia	0	1	1	0	2	0	0	1	0	2	1	1	0	0	2	2	0	2
Paroncheilus	2	1	1	0	2	2	1	2	1	2	1	2	1	1	0	3	0	1
Pristiapogon	2	1	1	2	2	0	0	$^{2}_{3}$	0	0	1	2	0	0	1	3	0	1
Pristicon	1	1	1	2	2	0	0	0	0	0	1	1	0	1	1	1	0	1
Ostorhinchus	1	1	1	0	2	$^{0}_{1}{}^{2}$	0	1	0	1	1	2	0	$^{0}_{1}$	1	2	$^{0}_{2}$	1
Yarica	1	0	1	0	0	0	0	0	0	2	1	1	0	1	0	1	1	1
Zapogon	1	1	1	0	2	0	0	0	0	2	2	2	1	1	0	1	0	2
Zoramia	1	1	3	0	2	1	0	2	0	2	1	$^{2}_{3}$	0	1	0	1	0	1
Cheilodipterus	$^{1}_{2}$	1	0	1	1	1	1	$^{1}_{2}$	$^{0}_{2}$	2	$^{1}_{2}$	$^{2}_{3}$	0	1	0	1	$^{0}_{1}$	1
Holapogon	1	0	1	0	0	0	0	0	0	2	0	2	0	0	2	0	1	1
Phaeoptyx	0	1	1	0	2	1	0	2	1	2	1	2	1	1	0	3	0	1

APPENDIX B.

Taxon by Character Matrix for the Apogonidae [Morphological and Osteological Characters (Fraser, 1972)]

Taxon	Character 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Apogon	0	1	0	0	1	0	2	0	2	1	0	2	1	0	2	0	0	0
Brephamia	0	3	0	0	1	0	2	0	2	3	0	3	1	0	2	2	0	0
Jaydia	0	2	0	0	1	0	?	1	2	1	0	1	?	1	1	2	0	0
Lepidamia	0	1	0	0	1	0	2	0	2	1	0	1	1	0	2	2	0	0
Paroncheilus	0	3	0	0	1	0	2	0	2	3	1	2	1	0	2	1	0	0
Pristiapogon	0	3	0	0	1	0	2	2	2	0	0	$^{2}_{3}$	1	2	2	2	0	0
Pristicon	0	2	0	0	1	0	2	2	2	0	0	0	1	2	2	2	0	0
Ostorhinchus	0	2	0	0	1	0	2	0	2	$^{0}_{1}{}^{2}_{3}$	2	2	1	0	2	2	0	0
Yarica	0	2	0	0	0	0	2	0	0	1	0	0	1	0	2	2	0	0
Zapogon	0	2	0	0	1	0	2	0	2	0	0	0	1	0	2	0	0	0
Zoramia	1	2	0	0	1	0	4	0	2	2	0	2	1	0	2	2	0	0
Apogonichthys	0	$^{1}_{2}$	0	1	1	0	2	0	1	0	0	$^{2}_{3}$	$^{0}_{1}$	0	0	2	0	0
Archamia	1	3	0	0	1	0	2	0	2	2	0	1	1	0	0	2	0	0
Astrapogon	0	1	0	2	1	0	2	0	2	0	0	2	1	0	0	2	0	0
Cercamia	0	3	1	2	1	0	0	0	2	$^{2}_{3}$	0	3	1	0	0	2	2	0
Cheilodipterus	0	$^{1}_{2}$	1	0	1	0	2	0	1	1	1	$^{1}_{2}$	1	0	$^{1}_{2}$	2	0	0
Coranthus	0	2	1	0	?	?	?	0	0	2	1	2	1	0	2	2	0	0
Foa	0	1	0	1	1	0	2	0	1	0	0	$^{1}_{2}{}^{3}$	1	0	0	2	0	0
Fowleria	0	0	0	2	1	0	1	0	1	0	0	3	1	0	0	2	0	0
Glossamia	0	2	0	$^{1}_{2}$	0	0	2	0	0	0	0	0	0	0	0	2	0	0
Holapogon	0	2	0	0	0	0	4	0	0	1	0	1	1	0	2	2	0	0
Lachneratus	0	4	1	?	?	0	?	?	2	0	1	$^{1}_{2}$	1	0	0	2	2	0
Neamia	0	$^{1}_{2}$	0	2	1	0	2	0	1	1	0	3	1	0	0	2	0	0
Phaeoptyx	0	1	0	$^{0}_{1}{}^{2}$	1	0	2	0	2	2	0	2	1	0	0	1	0	0
Pterapogon	1	3	0	0	?	0	?	0	2	2	0	3	1	0	2	2	0	0
Quinca	0	1	0	0	?	0	?	0	2	1	0	1	1	0	2	2	0	0
Bentuviaichthys	0	3	0	2	1	0	4	0	2	2	1	2	1	0	0	2	0	0
Rhabdamia	0	3	0	0	1	0	3	0	2	3	1	$^{2}_{3}$	1	0	0	2	0	0
Verulux	0	3	0	0	1	0	4	0	2	3	1	$^{2}_{3}$	1	0	0	2	0	0
Siphamia	0	3	0	2	1	0	4	0	2	1	0	2	1	0	2	2	0	0
Sphaeramia	1	2	0	0	1	0	4	0	2	0	0	0	1	0	2	2	0	0
Vincentia	0	2	0	2	1	0	2	0	2	0	0	2	1	0	2	2	0	0
Gymnapogon	0	3	1	2	0	1	3	0	2	2	1	0	1	0	0	-	1	1
Paxton	0	3	1	2	0	1	4	0	2	2	1	2	1	-	-	-	1	2
Pseudamia	0	4	1	2	0	1	4	0	2	2	1	0	0	0	0	2	0	0
Pseudamiops	0	4	1	2	0	1	4	0	2	2	1	0	0	0	0	2	0	0

APPENDIX B. CONTINUED

Taxon by Character Matrix for the Apogonidae [Morphological and Osteological Characters (Fraser, 1972)]

Taxon	Character																
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Apogon	$^{0}_{1}$	1	1	0	1	0	1	$^{0\,2}_{1}$	1	1	2	1	0	0	0	3	0	0
Brephamia	0	1	1	0	1	0	1	2	1	1	2	0	0	0	0	3	0	0
Jaydia	0	?	1	0	?	0	1	?	$^{0}_{1}$	0	2	1	0	0	0	2	$^{2}_{3}$	0
Lepidamia	0	1	1	0	1	0	1	1	0	0	1	2	0	0	0	2	0	0
Paroncheilus	0	1	1	0	1	0	1	2	1	1	2	0	0	0	0	3	0	0
0Pristiapogon	0	1	1	0	1	0	1	2	0	0	2	?	0	0	0	3	0	0
Pristicon	0	1	1	0	1	0	1	1	0	1	2	1	0	0	0	1	0	0
Ostorhinchus	0	1	1	0	1	0	1	2	0	$^{0}_{1}$	2	?	0	0	0	2	0	0
Yarica	0	1	1	0	1	0	1	1	0	1	2	0	0	0	0	1	0	0
Zapogon	0	3	1	0	1	0	1	2	1	1	2	0	0	0	0	1	0	0
Zoramia	0	1	1	0	1	0	1	?	0	1	2	0	0	0	0	1	0	0
Apogonichthys	0	2	1	1	$^{1}_{2}$	0	1	2	0	0	0	0	0	0	0	1	0	0
Archamia	0	1	1	0	1	1	1	2	0	1	2	2	0	0	0	1	0	0
Astrapogon	0	2	1	0	1	1	1	2	2	1	1	0	0	0	0	3	0	2
Cercamia	0	3	1	0	1	1	2	8	3	1	2	3	0	2	0	3	0	3
Cheilodipterus	0	$^{1}_{2}$	0	0	$^{1}_{2}$	0	1	$^{2}_{3}$	0	1	2	0	0	0	0	1	0	0
Coranthus	0	?	?	?	?	0	1	3	0	0	1	3	0	0	0	0	0	0
Foa	0	3	1	0	1	0	1	2	0	0	2	0	0	2	0	0	0	0
Fowleria	0	2	1	1	1	0	1	2	0	0	1	0	0	0	0	1	0	0
Glossamia	0	1	0	0	0	0	1	1	0	1	2	0	0	0	0	1	0	0
Holapogon	0	0	1	0	0	0	1	2	0	0	1	3	0	0	0	0	0	0
Lachneratus	0	?	?	?	?	0	1	7	3	1	2	?	0	2	0	3	0	3
Neamia	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	2	0	2
Phaeoptyx	1	1	1	0	1	0	1	2	1	1	2	0	0	0	0	3	0	2
Pterapogon	0	?	?	?	?	0	1	?	0	0	2	?	0	0	0	1	0	0
Quinca	0	?	?	?	?	0	1	?	0	0	2	?	0	0	0	1	0	0
Bentuviaichthys	0	1	1	0	1	0	1	3	1	0	2	0	0	2	0	2	0	3
Rhabdamia	0	3	1	0	1	0	1	3	1	1	2	0	0	2	0	3	0	3
Verulux	0	3	1	0	1	0	1	?	2	1	2	0	0	2	2	3	0	3
Siphamia	0	3	1	0	1	0	1	2	$^{1}_{2}$	$^{0}_{1}$	2	?	$^{0}_{1}$	$^{1}_{2}$	$^{0}_{2}$	3	0	2
Sphaeramia	0	1	1	0	1	0	1	2	0	1	1	2	0	0	0	1	0	0
Vincentia	0	2	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0
Gymnapogon	1	3	1	2	0	1	1	4	3	1	2	0	1	1	2	3	1	2
Paxton	1	3	0	2	1	1	1	2	3	1	2	0	1	2	2	3	1	2
Pseudamia	0	1	1	0	1	0	1	$^{1}_{2}$	$^{1}_{2}$	1	2	0	2	2	2	2	0	1
Pseudamiops	0	3	1	0	1	0	1	8	$^{1\,3}_{2}$	1	2	0	2	2	2	3	0	1

APPENDIX B. CONTINUED

Taxon by Character Matrix for the Apogonidae [Morphological and Osteological Characters (Fraser, 1972)]

Taxon	Character							
	37	38	39	40	41	42	43	44
Apogon	0	0	1	0	0	1	0	0
Bephamia	0	0	0	0	0	1	$^{0}_{1}$	0
Jaydia	0	0	2	0	0	1	0	2
Lepidamia	0	0	0	0	0	2	0	0
Paroncheilus	0	0	0	2	0	1	0	0
Pristiapogon	0	0	0	0	0	1	0	0
Pristicon	0	0	0	0	0	1	0	0
Ostorhinchus	0	0	$^{0}_{2}$	0	0	1	0	0
Yarica	0	0	1	0	0	1	0	0
Zapogon	0	0	0	0	0	2	0	0
Zoramia	0	0	0	0	0	1	0	0
Apogonichthys	1	0	2	0	0	1	0	0
Archamia	0	0	0	0	0	1	0	0
Astrapogon	1	0	2	2	0	1	0	0
Cercamia	?	1	0	1	1	1	?	0
Cheilodipterus	0	0	0	0	0	1	0	0
Coranthus	0	0	1	0	0	1	0	0
Foa	0	0	2	0	0	1	1	0
Fowleria	0	0	2	0	0	1	$^{0}_{1}$	0
Glossamia	0	0	$^{1}_{2}$	0	0	2	0	0
Holapogon	0	0	1	0	0	1	0	0
Lachneratus	?	0	0	2	1	1	2	0
Neamia	1	0	2	0	0	1	0	0
Phaeoptyx	0	0	0	0	0	1	0	0
Pterapogon	0	1	0	0	0	1	0	0
Quinca	0	1	0	0	0	1	0	0
Bentuviaichthys	3	0	0	1	0	1	0	0
Rhabdamia	3	0	0	1	0	1	0	0
Verulux	3	0	0	1	0	1	0	$^{0}_{2}$
Siphamia	1	0	0	1	0	1	0	1
Sphaeramia	0	1	0	0	0	1	0	0
Vincentia	0	0	$^{1}_{2}$	0	0	1	0	0
Gymnapogon	1	0	0	3	-	-	-	0
Paxton	1	0	1	3	-	-	-	0
Pseudamia	0	0	2	2	1	2	1	0
Pseudamiops	2	0	2	2	0	0	2	0

APPENDIX C.

Taxon by Character Matrix for the Apogonidae [Cephalic Lateralis, Morphological, and Osteological Characters]

Taxon	Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Apogon	0	1	0	0	1	0	2	0	2	1	0	2	1	0	2	0	0	0
Brephamia	0	3	0	0	1	0	2	0	2	3	0	3	1	0	2	2	0	0
Jaydia	0	2	0	0	1	0	?	1	2	1	0	1	?	1	1	2	0	0
Lepidamia	0	1	0	0	1	0	2	0	2	1	0	1	1	0	2	2	0	0
Paroncheilus	0	3	0	0	1	0	2	0	2	3	1	2	1	0	2	1	0	0
Pristiapogon	0	3	0	0	1	0	2	2	2	0	0	$^{2}_{3}$	1	2	2	2	0	0
Pristicon	0	2	0	0	1	0	2	2	2	0	0	0	1	2	2	2	0	0
Ostorhinchus	0	2	0	0	1	0	2	0	2	$^{0\,2}_{1\,3}$	2	2	1	0	2	2	0	0
Yarica	0	2	0	0	0	0	2	0	0	1	0	0	1	0	2	2	0	0
Zapogon	0	2	0	0	1	0	2	0	2	0	0	0	1	0	2	0	0	0
Zoramia	1	2	0	0	1	0	4	0	2	2	0	2	1	0	2	2	0	0
Apogonichthys	0	$^{1}_{2}$	0	1	1	0	2	0	1	0	0	$^{2}_{3}$	$^{0}_{1}$	0	0	2	0	0
Archamia	1	3	0	0	1	0	2	0	2	2	0	1	1	0	0	2	0	0
Astrapogon	0	1	0	2	1	0	2	0	2	0	0	2	1	0	0	2	0	0
Cercamia	0	3	1	2	1	0	0	0	2	$^{2}_{3}$	0	3	1	0	0	2	2	0
Cheilodipterus	0	$^{1}_{2}$	1	0	1	0	2	0	1	1	1	$^{1}_{2}$	1	0	$^{1}_{2}$	2	0	0
Coranthus	0	2	1	0	?	?	?	0	0	2	1	2	1	0	2	2	0	0
Foa	0	1	0	1	1	0	2	0	1	0	0	$^{1\,3}_{2}$	1	0	0	2	0	0
Fowleria	0	0	0	2	1	0	1	0	1	0	0	3	1	0	0	2	0	0
Glossamia	0	2	0	$^{1}_{2}$	0	0	2	0	0	0	0	0	0	0	0	2	0	0
Holapogon	0	2	0	0	0	0	4	0	0	1	0	1	1	0	2	2	0	0
Lachneratus	0	4	1	?	?	0	?	?	2	0	1	$^{1}_{2}$	1	0	0	2	2	0
Neamia	0	$^{1}_{2}$	0	2	1	0	2	0	1	1	0	3	1	0	0	2	0	0
Phaeoptyx	0	1	0	$^{0\,2}_{1}$	1	0	2	0	2	2	0	2	1	0	0	1	0	0
Pterapogon	1	3	0	0	?	0	?	0	2	2	0	3	1	0	2	2	0	0
Quinca	0	1	0	0	?	0	?	0	2	1	0	1	1	0	2	2	0	0
Bentuviaichthys	0	3	0	2	1	0	4	0	2	2	1	2	1	0	0	2	0	0
Rhabdamia	0	3	0	0	1	0	3	0	2	3	1	$^{2}_{3}$	1	0	0	2	0	0
Verulux	0	3	0	0	1	0	4	0	2	3	1	$^{2}_{3}$	1	0	0	2	0	0
Siphamia	0	3	0	2	1	0	4	0	2	1	0	2	1	0	2	2	0	0
Sphaeramia	1	2	0	0	1	0	4	0	2	0	0	0	1	0	2	2	0	0
Vincentia	0	2	0	2	1	0	2	0	2	0	0	2	1	0	2	2	0	0
Gymnapogon	0	3	1	2	0	1	3	0	2	2	1	0	1	0	0	-	1	1
Paxton	0	3	1	2	0	1	4	0	2	2	1	2	1	-	-	-	1	2
Pseudamia	0	4	1	2	0	1	4	0	2	2	1	0	0	0	0	2	0	0
Pseudamiops	0	4	1	2	0	1	4	0	2	2	1	0	0	0	0	2	0	0

APPENDIX C. CONTINUED

Taxon by Character Matrix for the Apogonidae [Cephalic Lateralis, Morphological, and Osteological Characters]

Taxon	Character																
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Apogon	$^{0}_{1}$	1	1	0	1	0	1	$^{0\,2}_{1}$	1	1	2	1	0	0	0	3	0	0
Brephamia	0	1	1	0	1	0	1	2	1	1	2	0	0	0	0	3	0	0
Jaydia	0	?	1	0	?	0	1	?	$^{0}_{1}$	0	2	1	0	0	0	2	$^{2}_{3}$	0
Lepidamia	0	1	1	0	1	0	1	1	0	0	1	2	0	0	0	2	0	0
Paroncheilus	0	1	1	0	1	0	1	2	1	1	2	0	0	0	0	3	0	0
0Pristiapogon	0	1	1	0	1	0	1	2	0	0	2	?	0	0	0	3	0	0
Pristicon	0	1	1	0	1	0	1	1	0	1	2	1	0	0	0	1	0	0
Ostorhinchus	0	1	1	0	1	0	1	2	0	$^{0}_{1}$	2	?	0	0	0	2	0	0
Yarica	0	1	1	0	1	0	1	1	0	1	2	0	0	0	0	1	0	0
Zapogon	0	3	1	0	1	0	1	2	1	1	2	0	0	0	0	1	0	0
Zoramia	0	1	1	0	1	0	1	?	0	1	2	0	0	0	0	1	0	0
Apogonichthys	0	2	1	1	$^{1}_{2}$	0	1	2	0	0	0	0	0	0	0	1	0	0
Archamia	0	1	1	0	1	1	1	2	0	1	2	2	0	0	0	1	0	0
Astrapogon	0	2	1	0	1	1	1	2	2	1	1	0	0	0	0	3	0	2
Cercamia	0	3	1	0	1	1	2	8	3	1	2	3	0	2	0	3	0	3
Cheilodipterus	0	$^{1}_{2}$	0	0	$^{1}_{2}$	0	1	$^{2}_{3}$	0	1	2	0	0	0	0	1	0	0
Coranthus	0	?	?	?	?	0	1	3	0	0	1	3	0	0	0	0	0	0
Foa	0	3	1	0	1	0	1	2	0	0	2	0	0	2	0	0	0	0
Fowleria	0	2	1	1	1	0	1	2	0	0	1	0	0	0	0	1	0	0
Glossamia	0	1	0	0	0	0	1	1	0	1	2	0	0	0	0	1	0	0
Holapogon	0	0	1	0	0	0	1	2	0	0	1	3	0	0	0	0	0	0
Lachneratus	0	?	?	?	?	0	1	7	3	1	2	?	0	2	0	3	0	3
Neamia	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	2	0	2
Phaeoptyx	1	1	1	0	1	0	1	2	1	1	2	0	0	0	0	3	0	2
Pterapogon	0	?	?	?	?	0	1	?	0	0	2	?	0	0	0	1	0	0
Quinca	0	?	?	?	?	0	1	?	0	0	2	?	0	0	0	1	0	0
Bentuviaichthys	0	1	1	0	1	0	1	3	1	0	2	0	0	2	0	2	0	3
Rhabdamia	0	3	1	0	1	0	1	3	1	1	2	0	0	2	0	3	0	3
Verulux	0	3	1	0	1	0	1	?	2	1	2	0	0	2	2	3	0	3
Siphamia	0	3	1	0	1	0	1	2	$^{1}_{2}$	$^{0}_{1}$	2	?	$^{0}_{1}$	$^{1}_{2}$	$^{0}_{2}$	3	0	2
Sphaeramia	0	1	1	0	1	0	1	2	0	1	1	2	0	0	0	1	0	0
Vincentia	0	2	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0
Gymnapogon	1	3	1	2	0	1	1	4	3	1	2	0	1	1	2	3	1	2
Paxton	1	3	0	2	1	1	1	2	3	1	2	0	1	2	2	3	1	2
Pseudamia	0	1	1	0	1	0	1	$^{1}_{2}$	$^{1}_{2}$	1	2	0	2	2	2	2	0	1
Pseudamiops	0	3	1	0	1	0	1	8	$^{1\,3}_{2}$	1	2	0	2	2	2	3	0	1

APPENDIX C. CONTINUED

Taxon by Character Matrix for the Apogonidae [Cephalic Lateralis, Morphological, and Osteological Characters]

Taxon	Character 37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
Apogon	0	0	1	0	0	1	0	0	1	1	2	2	0	2	3	1
Brephamia	0	0	0	0	0	1	$^{0}_{1}$	0	0	1	1	1	1	1	2	0
Jaydia	0	0	2	0	0	1	0	2	0	1	1	2	0	2	1	0
Lepidamia	0	0	0	0	0	2	0	0	1	1	0	1	0	2	3	0
Paroncheilus	0	0	0	2	0	1	0	0	0	1	1	2	0	2	2	0
Pristiapogon	0	0	0	0	0	1	0	0	1	1	1	2	0	1	2	0
Pristicon	0	0	0	0	0	1	0	0	0	1	2	2	0	2	2	0
Ostorhinchus	0	0	$^{0}_{2}$	0	0	1	0	0	1	2	1	1	0	2	3	0
Yarica	0	0	1	0	0	1	0	0	0	1	2	2	0	1	2	0
Zapogon	0	0	0	0	0	2	0	0	1	1	1	1	0	0	1	0
Zoramia	0	0	0	0	0	1	0	0	0	1	1	2	0	2	2	0
Apogonichthys	1	0	2	0	0	1	0	0	1	1	1	1	0	2	1	0
Archamia	0	0	0	0	0	1	0	0	0	1	1	1	1	2	2	1
Astrapogon	1	0	2	2	0	1	0	0	0	1	1	1	0	2	2	0
Cercamia	?	1	0	1	1	1	?	0	0	1	0	1	0	1	1	1
Cheilodipterus	0	0	0	0	0	1	0	0	0	2	2	2	0	2	3	1
Coranthus	0	0	1	0	0	1	0	0	0	2	2	2	0	2	3	0
Foa	0	0	2	0	0	1	1	0	0	1	1	1	0	2	1	0
Fowleria	0	0	2	0	0	1	$^{0}_{1}$	0	0	1	1	2	0	1	2	0
Glossamia	0	0	$^{1}_{2}$	0	0	2	0	0	0	1	1	1	0	0	1	0
Holapogon	0	0	1	0	0	1	0	0	1	2	2	2	0	2	3	0
Lachneratus	?	0	0	2	1	1	2	0	0	1	1	1	0	0	1	0
Neamia	1	0	2	0	0	1	0	0	0	1	1	1	0	1	2	0
Phaeoptyx	0	0	0	0	0	1	0	0	0	1	1	2	0	2	1	0
Pterapogon	0	1	0	0	0	1	0	0	0	1	1	1	0	2	1	0
Quinca	0	1	0	0	0	1	0	0	1	1	2	2	0	2	3	0
Bentuviaichthys	3	0	0	1	0	1	0	0	0	2	2	2	1	2	3	1
Rhabdamia	3	0	0	1	0	1	0	0	0	1	2	2	0	2	3	1
Verulux	3	0	0	1	0	1	0	$^{0}_{2}$	0	1	2	2	1	2	3	1
Siphamia	1	0	0	1	0	1	0	1	0	1	1	1	1	1	1	0
Sphaeramia	0	1	0	0	0	1	0	0	0	1	1	1	0	2	1	0
Vincentia	0	0	$^{1}_{2}$	0	0	1	0	0	1	1	1	2	1	2	3	0
Gymnapogon	1	0	0	3	-	-	-	0	0	1	1	0	0	0	1	0
Paxton	1	0	1	3	-	-	-	0	0	1	1	0	0	0	0	1
Pseudamia	0	0	2	2	1	2	1	0	0	0	0	0	0	0	0	1
Pseudamiops	2	0	2	2	0	0	2	0	0	1	1	0	0	0	1	0

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