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Paxton concilians: A New Genus and Species of Pseudamine Apogonid (Teleostei: Percoidei) from Northwestern Australia: The Sister Group of the Enigmatic *Gymnapogon*

CAROLE C. BALDWIN AND G. DAVID JOHNSON

Paxton concilians is described as a new genus and species of pseudamine apogonid from four specimens trawled off northwestern Australia. It differs most conspicuously from all other apogonids in having a continuous dorsal fin but shares with other members of the family certain specializations of the dorsal gill arches, last spinous dorsal fin pterygiophore, and cutaneous sensory system. We recognize two subfamilies of apogonids, the Apogoninae and Pseudaminae, and diagnose the latter on the basis of numerous derived features. We propose that *Paxton* be added as a fourth member of the Pseudaminae (with *Gymnapogon*, *Pseudamia*, and *Pseudamiops*) and provide strong evidence that *Paxton* is the sister group of *Gymnapogon*, a taxon whose phylogenetic position within the Apogonidae has never been well understood.

IN his comprehensive study of the osteology of cardinalfishes, Fraser (1972) followed Smith (1954) in recognizing the subfamily Pseudaminae for *Pseudamia* Bleeker, 1865, *Pseudamiops* Smith, 1954, and *Gymnapogon* Regan, 1905 (including *Henicichthys* Tanaka, 1915, *Australaphia* Whitley, 1936, and *Acanthapogon* Fowler, 1938). Fraser's (1972) classification of the group differed from Smith's (1954) only in his recognition of *Lachneria* Smith, 1954, as a synonym of *Pseudamiops*. Although a close relationship between *Pseudamia* and apogonids was obvious to Bleeker (1865), relationships of *Gymnapogon* have not always been so evident. As noted by Fraser (1972, and references therein), the genus has been placed in or associated with six families: Apogonidae, Gymnapogonidae, Gobiidae, Henicichthyidae, Pomatomidae, and Trichodontidae. Citing features of external anatomy and osteology, Regan (1940) argued that *Gymnapogon* is not closely related to pomatomids (which at the time included *Scombrops*) but rather to apogonids (formerly cheilodipterids). Smith (1954:776) first recognized that "... *Gymnapogon* Regan, 1905, . . . , is clearly and closely related to *Pseudamia* Bleeker. . . ." Fraser (1972: 32–33) also recognized similarities between *Gymnapogon* and *Pseudamia/Pseudamiops* but noted nevertheless that the "genus is not intimately related to apogonids or other percoid fishes." Among the characters of pseudamines that have elicited questions regarding their alignment with the typical shallow-water cardinalfishes are a weakly scaled body (scales deciduous or absent), canine teeth in the upper and lower jaws, a reduced number of supraneurals and epurals, and an elongate neurocranium (Fraser, 1972). *Gymnapogon* is further specialized in having a

well-developed preopercular spine, the parhypural fused to the lower hypural plate, and a single postcleithrum (Smith, 1954; Fraser, 1972). The Pseudaminae have not been diagnosed cladistically, and some pseudamine specimens continue to be misplaced in fish collections, often being shelved with eleotrids or gobiids.

Several years ago, the second author received from J. R. Paxton (Australian Museum, Sydney) four specimens of an unidentified percoid fish collected by trawl off northwestern Australia that were believed to represent an undescribed genus of grammistid serranid (Gloerfelt-Tarp and Kailola, 1984; Sainsbury et al., 1984; Paxton et al., 1989). Johnson's [unpubl. abstract, 70th Annual Meeting of the American Society of Ichthyologists and Herpetologists (ASIH), 1990] conclusion that the specimens represent a new genus of pseudamine apogonid was completely unexpected upon superficial examination of them: unlike all other apogonids, the northwestern Australian specimens have a continuous dorsal fin. In the process of identifying the specimens, a large number of lower percoids was examined, which ultimately resulted in the discovery of derived characters useful in diagnosing the Apogonidae (Johnson, 1993). Here we describe the external anatomy and osteology of *Paxton concilians*, compare the new genus to other apogonids, diagnose the Pseudaminae on the basis of derived characters, provide evidence of a pseudamine affinity for *Paxton*, and document with derived characters a sister-group relationship between *Paxton* and *Gymnapogon*. A phylogenetic analysis that includes all pseudamine species is in progress.

MATERIALS AND METHODS

Institutional abbreviations follow Leviton et al. (1985). Terminology and abbreviations of structures in the caudal skeleton follow Fujita (1990), the intermusculars Patterson and Johnson (1995), and the pelvic girdle Stiassny and Moore (1992). The osteological description of *P. concilians* is based primarily on examination of a single cleared-and-stained specimen, CSIRO H.2254-1. Drawings were made with the aid of a camera lucida. Scale bars in all illustrations represent 1 mm.

In hypothesizing character polarity for the Apogonidae, numerous lower percoids were examined (see Material Examined). In polarizing characters of the Pseudaminae, other apogonids were considered the first outgroup and the same selection of lower percoids the second. Autapomorphic characters of *Paxton* were identified using other pseudamines as the first outgroup and apogonines as the second, based on the hypotheses of apogonid relationships proposed herein.

Comparative cleared-and-stained apogonid and percoid material examined included the following: Acropomatidae—*Acropoma* sp. USNM 287444, 2 specimens; *Synagrops bella* USNM 218918, 1; Apogonidae—*Apogon lateralis* USNM 169600, 1; *A. moluccensis* USNM 213380, 1; *Apogonichthys ocellatus* USNM 318066, 1; *Apogonops anomalous* USNM 287447, 1; *Archamia zosterophora* USNM 218801, 2; *Astrapogon stellatus* USNM 339373, 1; *Cercamia cladara* USNM 341821, 1; *C. eremia* USNM 334713, 1; *Cheilodipterus quinque-lineatus* USNM 218806, 2; *Fowleria variegata* USNM 218804, 2; *Glossamia aprion* USNM 212197, 1; *Gymnapogon annona* USNM 205671, 1; *G. philippinus* USNM 268313, 4; 262171, 4; *G. urospilatus* USNM 288032, 1; *Gymnapogon* sp. no data, 3; *Neamia octospina* USNM 203779, 1; *Phaeoptyx conklini* USNM 327788, 9; *Pseudamia gelatinosa* USNM 218802, 1; *P. hayashii* USNM 268333, 1; *Pseudamiops gracilicauda* USNM 324809, 1; *P. pellucidus* USNM 268330, 2; *Rhabdamia gracilis* USNM 213041, 2; Centropomidae—*Centropomus parallelus* USNM 306578, 1; Epigonidae—*Brinkmanella elongata* USNM 206944, 1; *Epigonus* sp. USNM 218803, 1; *Incerta cedis*—*Howella* sp. USNM 306589, 1; Polyprioniidae—*Polyprion americanus* USNM 269542, 1; Scombroptidae—*Scombroptus boops* USNM 049933, 1; Serranidae—*Plectropomus maculatus* USNM 218818, 1; Symphysanodontidae—*Symphysanodon berryi* USNM 269465, 1.

Paxton, gen. nov.

Diagnosis.—A pseudamine apogonid uniquely possessing each of the following features: a con-

tinuous dorsal fin, dorsal fin rays VI,19; anal fin rays I,15–16; caudal peduncle short and deep; entire margin of preopercle obscured by skin; distal margin of dorsal fin with band of dark pigment; neurocranium with a “postfrontal” bone; fifth and sixth infraorbitals widely separated from rest of circumorbital series; third epibranchial lacking a toothplate; fifth hypural fused to upper hypural plate; and pelvic girdle lacking anterior and posterior processes.

Type species.—*Paxton concilians*, new species.

Etymology.—The generic name is the surname of our friend and colleague John R. Paxton, who provided the specimens of the new species. We are pleased to honor John with this gesture and to provide him with a good-natured reminder that “you can’t judge a fish by its cover.”

Paxton concilians, new species

Figures 1–2, Table 1

Grammistidae gen. and sp. nov. Gloerfelt-Tarp and Kailola, (1984):326.

Grammistidae gen. and sp. nov. Sainsbury et al. (1984):338.

Grammistidae gen. and sp. nov. Paxton et al. (1989):516.

Holotype.—CSIRO H.1067-1. A 63.6-mm SL specimen collected off northwestern Australia, northeast of Monte Bello Islands, 20°07.2'S, 115°51.7'E to 20°07.1'S, 115°50.0'E, 63–65 m, Frank and Bryce demersal trawl, FRV SOELA, 9 October 1987.

Paratypes.—All from northwestern Australia: CSIRO H.2254-1, 49.0 mm SL (cleared and stained), northeast of Monte Bello Islands and northwest of Dampier Archipelago, 20°13.8'S, 116°13.4'E to 20°12.9'S, 116°13.9'E, 46–47 m, Frank and Bryce demersal trawl, FRV SOELA, 30 September 1987; AMS I.22672001, 75.5 mm SL, northeast of Monte Bello Islands, 19°55'S, 115°59'E to 19°54'S, 115°57'E, 80 m, demersal trawl, FRV COURAGEOUS, 21 July 1979; WAM P.27219035, 66.5 mm SL, Hummock Island, Abrolhos, 28°48'S, 113°03'E, D. Heald, 22 November 1980.

Description.—Counts and measurements of holotype, followed parenthetically by those of paratypes if different from holotype: Dorsal fin rays VI,19 (one paratype with 15 dorsal soft rays, but pterygiophores of posterior end of fin abnor-

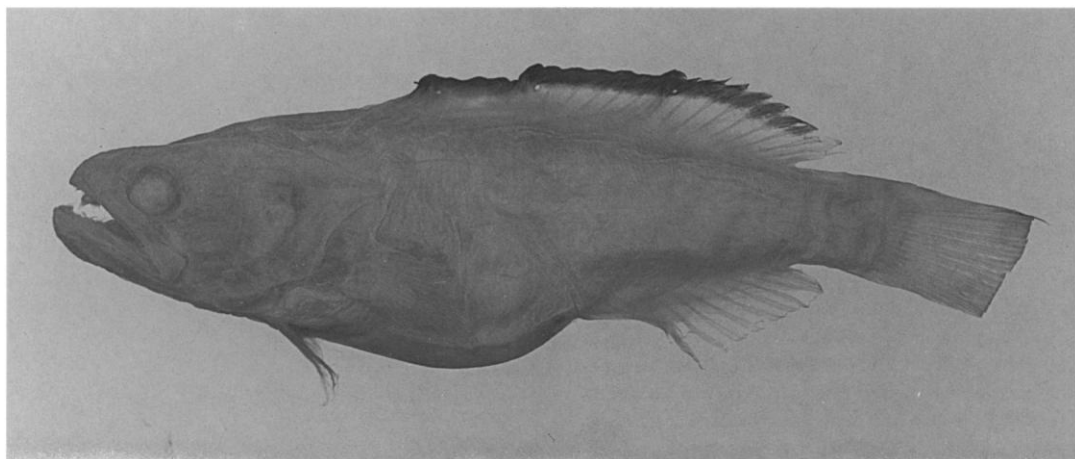


Fig. 1. Holotype of *Paxton concilians*, CSIRO H.1067-1, 63.6 mm SL. Photograph by Don Hurlbert, National Museum of Natural History.

mal in shape and configuration and thus this count presumably anomalous); anal fin rays I,15 (two paratypes with I,16); pectoral fin rays 18 (one paratype with 17 on right side); principal caudal fin rays 9 + 8, branched; procurrent caudal fin rays 10 + 9, unbranched; total gillrakers

on first arch 11, 1 on upper limb, 10 on lower limb; all paratypes also with 1–3 rudimentary rakers on upper limb or divided between upper and lower limbs; branchiostegal rays 7; vertebrae 10 + 14 = 24; no supraneurals.

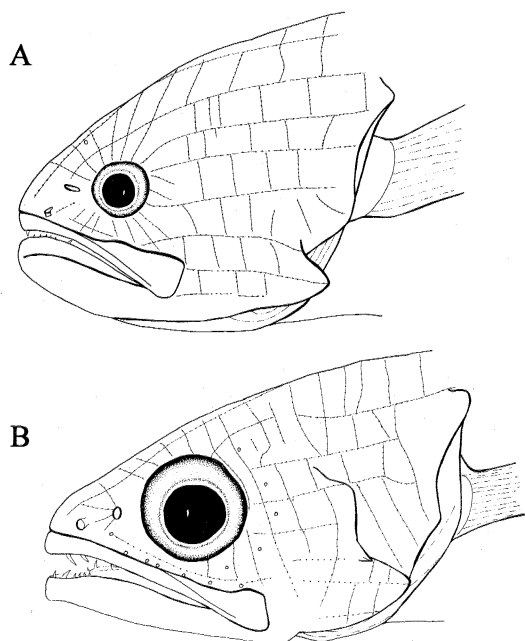


Fig. 2. Details of head morphology in (A) *Paxton concilians*, Paratype, AMS P.27219035, 66.5 mm SL; and (B) *Gymnapogon* sp., USNM 262166, 32 mm SL. Lines of sensory papillae drawn as a composite from left and right sides of illustrated specimen and from examination of other available specimens when necessary.

TABLE 1. PROPORTIONAL MEASUREMENTS OF TYPE SPECIMENS OF *Paxton* EXPRESSED AS A PERCENTAGE OF THE STANDARD LENGTH.

	Holotype	Paratypes	
	CSIRO H.1067-01	AMS I.22672001	WAM P.27219035
Standard length (mm)	63.6	75.5	66.5
Body depth	27	28	28
Body width	12	13	14
Head length	40	41	41
Snout length	7.2	7.3	9.0
Orbit diameter	6.3	6.4	6.5
Interorbital width	7.7	7.4	8.1
Caudal peduncle depth	10	12	12
Caudal peduncle length	11	11	12
Predorsal length	42	40	41
Preanus length	63	61	57
Length of first dorsal spine	3.6	4.4	4.5
Length of longest dorsal spine	5.8	7.5	7.6
Length of first dorsal ray	9.0	10	11
Length of anal spine	4.1	5.6	6.5
Length of first anal ray	7.2	8.1	9.8
Length of longest anal ray	16	14	15
Length of caudal fin	24	22	24
Length of pectoral fin	20	18	20
Length of pelvic fin	15	14	13

Body elongate, depth at origin of dorsal fin 3.7 (3.5–3.6) in SL, and compressed, width 2.2 (2.0–2.2) in depth. Head length 2.5 in SL, orbit diameter 6.3 in head. Snout short, rounded, length 5.5 (4.9–5.7) in head. Interorbital flat, the least width 5.1 (5.0–5.4) in head. Caudal peduncle short, length 9.1 (8.7–9.1) in SL; caudal peduncle depth slightly less than length in holotype, 9.6 in SL (depth slightly greater than length in paratypes, 8.4–8.5 in SL).

Mouth oblique, anteriorly forming an angle of about 20° with the horizontal, but angle increasing posteriorly as mouth curves ventrally. Lower jaw projecting slightly beyond upper jaw; upper jaw long, extending posteriorly to vertical well beyond posterior edge of orbit. Upper margin of maxilla obscured by lacrimal for part of its length. Upper and lower jaws each with about 3–5 rows of small conical teeth; premaxilla with several larger, slightly recurved canine teeth anteriorly, and dentary also with several enlarged canine teeth, the largest about half way back along the tooth-bearing surface. No supramaxilla.

Anterior nostril in short tube with very small flap posteriorly; anterior nostril located just posterior to upper lip. Posterior nostril situated at anterior edge of orbit, just slightly above center of eye; posterior nostril ovoid and large, the greatest axis approximately one-half pupil diameter. Eye slightly recessed; cornea thick and whitish.

Opercle with wide fleshy posterior margin that ends posterodorsally in pointed flap. Margin of preopercle covered by skin, not exposed; a long, fleshy, bluntly pointed flap extending posteriorly from ventral preopercular limb.

Head and body without scales but with numerous papillar neuromasts. Larger papillae forming rows that radiate from orbit. Rows of papillae generally crossing other rows at about right angles, and thus a cross-hatch pattern visible on many areas of head and body.

Dorsal fin originating above posterior tip of opercular flap. Spinous and soft dorsal fins continuous, a gap between ultimate and penultimate dorsal fin spines lacking. Spinous dorsal fin low, slightly lower than soft dorsal fin; first dorsal fin spine 11 (9.3–10) in head, longest dorsal fin spine, the fifth, 6.8 (5.3–5.4) in head; first dorsal fin soft ray 4.4 (3.8–3.9) in head. First anal fin spine 5.5 (6.3–7.3) in head; longest anal fin soft ray (usually 9th–11th) 2.5 (2.6–2.9) in head. Caudal fin truncate (slightly round), greatest length 4.2 (4.2–4.5) in SL. Pectoral fin falling well short of anus, reaching vertical through approximately the sixth dorsal fin spine; greatest pectoral fin length 5.1 (5.1–5.4).

Pelvic fin short, 6.6 (7.1–7.8) in SL, reaching only several millimeters beyond base of pectoral fin.

Color in life: body bright yellow; all fins pale except dorsal margin of dorsal fin with wide band of dark brown pigment, and dorsal margin of caudal fin dusky; abdomen and cheek silvery. Color of holotype in alcohol: entire body pale tan except dorsal fin with band of dark pigment along outer margin of entire fin; gut dusky. Dense patch of spots preceding dorsal fin and extending along anterior edge of membrane of first dorsal fin spine; 17th dorsal fin ray with tiny bit of pigment distally (none in paratypes); last two dorsal fin soft rays unpigmented (last with small bit of pigment on posterior margin of membrane, about half way up length of ray). Many scattered spots on dorsal portion of caudal peduncle, extending onto dorsal margin of anterior part of caudal fin. Sparse pigment on distal ends of uppermost principal caudal fin rays (absent in WAM paratype). A few scattered spots on ventral portion of caudal peduncle and posteriormost ventral procurent rays (both absent in WAM paratype).

Comparisons.—*Paxton* can be distinguished from all other apogonids on the basis of its continuous dorsal fin and in having fewer dorsal and anal fin spines (VI and I, respectively, vs VII–IX and II, respectively, in other members of the family), more dorsal fin soft rays (usually 19 vs 7–13), and usually more anal fin soft rays [15 or 16 vs 7–13, except the apogonine *Archamia* with 13–18 (Fraser, 1972)]. Additionally, the caudal peduncle in *Paxton* is very short and sometimes deeper than long versus approximately 1.3–2.0 times as long as deep in most apogonines, as much as twice as long as deep in *Pseudamia* (Randall et al., 1985) and *Gymnapogon* (e.g., Regan, 1905; Lachner, 1953), and three times as long as deep in *Pseudamiops* (Lachner, 1953; Smith, 1954). Finally, the entire margin of the preopercle is obscured by skin in *Paxton* (Fig. 2A), whereas the entire margin is exposed in apogonines, *Pseudamia*, and *Pseudamiops*, and the dorsal margin of the preopercle is exposed in *Gymnapogon* (Fig. 2B).

Paxton is most similar to *Gymnapogon*. Both lack scales, have a bluntly pointed fleshy flap extending posteriorly from the ventral margin of the preopercle (Fig. 2), and have little body pigment. The Atlantic apogonine genus *Phaeoptyx* also has a large fleshy preopercular flap (Fraser and Robins, 1970), but it is not present in other apogonines or pseudamines (some apo-

gonines have an unossified ventral preopercular margin; see Fraser and Struhsaker, 1991).

Etymology.—The specific name *concilians* is derived from the Latin *concilio*, to unite separate parts into a whole, in reference to the single dorsal fin of the new species.

Remarks.—*Paxton concilians* is known only from the northwestern coast of Western Australia. All specimens were taken by trawl at depths of 46 m or greater, whereas other pseudamines typically inhabit crevices and caves in shallow lagoons, estuaries, mangroves, tidal reefs, or coral rubble and usually are taken with ichthyocides. Possibly, small specimens of the new species live more cryptically and at shallower depths, as is the case with *Pseudamia nigra*. Allen (1992) described *P. nigra* from 28 specimens, 13.5–49.6 mm SL, all taken at depths less than 2 m and at a locality approximately 8 km upstream from a river mouth; however, we have recently identified two larger specimens (67 and 69 mm SL) as *P. nigra* (CSIRO H.3384-02 and H.3473-01) that were taken by trawl at 27 m and 50 m, respectively, off the coast of northern or northeastern Australia. Similarly, we have identified an 80-mm SL specimen of *Pseudamia* taken by trawl at 40–45 m in the Philippines as *P. hayashii* (USNM 270295), whereas all 55 specimens of *P. hayashii* listed in the original description of the species are smaller (16.5–62 mm SL) and were collected with rotenone from caves or crevices or beneath ledges of corals in lagoonal and exposed outer reefs (Randall et al., 1985). *Gymnapogon* also apparently exhibits the same depth/size relationship; for example, the largest specimen of the genus in collections at USNM (*G. philippinus*, 73 mm SL, USNM 332337) was taken in a trawl deployed to 80.5 m. Other *Gymnapogon* in USNM collections, including many type specimens of the various species, are smaller and were taken in shallow areas of coral debris.

Osteology of *Paxton*

Neurocranium.—Neurocranium (Fig. 3) elongate, length about four times greatest depth (through otic bulla). Vomer with one very large canine tooth on anterior margin (two in other paratypes, and one large and one small in holotype) and a semicircular patch of smaller teeth posteriorly; dorsal margin of vomer flat and separated from mesethmoid by large ethmoid cartilage. Orbit narrow and bordered dorsally by the frontal, anteriorly by the ethmoid cartilage and posterodorsal tip of lateral eth-

moid, ventrally by the parasphenoid, and posteriorly almost entirely by the dorsal limb of the parasphenoid, although the sphenotic and pterosphenoform the posterodorsal corner. Prootic excluded from orbit, the dorsal limb of the parasphenoid articulating directly with the pterosphenoform. Several pairs of bones of the post-orbital/otic region of the neurocranium articulating with one another through interdigitating sutures: sphenotic (ventral margin) and prootic (anterodorsal margin), epioccipital (anterior margin) and pterotic (posterodorsal margin), and exoccipital (anterior margin) and pterotic (posterior margin). Intercalar elongate, overlying portions of exoccipital, pterotic, and prootic; intercalary forming part of otic bulla, but intercalary facet not on otic bulla. No high frontal or supraoccipital crests.

A flat, triangular bone overlying posterior end of sphenotic, anterior end of pterotic, and ventral tip of parietal; this bone clearly separate from pterotic. C. Patterson (BMNH) examined the neurocranium of *Paxton* and suggested (pers. comm.) that the unidentified bone most closely resembles the postfrontal of Taverne (1974), or intertemporal of Le Danois (1967) and Kershaw (1970). See Taverne (1974, figs. 31–32) for an illustration of the postfrontal in *Pantodon*. It is not possible to tell from radiographs whether a “postfrontal” is present in the holotype and other paratypes of *Paxton*.

Comparisons.—Fraser (1972) did not identify any feature of the neurocranium unique to apogonids, but he noted several distinctive characters of the pseudamine braincase: the shape [Fraser did not specify the diagnostic aspect of shape, but presumably he meant the elongate nature of the neurocranium in pseudamines; we determined that the length of the pseudamine neurocranium is about four times the greatest depth (Fig. 3A), vs length about 2–2.5 times greatest depth in other apogonids (Fig. 3C)]; absence of a basisphenoid [present in many apogonines, but also reduced or absent in *Glossamia*, *Apogonichthys*, *Foa*, *Rhabdamia* (*Bentuviaichthys*), *Neamia*, *Astrapogon*, *Vincentia*, *Siphamia*, *Fowleria*, and sometimes *Phaeoptyx*]; intercalary facet not included on otic bulla [also not included on otic bulla in *Glossamia*, *Holapogon*, and *Apogon* (*Yarica*) among apogonines; see Fraser, 1972, 1973]; and parasphenoid not separated from pterosphenoform by prootic (unique to pseudamines). *Paxton* has all of those pseudamine features and an additional one not noted by Fraser: the dorsal aspect of the vomer is nearly flat and separated from the mesethmoid by a large ethmoid cartilage (Fig. 3A); in most other

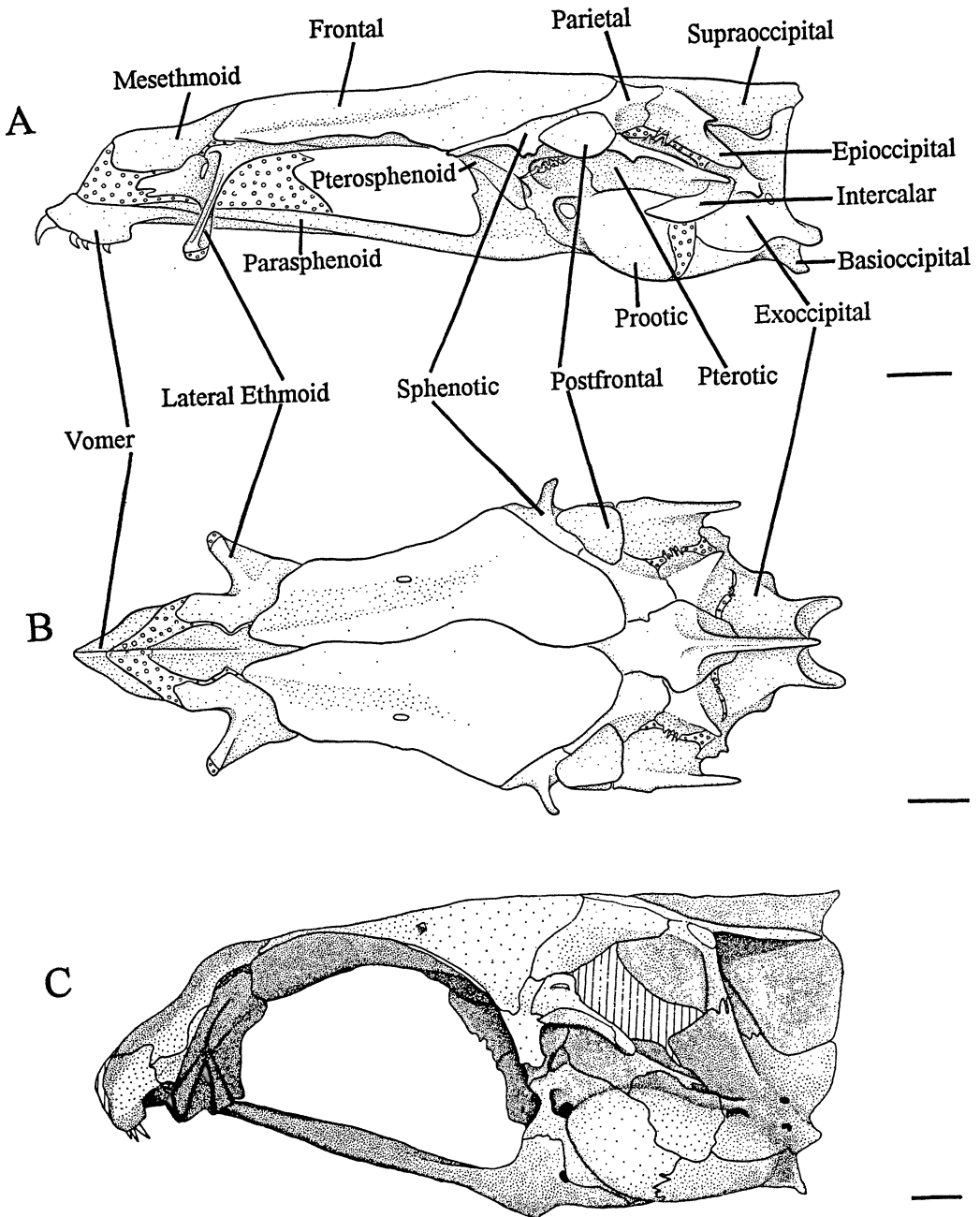


Fig. 3. Neurocranium. (A), (B) *Paxton concilians*, CSIRO H.2254-1, 49.0 mm SL, left lateral view and dorsal view, respectively; (C) *Phaeoptyx pigmentaria*, 53.1 mm SL (from Fraser, 1972:plate 36).

apogonids, there is a dorsal projection on the vomer that articulates with the mesethmoid (e.g., as in *Phaeoptyx*; Fig. 3C) or nearly does, in which case it is separated from the mesethmoid by a small area of the ethmoid cartilage. Fraser (1972, plate 33) illustrated the apogonine *Siphamia* with the vomer separate from the mesethmoid by cartilage (although the dorsal as-

pect of the vomer is not flat as it is in pseudamines). *Gymnapogon* exhibits variation in this character. In *G. annona* (Fraser, 1972, plate 42) and *G. urospilotus*, the vomer is connected to some extent to the mesethmoid, whereas there is no bony connection in *G. philippinus*, and the condition is nearly identical to that of *Paxton*, *Pseudamia*, and *Pseudamiops*. The intercalar also

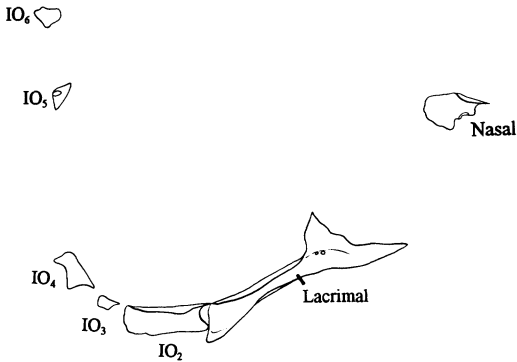


Fig. 4. Circumorbital and nasal bones of *Paxton concilians*, CSIRO H. 2254-1, 49.0 mm SL, right lateral view. $IO_n = n$ th infraorbital.

seems to be more elongate in pseudamines, although it is quite long in some apogonines (see Fraser, 1972). We found no features of the neurocranium unique to *Paxton* and any subgroup of pseudamines, and the presence of a postfrontal appears to be autapomorphic for *Paxton*.

Circumorbital bones.—This series (Fig. 4) comprising six bones, the lacrimal much larger than the others. Third infraorbital tiny and not bearing a subocular shelf. Only the first and second infraorbitals contiguous; the third close to the second and fourth but not in contact with them; the fifth small, poorly ossified, and greatly separated from fourth below and sixth above. Edges of all infraorbitals entire.

Comparisons.—*Paxton* shares with other apogonids and many percoids the presence of six infraorbitals (epigonids, for example, have seven or eight; Fraser, 1972). *Paxton*, *Pseudamia*, and *Pseudamiops* lack a subocular shelf on the third infraorbital. A subocular shelf is present in most apogonines but lacking in, for example, *Rhabdamia* (*Verulux*), *R. (Bentuviaichthys)*, *Apogon* (*Zoramia*)—(Fraser, 1972). *Gymnapogon* is the only pseudamine with a subocular shelf, but it has a small shelf compared to the well-developed shelf of most apogonines (and lower percoids). *Paxton* differs from all other apogonids in having the fifth and sixth infraorbitals widely separated from the rest of the series.

Nasal bone.—A simple, relatively flat bone (Fig. 4) lying above dorsolateral surface of rostral car-

tilage; anteriorly, edges of nasal bone curled dorsally forming shallow canal for passage of branch of cephalic lateral line.

Comparisons.—The shape of the nasal bone in *Paxton*, *Gymnapogon*, and *Pseudamia* is nearly identical, each having a somewhat broad laminar flange extending ventrally from the posterior half of the bone. The nasal is not so shaped in other apogonids, including *Pseudamiops*, in which it is a simple tube with an opening at each end.

Jaws, suspensorium, opercular series.—Premaxilla and dentary armed with numerous small conical teeth and several larger canine teeth (Fig. 5A). Supramaxilla lacking. Hyomandibular articulating ventrally with symplectic but not metapterygoid. Metapterygoid with two ventrally directed rami separated by laminar bone and bound synchondrally to two dorsally directed rami of quadrate also separated by laminar bone. Between the anterior and posterior synchondral joints, quadrate and metapterygoid loosely sutured with interdigitating struts of laminar bone.

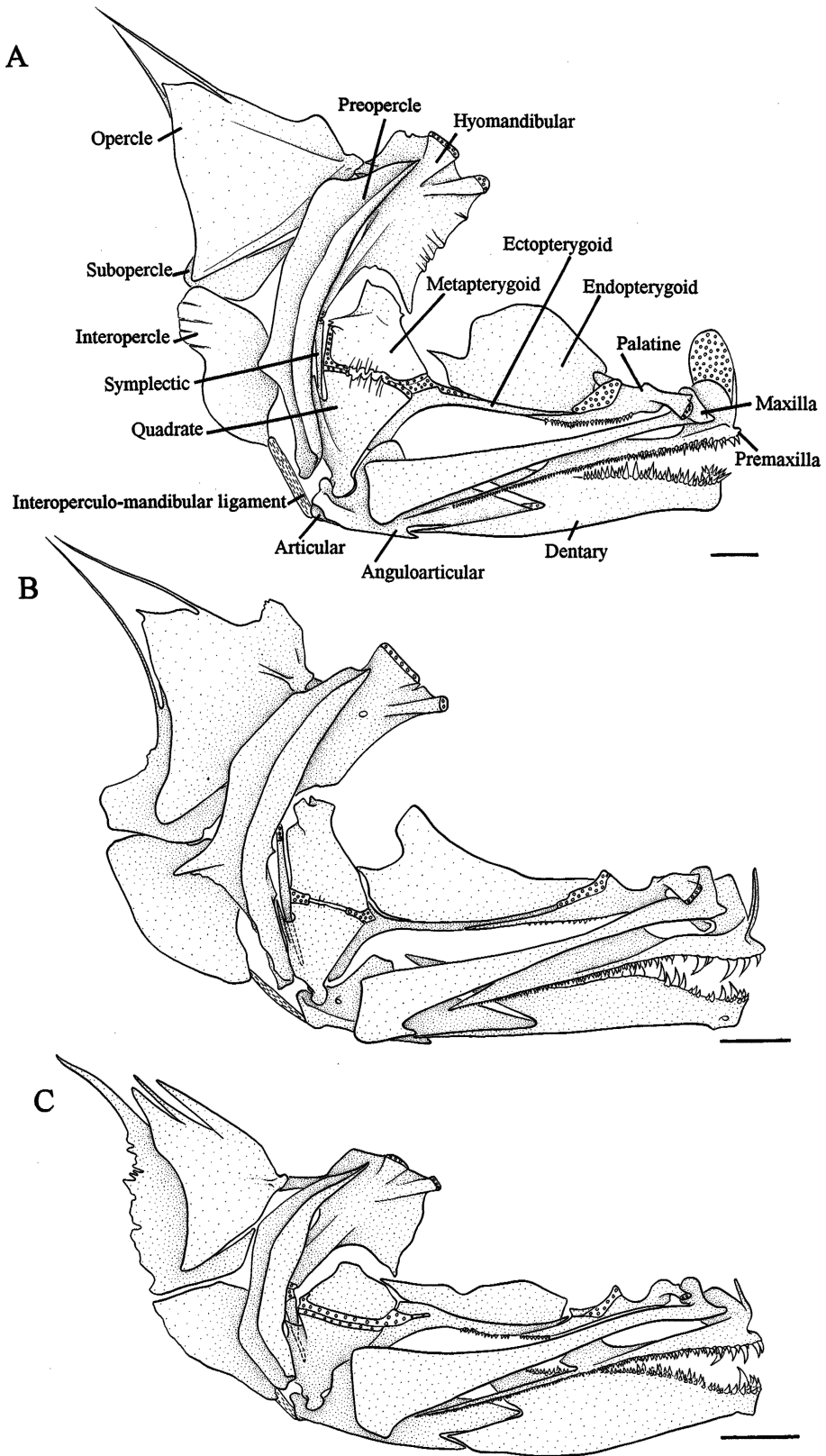
Ectopterygoid and endopterygoid without teeth, palatine with long series of small conical teeth. Endopterygoid lying above dorsal limb of ectopterygoid and giving rise posteriorly to a spine that extends toward the metapterygoid.

Opercle bearing a single spine on posterior margin; opercle poorly ossified dorsally and giving rise posterodorsally to a long bony filament; ventral part of opercle overlapping subopercle, the posterior ramus of which is also prolonged into a thin, posteriorly directed, bony filament. Preopercle with a single blunt spine on posterior margin at a point about one-third the length of the bone from its ventral terminus. Interopercle large, weakly ossified ventrally, and joined by a long ligament (approximately half the length of the long axis of the interopercle) to the retroarticular.

Comparisons.—*Paxton* (Fig. 5A) shares with most other apogonids and some percoids a single spine on the posterior opercular margin (e.g., as in *Gymnapogon*, Fig. 5B); opercle with deep indentations on either side of the spine in some taxa (e.g., as in *Pseudamiops*, Fig. 5C), creating the impression of three opercular spines. *Paxton*

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Fig. 5. Jaws, suspensorium, and opercular series, right lateral view. (A) *Paxton concilians*, CSIRO H.2254-1, 49.0 mm SL; (B) *Gymnapogon philippinus*, USNM 268314, 35.0 mm SL; (C) *Pseudamiops pellucidus*, USNM 268330, 37.0 mm SL.



also shares with other apogonids and many lower percoids the extension of the subopercle posteriorly via a slender bony filament (Fig. 5A–C). With other pseudamines, *Paxton* shares enlarged canine teeth in the lower jaw and at least some slightly enlarged teeth on the premaxilla (Fig. 5A–C). Among apogonines, slightly enlarged or canine teeth are found in *Cheilodipterus*, *Coranthus*, *Rhabdamia* (*Bentuviaichthys*), *Lachneratus*, and *Apogon affinis* (Fraser, 1972, 1973; Fraser and Struhsaker, 1991), the relationships of which to pseudamines are unclear.

The opercular series and suspensorium of *Paxton* (Fig. 5A) and *Gymnapogon* (Fig. 5B) are remarkably similar. Those genera are unique among apogonids in having a long bony strut from the dorsal part of the opercle and in having a spine on the posterior margin of the preopercle. The preopercular spine is blunt in *Paxton*, slightly larger and more pointed in *Gymnapogon*, but it is located in the same position at a point approximately one-third the vertical length of the preopercle from the ventral end in both genera (the spine is visible externally in *Gymnapogon*, Fig. 2B, unexposed in *Paxton*, Fig. 2A). The posterior preopercular margin in apogonines may be smooth or serrate (Fraser, 1972), and *Cercamia* may have 2–5 short spines (Randall and Smith, 1988; Hayashi, 1991), but a single spine in the position described above for *Gymnapogon* and *Paxton* is unique to those genera. A striking similarity between *Paxton* and *Gymnapogon* is the articulation of the quadrate and metapterygoid. Rather than articulating at a single synchondral joint as in other apogonids (e.g., as in *Pseudamiops*, Fig. 5C), the quadrate and metapterygoid articulate at two separate synchondral joints, one anteriorly and one posteriorly. Between these anterior and posterior joints is bone, sometimes with weakly (some species of *Gymnapogon*) or strongly (*Paxton*) developed struts that form an interdigitating suture. *Gymnapogon* also shares with *Paxton* a similarly shaped endopterygoid characterized by a posteriorly directed spine and a significantly longer interoperculohyoid ligament than in other apogonids [this ligament 40–50% the length of the long axis of the interopercle in *Paxton* and *Gymnapogon*, < 25% in other apogonids (Fig. 5A–C)].

Lower hyoid arch.—Anterior and posterior ceratohyals sutured to one another on medial surface by several bony interdigitating struts; anterior ceratohyal supporting five branchiostegals, posterior ceratohyal two; anterior ceratohyal not perforated (McAllister, 1968), and upper margin of the bone nearly straight (Fig. 6).

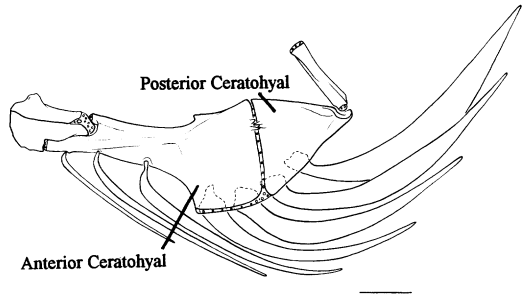


Fig. 6. Lower hyoid arch of *Paxton concilians*, CSIRO H.2254-1, 49.0 mm SL, right medial view.

Comparisons.—*Paxton* shares with other apogonids and many percoids the presence of seven branchiostegals (one fewer on the anterior ceratohyal than in, e.g., beryciforms) and the absence of a perforated anterior ceratohyal (except in *Holapogon*; Fraser, 1973). *Paxton* differs from all apogonids (except *Glossamia* according to Fraser, 1972) in having a small bit of bony suturing between the medial surfaces of the anterior and posterior ceratohyals.

Gill arches.—Gill arches comprising three ossified basibranchials, the third greatly exceeding the first and second in length, a small fourth basibranchial cartilage, three hypobranchials, five ceratobranchials, four epibranchials, two pharyngobranchials, a fourth upper pharyngeal toothplate, and an interarcual cartilage between the dorsal portion of the first and second arches (Fig. 7). First and fourth pharyngobranchials lacking. Gillrakers (distinguished from gill plates or rudimentary rakers by being longer than wide) present on the first hypobranchial, first and second ceratobranchials, and first and sometimes second epibranchials; gill plates present on all three hypobranchials, first through fourth ceratobranchials, and first through third epibranchials (Fig. 7; gillrakers and plates on epibranchials not illustrated).

First epibranchial terminating distally as a long thin cartilage but no separate first pharyngobranchial present (Fig. 8A). A very long, slender interarcual cartilage extending from uncinat process of first epibranchial to anterior tip of second pharyngobranchial. Second pharyngobranchial with a single cartilaginous condyle that articulates with the interarcual cartilage (Fig. 8A). No direct connection between second pharyngobranchial and second epibranchial (Fig. 8A–B), the latter medially articulating only with a laterally directed cartilaginous condyle of the third pharyngobranchial (Fig. 8A). Medial end of third epibranchial greatly

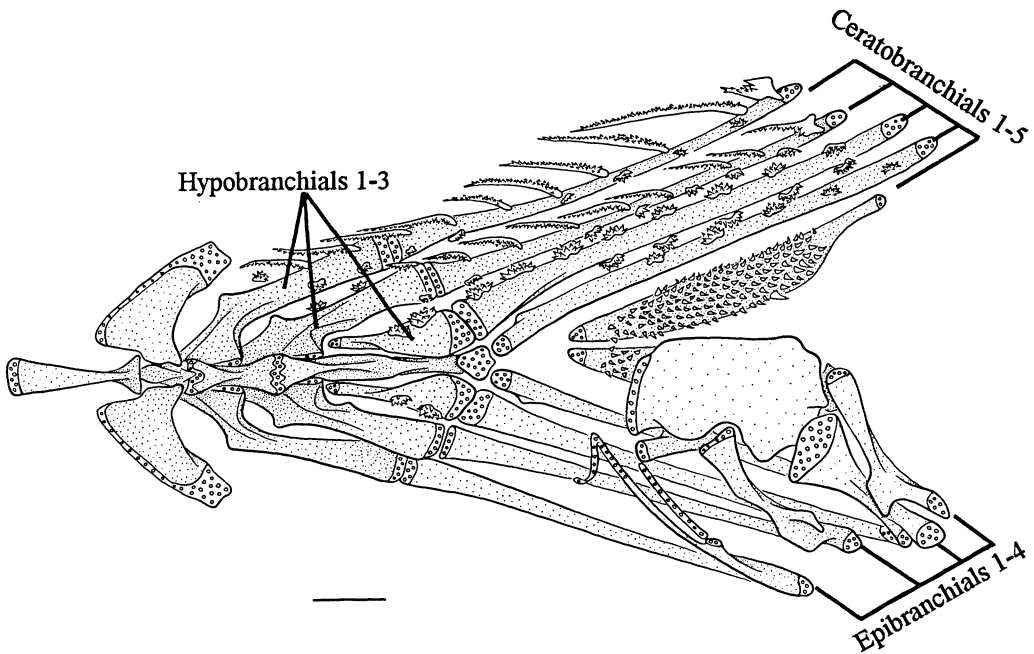


Fig. 7. Branchial skeleton of *Paxton concilians*, CSIRO H.2254-1, 49.0 mm SL, dorsal view, dorsal gill arches removed from right side.

expanded where it articulates with a very large third pharyngobranchial. Fourth epibranchial slender (Figs. 7, 8A). Second and third pharyngobranchials bearing well-developed fused toothplates ventrally, the third pharyngobranchial very large (Fig. 8A). A small fourth upper pharyngeal toothplate present, but fourth pharyngobranchial cartilage lacking. Fifth ceratobranchial bearing long patch of small teeth, about seven rows of teeth at greatest width (Fig. 7). Epibranchial toothplates lacking.

Comparisons.—The dorsal gill arches of *Paxton* resemble those of *Gymnapogon* in lacking a first pharyngobranchial and in having the medial end of the first epibranchial terminating as an attenuated cartilage (Fig. 8A,C). Additionally, the interarcual cartilage is very long and slender in both genera (also somewhat elongate in some apogonines, e.g., *Apogonichthys*, Fig. 8E, relative to the very short interarcual cartilage in other apogonids, e.g., *Pseudamia*, Fig. 8D), and gillrakers are present on the first and second arches (vs on only the first in all other apogonids examined except on first and second arches in *Archamia*, *Astrapogon*, and *Cercamia*). Finally, *Paxton* and *Gymnapogon* have a single cartilage-tipped process at the distal end of the second pharyngobranchial that articulates with the interarcual cartilage (Fig. 8A,C). In addition to this process, other pseudamines and many apo-

gonines have a second cartilage-tipped process that terminates in close proximity to the cartilaginous head of the third pharyngobranchial (e.g., *Apogonichthys*, Fig. 8E, and *Pseudamia* Fig. 8D).

Fraser (1972) noted that the first pharyngobranchial is poorly ossified in *Gymnapogon* and lacking in *Apogonichthys*, *Fowleria*, and *Astrapogon*. In our specimens, the first pharyngobranchial is lacking in *Gymnapogon* (Fig. 8C) but present and ossified in *Astrapogon stellatus*. In *Apogonichthys* (Fig. 8E) and *Fowleria* (Fig. 8F), there is usually no separate first pharyngobranchial (one specimen of *Fowleria* examined has a separate first pharyngobranchial on one side), but within an elongate blue-stained cartilage extending from the tip of the first epibranchial in those taxa, there is a more darkly blue-stained cartilaginous nubbin in *Apogonichthys* and a red-stained ossified rod in *Fowleria*. Presumably these structures are the developing first pharyngobranchials, and thus in *Apogonichthys* and *Fowleria* the first pharyngobranchial apparently develops within the cartilaginous tip of the first epibranchial rather than separately as is typical for perciforms. A more comprehensive survey of the ontogeny of dorsal gill arches in apogonids is needed but is beyond the scope of this study. Of relevance here is that there is no evidence of development or ossification of a first

pharyngobranchial within the cartilage extending from the first epibranchial in *Paxton* and *Gymnapogon* (Fig. 8A,C), and we interpret the condition in those genera as distinct from the conditions in *Apogonichthys* and *Fowleria*; that is, *Paxton* and *Gymnapogon* uniquely lack a first pharyngobranchial. *Paxton* is unique among apogonids in lacking a toothplate fused to the third epibranchial (Fig. 8A).

Postcranial axial skeleton.—Twenty-four vertebrae (10 + 14), usually eight pairs of ribs (on vertebrae 3 through 10), and eight pairs of epineural bones (Fig. 9); holotype with seven pairs of ribs, the series ending on vertebra 9; epineurals originating from neural arches on first and second vertebrae, but origin descending to rib on third and fourth vertebrae; remaining epineurals free from axial skeleton. Origin of ribs descending from dorsolateral portion of centrum on third and fourth vertebrae to ventrolateral region of centrum on fifth, and to medial surface of parapophysis on the sixth through ninth; rib on 10th vertebra free from axial skeleton, originating ventral to ventral tip of parapophysis. Ribs preformed in cartilage, as indicated by their cartilaginous ventral tips. All neural arches fused to centra, and left and right sides of all neural spines fused.

Comparisons.—Fraser (1972) considered a reduced number (2–7) of epineurals (his epipleurals) as a character uniting pseudaminies, but *Paxton* has eight, as do many apogonines, and several apogonine genera have seven. *Cercamia* and *Pseudamiops* appear to be unique among apogonids in having only two pairs of epineural bones (Fraser, 1972; Randall and Smith, 1988).

Median fins.—Dorsal fin not preceded by supraneurals. “Predorsal pattern” of Ahlstrom et al. (1976): //1/1+1/1/1/1/I+s/s+s/ etc., (where / = neural spine, 1 = pterygiophore bearing spine in supernumerary association, I = pterygiophore with no supernumerary element, s =

pterygiophore bearing soft ray in supernumerary association); Figure 9.

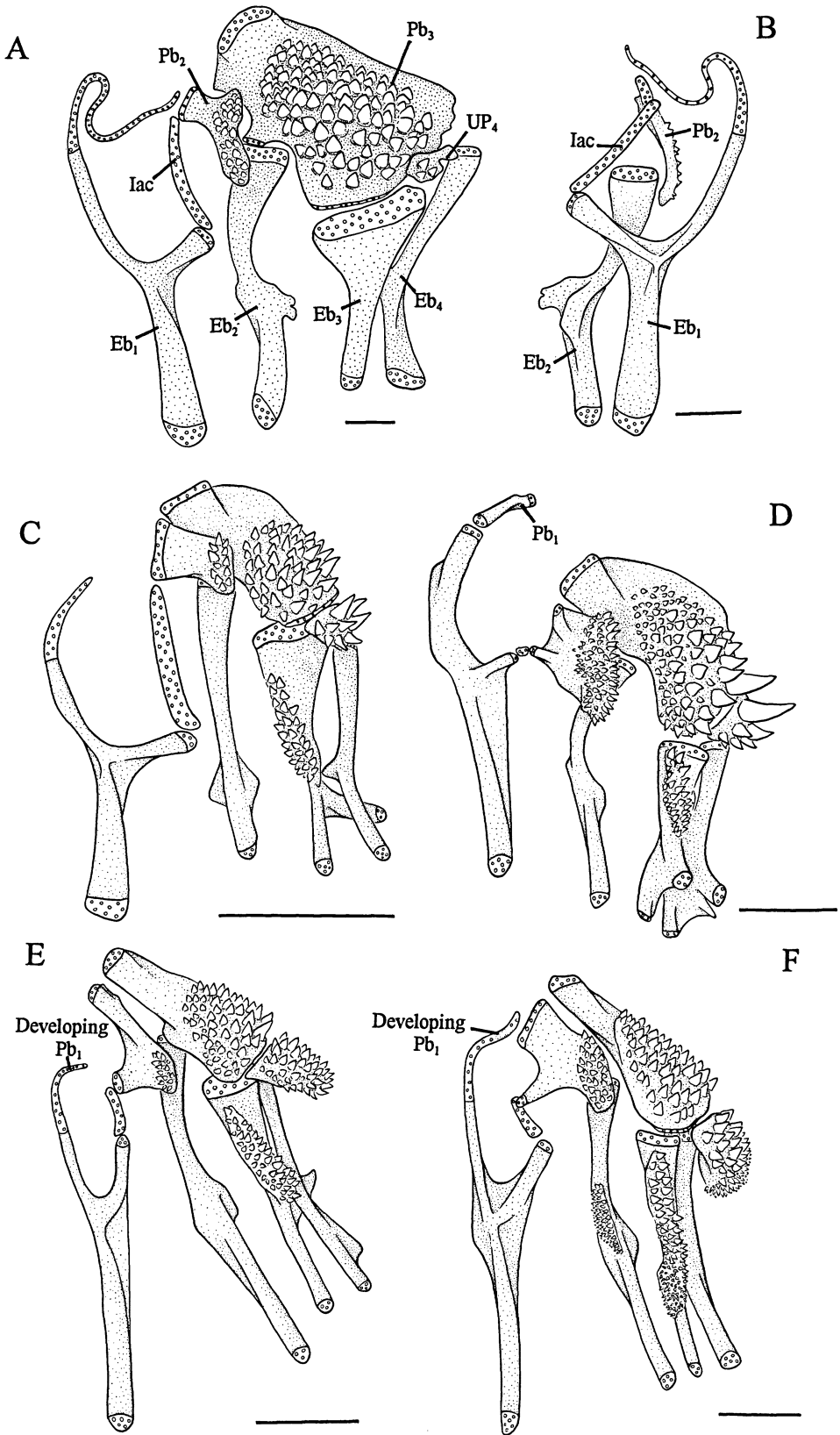
Dorsal fin rays modally VI,19 (see Description above), last spine not separated from penultimate spine by a gap externally. First dorsal fin pterygiophore bearing one spine in supernumerary association. Each spine-bearing proximal-middle pterygiophore lacking posteriorly projecting shelf for articulation with its serially associated distal radial and thus separated from radial by large gap (Fig. 9). Sixth dorsal fin pterygiophore lacking serially associated spine, but a small, free cartilaginous distal radial present. A very small, free cartilaginous element in anterior portion of spinous dorsal fin preceding distal radial serially associated with first pterygiophore.

Anal fin comprising one spine and 15 or 16 soft rays. One supernumerary spine present on first pterygiophore (Fig. 10). Cartilaginous stay present at posterior base of both dorsal fin and anal fin.

Comparisons.—*Paxton* (Fig. 9) shares with most apogonids (e.g., *Gymnapogon*, Fig. 11A) the absence of a spine serially associated with the sixth dorsal fin pterygiophore [this spine present as a nubbin or tiny spine in some apogonines, e.g., *Apogon*, *Apogonichthys*, *Astrapogon* (Fig. 11B), *Fowleria*, *Holapogon*, and *Vincentia*; fully developed in e.g., *Neamia* (Fraser, 1972, 1973; this study)]. The missing spine in *Paxton* does not result in an external gap in the dorsal fin as it does in other apogonids for two reasons: (1) the sixth and seventh pterygiophores in *Paxton* are much closer to one another than in, for example, *Gymnapogon*, where a wide gap between those pterygiophores internally corresponds to a wide gap between the sixth and seventh dorsal fin spines externally (Fig. 11A); and (2) the sixth and seventh pterygiophores lack long posterior shelves, such as those in, for example, *Astrapogon* (Fig. 11B). Although the main bodies of the sixth and seventh pterygiophores are in close proximity in *Astrapogon* and many other apogonids, the long posterior shelves on the

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Fig. 8. Dorsal gill arches. (A) *Paxton concilians*, CSIRO H.2254-1, 49.0 mm SL, left side, ventral view; (B) *Paxton concilians*, CSIRO H.2254-1, 49.0 mm SL, left side, dorsal view, the second epibranchial rotated counterclockwise; note that the second pharyngobranchial overlaps but does not articulate with distal end of second epibranchial; (C) *Gymnapogon philippinus*, USNM 268314, 35.0 mm SL, left side, ventral view; (D) *Pseudamia gelatinosa*, USNM 218802, 53.0 mm SL, right side (drawing reversed), ventral view; (E) *Apogonichthys ocellatus*, USNM 318066, 36 mm SL, left side, ventral view; (F) *Fowleria variegatus*, USNM 218804, 40.5 mm SL, left side, ventral view. Eb_n = nth epibranchial, Pb_n = nth pharyngobranchial, UP₄ = fourth upper pharyngeal toothplate, Iac = interarcual cartilage.



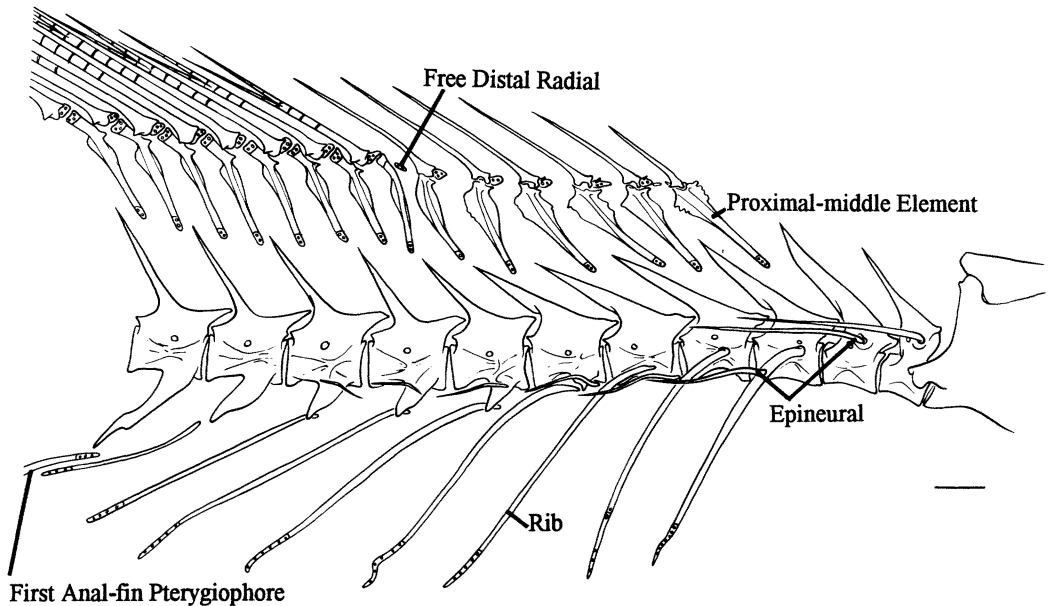


Fig. 9. Anterior portion of axial and dorsal fin skeletons of *Paxton concilians*, CSIRO H.2254-1, 49.0 mm SL, right lateral view.

sixth and seventh pterygiophores result in a large gap between the spine in supernumerary association with the sixth pterygiophore (the penultimate spine) and the spine serially associated with the seventh pterygiophore (the ultimate spine).

Paxton also differs from other apogonids in having only six dorsal fin spines, the seventh pterygiophore serially supporting a soft ray rather than a spine. Finally, it is unique within the family in having the fourth through last (sixth)

dorsal spines nearly subequal and longest (Fig. 9); in other apogonids, the penultimate spine is typically smaller than the preceding and ultimate spines (Fig. 11).

Paxton and other pseudamines have a gap between the proximal-middle and distal elements of at least some spine-bearing pterygiophores (Figs. 9, 11A), whereas those elements are contiguous in most apogonines (e.g., *Astrapogon*, Fig. 11B). In *Paxton*, the proximal-middle elements of all spine-bearing pterygiophores are separated from their distal radials by a gap (Fig. 9). The proximal-middle element of each of the anteriormost two or three pterygiophores may be in contact with its distal radial in *Gymnapogon* (Fig. 11A), *Pseudamia*, and *Pseudamiops*, but further posteriorly, proximal-middle elements are always well separated from their distal radials (when present; distal radials are lost or greatly reduced posteriorly in *Pseudamia* and *Pseudamiops*). Among apogonines, we have observed separation of proximal-middle and distal elements only in *Apogonichthys* and *Fowleria*, the gaps occurring on the fourth through sixth pterygiophores.

Paxton shares with *Gymnapogon* the absence of supraneurals. Fraser (1972) noted that *Astrapogon* lacks supraneurals, but in our cleared-and-stained specimen of *A. stellatus*, a single ossified supraneural is present (Fig. 11B), suggesting that there may be some variation within the genus. Supraneurals also are lacking in *Cercamia*

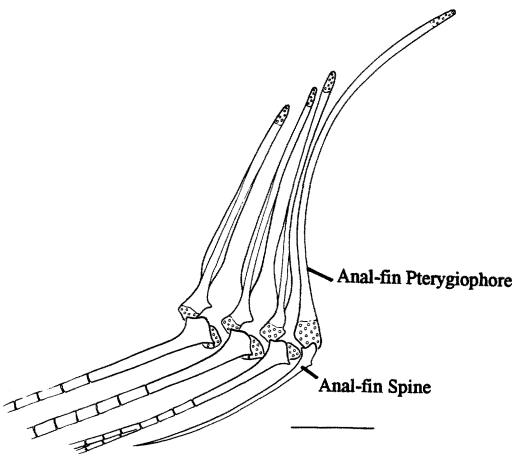


Fig. 10. Anterior elements of anal fin of *Paxton concilians*, CSIRO H.2254-1, 49.0 mm SL, right lateral view.

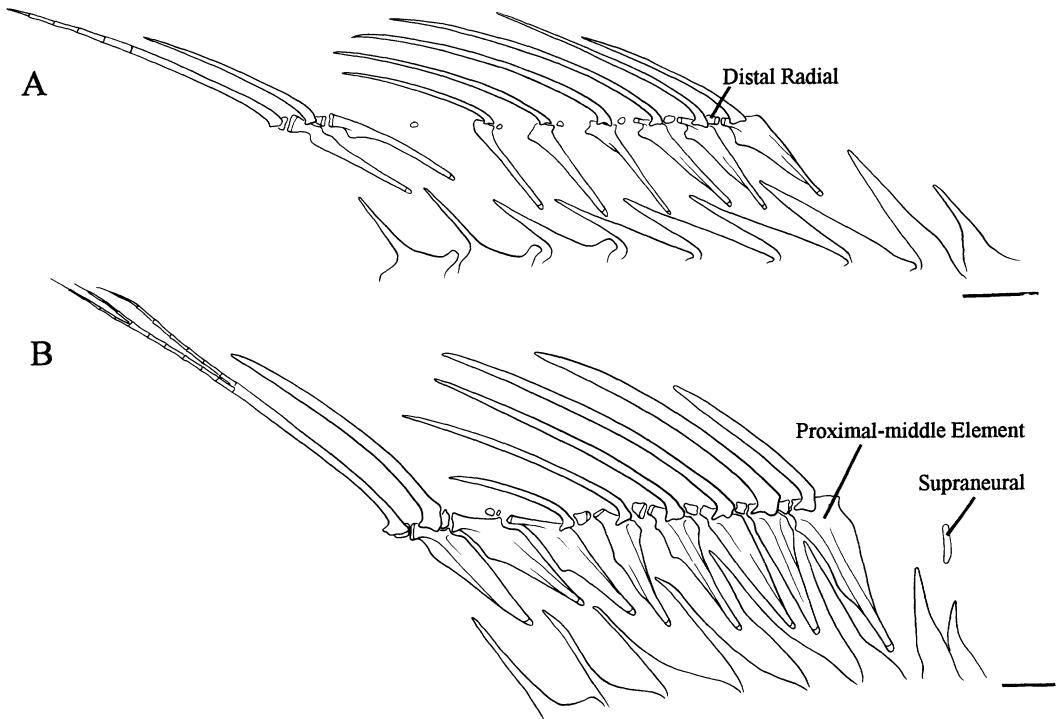


Fig. 11. Anterior elements of dorsal fin, right lateral view. (A) *Gymnapogon philippinus*, USNM 268314, 35.0 mm SL; (B) *Astrapogon stellatus*, USNM 339373, 41.0 mm SL.

(Randall and Smith, 1988; Hayashi, 1991) and *Lachneratus* (Fraser and Struhsaker, 1991).

Paxton shares with all apogonids a reduction in number of anal fin spines from the primitive percoid complement of three; however, it is unique among apogonids in having a single anal fin spine. (Allen, 1992, reported I,10 for *Pseudamia nigra*, but specimens examined in this study have II,9.) Most apogonids, including other pseudamines, have two anal fin spines, one in supernumerary association with the first pterygiophore, the second associated serially. Although the first anal fin element in *Paxton* is a spine in supernumerary association with the first pterygiophore, the serially associated element is a soft ray (Fig. 10). Johnson (1984) noted that the presence of two anal fin spines in apogonids and epigonids is not indicative of a close relationship between those families because in epigonids the two spines are both in supernumerary association with the first pterygiophore (i.e., the third spine of primitive percoids fails to transform from a ray); in apogonids, only the first spine is in supernumerary association with the first pterygiophore (i.e., the first supernumerary spine of primitive percoids has been lost). We note that a few apogonids (e.g., *Apogon moluccensis*, *A. lateralis*, *Neamia oc-*

tospina) have both anal fin spines in supernumerary association with the first pterygiophore, but in those taxa, the first pterygiophore is a large, apparently compound structure presumably resulting from fusion of the first and second pterygiophores. *Paxton* also has more anal fin soft rays than most apogonids [15–16 vs. 7–13 in all apogonid genera except *Archamia* with 12–18 (Fraser, 1972)].

Caudal skeleton.—Principal caudal fin rays 17 (9 + 8), all branched, segmented, and articulating with hypural plates (Fig. 12A). Procurrent rays 10 + 9, all unbranched and articulating with epurals, haemal spine of second preural centrum (PU_2), or caudal cartilages; procurrent rays not articulating with neural and haemal spines of third preural centrum (PU_3), which are enveloped distally by cartilage. Posterior-most three or four procurrent rays of upper and lower caudal fin lobes segmented. Contralateral hemitrichs of procurrent rays not fused to one another. Two epurals and two hypural plates, the lower plate autogenous and comprising the fused parhypural + hypurals 1 and 2, the upper fused to terminal centrum and including fused hypurals 3 and 4 (and 5?). A separate hypural 5 lacking. Uroneurals absent. The interneural-

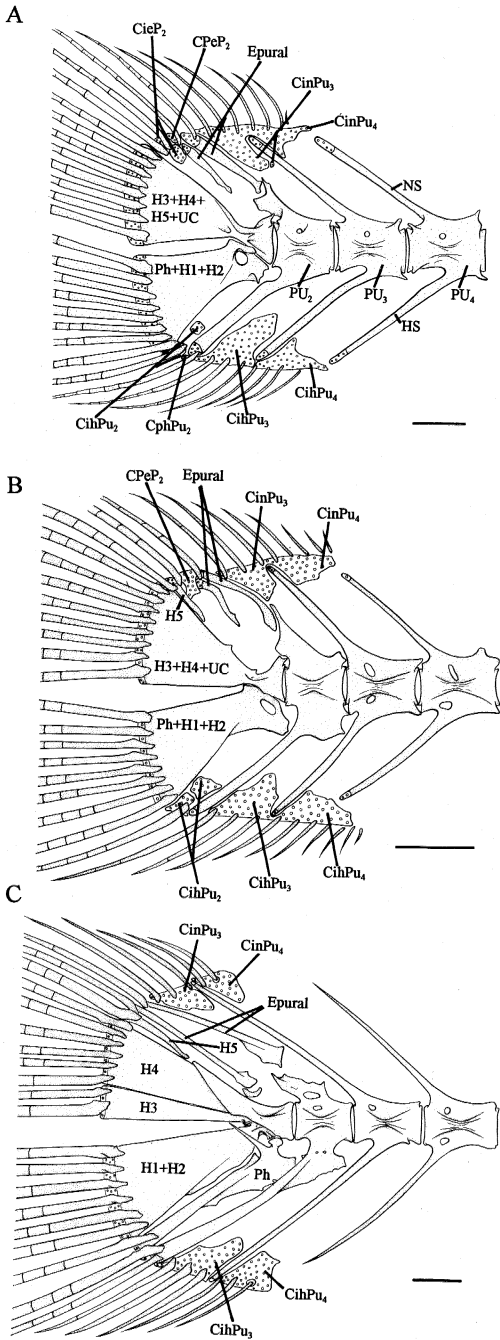


Fig. 12. Caudal skeleton. (A) *Paxton concilians*, CSIRO H.2254-1, 49.0 mm SL, left side (drawing reversed); (B) *Gymnapogon philippinus*, USNM 268314, 33.0 mm SL, right side; (C) *Pseudamia gelatinosa*, USNM 218802, 53.0 mm SL, right side. CieP_n = interepural n cartilage, CihPu_n = interhaemal spine cartilage of nth preural vertebra, CinPu_n = interneural spine cartilage of nth preural vertebra, CPeP_n = postepural n cartilage, CphPu_n = posthaemal spine cartilage of nth preural vertebrae, H_n = nth hypural, HS

spine cartilages of fourth preural centrum (PU₄) and PU₃ well developed, fused distally, and enveloping distal third of neural spine of PU₃. An additional tiny round interneural-spine cartilage present along posterior edge of neural spine of PU₃ at posteroventral tip of fused third and fourth interneural-spine cartilages. A single postepural 2 cartilage and two interepural 2 cartilages present. Interhaemal-spine cartilages of PU₄ and PU₃ large, separate but abutting one another distally and enveloping distal third of haemal spine of PU₃. One posthaemal-spine cartilage and two interhaemal-spine cartilages of PU₂.

Comparisons.—*Paxton* (Fig. 12A) and other pseudamines (Fig. 12B,C) have two epurals; all other apogonids except *Rhabdamia* (*Verulux*) and some *Siphamia* have three (Fraser, 1972). Among apogonids, *Paxton* (Fig. 12A) and *Gymnapogon* (Fig. 12B) are unique in having (1) the parhypural fused with hypurals 1 and 2, and (2) the upper but not lower hypural plate fused to the urostylar centrum. Those genera also have the neural and haemal spines of PU₃ shortened and surrounded distally by cartilage; in *Pseudamia* (Fig. 12C) and most other apogonids, the neural and haemal spines of PU₃ are not shortened or surrounded distally by cartilage. (*Pseudamiops* has an intermediate condition in which the spines are not noticeably shortened, but they are surrounded distally by a thin layer of cartilage.) *Paxton* is unique among apogonids in lacking a separate hypural 5.

Pectoral girdle.—Extrascapulars lacking. Posttemporal forked anteriorly, upper limb articulating with epioccipital, lower limb with intercalar. Posterior margin of posttemporal mostly smooth, ventralmost portion overlying dorsal tip of supracleithrum (Fig. 13A). Supracleithrum a simple elongate bone overlying anterodorsal part of cleithrum. Cleithrum with dorsally directed projection at anterodorsal corner. Cleithrum fan-shaped posterodorsally and narrowing ventrally where it covers anterior margins of scapula and coracoid. Scapula approximately square and bearing a central fossa and posterodorsal facet for articulation of first pectoral fin ray. Coracoid roughly rectangular, ventral half comprising two diverging bony stems of approximately equal length that are flanked on all sides by laminar bone; one stem projecting antero-

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= haemal spine, NS = neural spine, Ph = parhypural, PU_n = nth preural vertebra, UC = urostylar centrum.

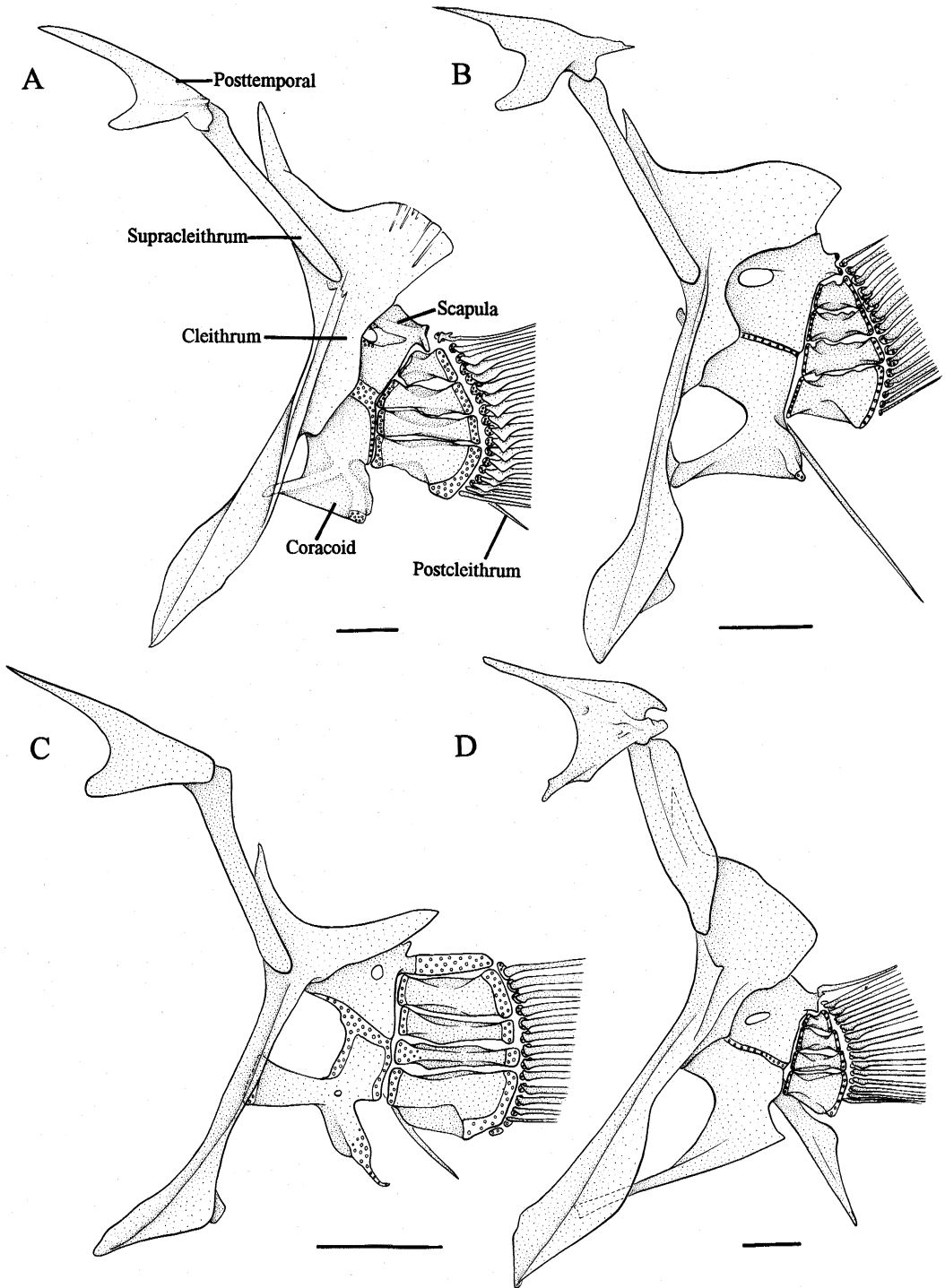


Fig. 13. Pectoral girdle, left side. (A) *Paxton concilians*, CSIRO H.2254-1, 49.0 mm SL; (B) *Gymnapogon urosipilotus*, USNM 288032, 35.5 mm SL; (C) *Pseudamiops pellucidus*, USNM 268330, 37.0 mm SL; (D) *Fowleria variegatus*, USNM 218804, 46.0 mm SL.

ventrally and articulating with cleithrum (at a point approximately one-third the length of cleithrum from its ventral tip), other stem directed ventrally and tipped in cartilage. Coracoid separated dorsally from scapula by cartilage that continues ventrally along posterior margin of coracoid. Scapula and coracoid supporting four large radials. Pectoral fin comprising 18 (rarely 17) rays, lateral and medial heads of each, except dorsalmost one and ventralmost two, embracing small cartilaginous distal radial. Dorsalmost ray embracing ovoid cartilage, the ontogenetic origin of which Johnson and Brothers (1993:463) described as equivocal. As noted by those authors, typically in teleosts, this cartilage eventually fuses to the base of the medial half of the first ray, ossifying as a facet that articulates with the scapular condyle. Single, slender, elongate postcleithrum present.

Comparisons.—*Paxton* (Fig. 13A) shares with pseudamines (e.g., *Gymnapogon* and *Pseudamiops*, Fig. 13B–C) a ventrally directed stem on the posteroventral portion of the coracoid. In other apogonids (e.g., *Fowleria*, Fig. 13D), there is no distinct coracoid stem posteroventrally, although there may be a posteriorly or postero-dorsally pointed projection. The location of the coracoid articulation with the cleithrum also supports a pseudamine affinity for *Paxton*. In most apogonids, the coracoid articulates at the ventral tip of the cleithrum or slightly more dorsally (up to a point approximately one-quarter the length of the cleithrum from the ventral tip, Fig. 13D), whereas in *Paxton* and pseudamines, the coracoid articulates at a point one-third or more the length of the cleithrum from the ventral tip (Fig. 13A–C). *Paxton* and *Gymnapogon* are unique among apogonids in having a single postcleithrum.

Pelvic girdle.—Pelvic girdle comprising paired basipterygia, each supporting on its posterior margin one spine and five soft rays (Fig. 14). The two halves of girdle in close proximity posteriorly, where medial processes approach one another at ventral midline; bony interdigitating suture as described by Stiassny and Moore (1992:217) for higher percomorphs lacking. Central processes well separated from one another anteriorly. Small laterally directed spine present on external dorsal wing of central process near its origin posteriorly. Little three-dimensional structure to girdle because external ventral wing almost imperceptible. Anterior and posterior processes lacking. Median wishbone-shaped cartilage lying just posterior to posterior

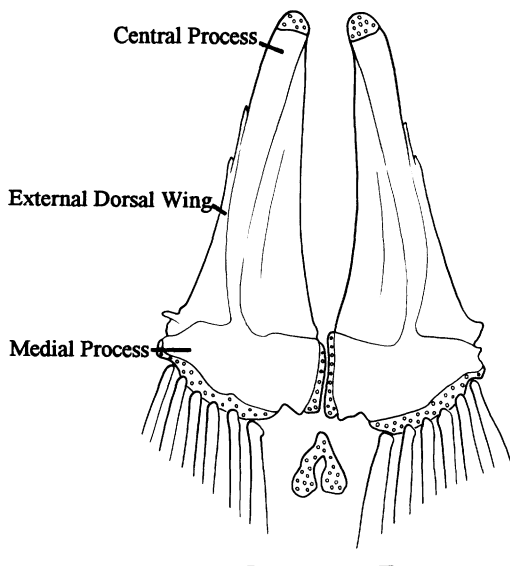


Fig. 14. Pelvic girdle of *Paxton concilians*, CSIRO H.2254-1, 49.0 mm SL.

margins of central processes between bases of pelvic fin spines.

Comparisons.—*Paxton* shares with other pseudamines a very reduced external ventral wing and thus the pelvic girdle has little three-dimensional form. *Paxton* shares with *Gymnapogon* the laterally directed spine near the posterior end of the external dorsal wing. *Paxton* is unique among apogonids in lacking anterior and posterior processes and in having the median wishbone-shaped cartilage, a feature we have not observed in any other fishes.

RELATIONSHIPS

In his comparative osteological treatment of the Apogonidae, Fraser (1972) recognized three subfamilies, the Apogoninae (apogonids proper, i.e., primarily shallow-water reef forms), Pseudaminae (small to minute elongate fishes often with translucent or transparent bodies with slimy or gelatinous skin, feeble or no squamation, conspicuous intersecting lines of papillae on the head and body, etc.), and Epigoninae (relatively deep-water forms that differ from apogonines and pseudamines in having, e.g., two pairs of uroneurals and 25 vertebrae). Fraser hypothesized that epigonines are primitive with respect to apogonines and pseudamines, and Johnson (1984) subsequently removed epigonines from the Apogonidae. Johnson suggested that *Brinkmanella*, *Epigonus*, *Florenciella*, *Rosenblattia*, and *Sphyraenops* constitute a distinct

family, the Epigonidae, characterized by several specializations of the jaws, suspensorium, and infraorbitals. Johnson (1993) provided further evidence that epigonids are not closely related to apogonids by identifying synapomorphies of apogonines + pseudamines that are lacking in epigonids: (1) absence of a direct articulation between the second epibranchial and second pharyngobranchial (Fig. 8); (2) expanded third epibranchial and narrow fourth epibranchial (Fig. 8); (3) small fourth upper pharyngeal toothplate lacking a fourth pharyngobranchial cartilage (Fig. 8); (4) very short distal radial associated with last dorsal fin spine, the serially associated proximal-middle element nearly contacting last spine (Fig. 11A–B); and (5) horizontal and vertical rows of superficial neuromasts on head and body (Fig. 2; see also Smith, 1954, fig. 3; Hayashi, 1991, fig. 11).

Although rare among percoids examined, some of those features are present elsewhere: *Epigonus* is superficially similar to apogonids in having a relatively large third epibranchial and slender fourth; *Scombrops* has a reduced distal radial associated with the last dorsal fin spine; *Pempheris* and *Glaucosoma* lack an articulation between the second epibranchial and second pharyngobranchial (Johnson, 1993); and *Kurtus* has most of the diagnostic features of apogonids and may be closely related to the family (Johnson, 1993). We only tentatively include the presence of horizontal and vertical rows of neuromasts as a synapomorphy of apogonids because ongoing work by L. R. Parenti and J. Song (USNM, pers. comm.) suggests that similar linear patterns are found in more teleosts than previously recognized. Identification of the closest relatives of apogonids is needed to test the polarity of all proposed apogonid synapomorphies, but they appear to be derived relative to the general percoid conditions: (1) second epibranchial and second pharyngobranchial articulate synchondrally, (2) the third and fourth epibranchials are not greatly enlarged or reduced, (3) a small fourth pharyngobranchial cartilage is associated with the fourth upper pharyngeal toothplate, (4) the distal radial associated with the last dorsal fin spine is elongate, and (5) there are no conspicuous rows of sensory papillae on the head and body. Fraser (1972) noted that apogonines and pseudamines (Apogonidae herein) share two anal fin spines, a swimbladder with an anterodorsal oval, 10 + 14 vertebrae, and no developed axillary scale at the base of the pectoral fin. Of those, we tentatively consider two as synapomorphic for apogonids: (6) two anal fin spines, one supernumerary on the first pterygiophore (Fig. 10); (7)

swimbladder with anterodorsal oval (see Fraser, 1972, plate 1). The number of anal fin spines has increased and decreased a number of times in the Percoidei from the primitive condition of three, but the presence of two spines is nevertheless uncommon in the group (Johnson, 1984, table 120). Furthermore, some groups that have two spines (e.g., epigonids, sciaenids, *Kurtus*) have both spines in supernumerary association with the first pterygiophore rather than one (Johnson, 1984, but see note about anal fin spines in comparisons section of Median Fins above). Nearly all apogonines and pseudamines for which Fraser (1972) examined swimbladders have the oval at the anterodorsal end, whereas epigonids have the oval posterodorsally. Fraser (1972) considered the latter to be the primitive state for his Apogonidae, but further investigation of percoid swimbladder morphology is needed to corroborate this hypothesis. A vertebral count of 10 + 14 and absence of an axillary scale at the base of the pectoral fin are common percoid features and thus of little value in defining the Apogonidae.

Despite lacking one of the apogonid hallmarks, separate dorsal fins, *Paxton* is clearly an apogonid, as it shares with other members of the family most of the diagnostic features listed above (*Paxton* is specialized with respect to other apogonids in having a single anal fin spine). Furthermore, the differences in dorsal fin configuration between *Paxton* and other apogonids are minimal, and the continuity of the dorsal fin in *Paxton* is clearly secondarily derived. Like most other apogonids, *Paxton* lacks a spine serially associated with the sixth dorsal fin pterygiophore (Fig. 9). An external gap in the fin fails to form because the sixth and seventh dorsal fin pterygiophores are closely spaced, and both pterygiophores lack long posterior projections (see discussion under Median Fins above). We do not consider separate dorsal fins as a synapomorphy of apogonids because many lower percoids have this feature, and it is unclear how many times it has evolved.

Within the Apogonidae, *Paxton* superficially bears little resemblance to any described genus, but reductive features such as absence of scales and supraneurals suggest it is related to the pseudamine genera *Pseudamia*, *Pseudamiops*, and *Gymnapogon*. None of those genera is defined on the basis of derived features, and a phylogenetic analysis of all pseudamine species is needed to better understand generic limits and relationships within the group. Such a study is in progress, and results will be reported later. Of relevance to the present study are the following: Is the subfamily Pseudaminae a natural as-

semblage? If so, is *Paxton* a pseudamine? And, if so, what are its affinities within the group?

Our investigation supports monophyly of Fraser's (1972) Pseudaminae and Johnson's (unpubl. abstract, 70th Annual ASIH Meeting, 1990) conclusions that *Paxton* is a member of that group and the sister group of *Gymnapogon*. From our preceding comparisons of the osteology of *Paxton* with that of other apogonines and from our survey of the pertinent literature, we hypothesize that the following characters are derived for the Pseudaminae with respect to apogonines and lower percoids: (1) neurocranium elongate (length approximately four times depth; Fig. 3); (2) parasphenoid contiguous with pterosphenoid (Fig. 3); (3) basisphenoid absent (Fig. 3); (4) dorsal aspect of vomer nearly flat and widely separated from mesethmoid by large ethmoid cartilage (Fig. 3); (5) upper and lower jaws with canine teeth (Fig. 5); (6) two or fewer supraneurals; (7) one or more spinous dorsal fin pterygiophores with proximal-middle and distal elements separated from one another by a gap (Figs. 9, 11); (8) two epurals (Fig. 12); (9) coracoid with cartilage-tipped ventrally directed stem on posteroventral portion (Fig. 13); (10) coracoid articulating with cleithrum at a point one-third the length of the cleithrum or more from its ventral tip (Fig. 13); (11) pelvic girdle with little three-dimensional form, the external ventral wing of the basipterygium small (Fig. 15); and (12) scales cycloid and deciduous or lacking.

Primitive apogonid states for those features appear to be (1) a deeper neurocranium (length approximately 2–2.5 times greatest depth); (2) parasphenoid separated from pterosphenoid by prootic; (3) basisphenoid present; (4) dorsal aspect of vomer with dorsal projection that meets the mesethmoid or nearly does; (5) canine teeth lacking; (6) three supraneurals; (7) proximal-middle elements of all dorsal fin pterygiophores with posterior shelf that articulates with distal radial; (8) three epurals; (9) posteroventral portion of coracoid without ventral stem; (10) coracoid articulates with cleithrum near its ventral tip; (11) external ventral wing of basipterygium well developed, promoting three-dimensional nature of pelvic girdle; and (12) scales usually ctenoid, cycloid or weakly ctenoid (but not deciduous) in several apogonine genera.

Four of the putative synapomorphies of pseudamines recognized herein, absence of a basisphenoid, two or fewer supraneurals, two epurals, and canine teeth in the jaws, are only tentatively considered derived for the Pseudaminae because they occur in a number of apogonines,

and variation in most of those characters is common within the Percoidei. Among apogonines, the basisphenoid is reduced or absent in *Apogonichthys*, *Astrapogon*, *Foa*, *Fowleria*, *Neamia*, *Phaeoptyx*, *Rhabdamia* (*Bentuviaichthys*), *Siphamia*, and *Vincentia*; *Phaeoptyx*, *Rhabdamia*, *Siphamia*, and some subgenera of *Apogon* have one or two supraneurals, and supraneurals are apparently lacking in *Astrapogon alutus* (Fraser, 1972), *Cercamia* (Hayashi, 1991; this study), and *Lachneratus* (Fraser and Struhsaker, 1991); *Rhabdamia* (*Verulux*) and some species of *Siphamia* have two epurals; and *Apogon affinis*, *Cheilodipterus*, *Coranthus*, *Rhabdamia* (*Bentuviaichthys*), and *Lachneratus* have some slightly enlarged or canine teeth in the upper and lower jaws. Nevertheless, Fraser (1972) hypothesized that primitive apogonine states for those four characters are presence of a basisphenoid, three supraneurals, three epurals, and jaws with bands of villiform teeth, and Fraser (1973) found those presumably primitive features in *Holapogon*, a genus he considered to be "near the ancestor which gave rise to all the living Apogoninae" (Fraser 1973: 1). Johnson (1984) noted that three epurals and three supraneurals appear to be primitive states for percoids. A cladistic reconstruction of apogonine phylogeny is needed to further investigate primitive apogonine states of all pseudamine characters.

Randall and Smith (1988) noted that *Cercamia* resembles *Pseudamiops* in having only two pairs of epipleural ribs (epineural bones), and Hayashi (1991) illustrated the caudal skeleton of *C. eremia* with two epurals, a condition that we believe, as noted above, may be a synapomorphy of pseudamines. However, a cleared-and-stained specimen of *C. eremia* examined in this study has two ossified epurals and another small, cartilaginous epural posterior to those. *Cercamia cladara* has three ossified epurals, and thus Randall and Smith's (1988) description of the genus as being characterized by three epurals appears to be correct. A reduced number of epineural bones is apparently independently derived in *Cercamia* and *Pseudamiops*, as our examination of *C. eremia* and *C. cladara* with respect to the diagnostic features of pseudamines listed above suggests that *Cercamia* is not a member of the Pseudaminae. *Cercamia* lacks all pseudamine characters except for two, a reduction in number of supraneural bones (*Cercamia* lacks them) and absence of a basisphenoid. Further study is needed to hypothesize whether the presence of those features in *Cercamia* and other apogonines is independent of that in pseudamines or if the Apogoninae are paraphyletic,

with some genera being more closely related to the Pseudaminae.

Paxton has all of the characters listed above as diagnostic for the Pseudaminae. Within the subfamily, *Paxton* shares numerous specializations with *Gymnapogon*, represented in our study by cleared-and-stained specimens of *G. anona*, *G. philippinus*, and *G. urosphilotus*, an intact syntype of the type species, *G. japonicus* Regan, 1905, and the holotype of *G. africanus* Smith, 1954. From our preceding comparisons of *Paxton* with other pseudamines, we propose that the following features are derived within the Pseudaminae and represent synapomorphies of *Paxton* and *Gymnapogon*: (1) bluntly pointed, fleshy flap extending posteriorly from ventral margin of preopercle (Fig. 1; see also Smith, 1954, fig. 3); (2) scales lacking; (3) dorsal edge of opercle with long posteriorly directed bony strut (Fig. 5); (4) preopercle with well-developed spine at angle (Fig. 5); (5) articulation of quadrate and metapterygoid characterized by anterior and posterior synchondral joints separated by laminar bone that sometimes comprises interdigitating bony struts (Fig. 5); (6) endopterygoid with posteroventrally directed spine (Fig. 5); (7) interoperculo-mandibular ligament long, 40–50% of the length of the long axis of the interopercle (Fig. 5); (8) first pharyngobranchial lacking, and distal end of first epibranchial with long thin cartilaginous tip (Fig. 8); (9) interarcual cartilage long and slender (Fig. 8); (10) gillrakers present on first and second arches (Fig. 7); (11) supraneurals lacking (Figs. 9, 11); (12) parhypural fused with hypurals 1 + 2 (Fig. 12); (13) upper hypural plate fused to urostylar centrum (Fig. 12); and (14) a single postcleithrum (Fig. 13).

Primitively in pseudamines (1) there is no fleshy flap on the margin of the preopercle; (2) the body is weakly scaled; (3) there is no long bony strut extending posteriorly from the opercle; (4) there is no spine at the angle of the preopercle; (5) the quadrate and metapterygoid articulate via a single synchondral joint; (6) the endopterygoid lacks a posteroventrally directed spine; (7) the interoperculo-mandibular ligament is short, < 25% of the length of the long axis of the interopercle; (8) the suspensory pharyngobranchial is present and ossified, and the medial end of the first epibranchial has a small cartilaginous tip; (9) the interarcual cartilage is short; (10) gillrakers are present on the first arch only; (11) the dorsal fin is preceded by one or two supraneurals; (12) the parhypural is autogenous; (13) neither the upper nor lower (*Pseudamia*) or only the lower hypural plate (*Pseudamiops*) is fused to the cen-

trum; and (14) there are two postcleithra. Fraser (1972, plate 12G) depicted *Pseudamiops pelucidus* without supraneurals, but all specimens that we examined have one or two small cartilaginous supraneural elements.

Although obviously its sister taxon, *Paxton* differs notably from *Gymnapogon* in some aspects of its morphology. Autapomorphies of *Paxton* (with respect to other pseudamines and apogonines) include the following: (1) dorsal fin continuous (Figs. 3, 9); (2) six dorsal fin spines (Fig. 9); (3) fourth through sixth dorsal fin spines approximately subequal and longest (Fig. 9); (4) one anal fin spine (Fig. 10); (5) entire margin of preopercle covered by skin (Fig. 2A); (6) postfrontal bone present (Fig. 3); (7) small bit of bony suturing present between anterior and posterior ceratohyals (Fig. 6); (8) fifth and sixth infraorbitals widely separated from rest of series (Fig. 4); (9) third epibranchial toothplate lacking (Fig. 8); (10) a separate fifth hypural lacking (Fig. 12); (11) anterior and posterior pelvic-girdle processes lacking (Fig. 14); and (12) an autogenous wishbone-shaped cartilage present between proximal bases of left and right pelvic fins (Fig. 14).

Other apogonids typically have (1) separate dorsal fins; (2) seven to nine dorsal fin spines; (3) the penultimate dorsal fin spine much smaller than the ultimate; (4) two anal fin spines; (5) the entire margin of preopercle exposed (dorsal limb of margin exposed in *Gymnapogon*, Fig. 2B); (6) no postfrontal bone; (7) no suturing between anterior and posterior ceratohyals (except in *Glossamia*; see Fraser, 1972); (8) fifth and sixth infraorbitals in series with other infraorbitals; (9) a toothplate fused to the third epibranchial; (10) fifth hypural autogenous; (11) anterior and posterior processes of pelvic girdle present; and (12) no autogenous cartilage between bases of pelvic fins.

SUMMARY

Four specimens of an unidentified percoid fish from northwestern Australia are described as a new genus and species of pseudamine apogonid, *Paxton concilians*. The pseudamine genus *Gymnapogon* has been referred to as “puzzling” and “aberrant” (Smith, 1954:775) and “not intimately related to apogonids or other percoid fishes” (Fraser, 1972:32). Our investigation clearly supports a sister-group relationship between *Gymnapogon* and *Paxton* and suggests that those genera, along with *Pseudamia* and *Pseudamiops*, form the well-defined subfamily Pseudaminae, diagnosed here on the basis of 12 derived characters. Although diagnostic features

of *Paxton* are numerous, most of the characters previously used to diagnose *Gymnapogon* (a large preopercular spine, absence of scales, absence of ectopterygoid teeth, parhypural fused to lower hypural plate, and a single postcleithrum; Fraser, 1972) are also present in *Paxton*. Further investigation of *Gymnapogon* monophyly is needed. One feature that may be useful in diagnosing the genus is a subocular shelf on the third infraorbital, which is lacking in other pseudamines but present in most apogonines and lower percoids (and thus possibly a reversal in *Gymnapogon*). We anticipate that our ongoing work on pseudamine phylogeny will resolve questions about the monophyly of all pseudamine genera as well as provide corroborative evidence for hypotheses of relationships outlined herein.

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