

MONOPHYLY OF THE GRAMMATIDAE AND OF THE NOTOGRAPTIDAE, WITH EVIDENCE FOR THEIR PHYLOGENETIC POSITIONS AMONG PERCIFORMS

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ABSTRACT

Monophyly of a redefined Grammatidae consisting only of *Gramma* Poey and *Lipogramma* Böhlke is supported by synapomorphic modification of the cheek musculature: adductor mandibulae with a separate $A_{1\beta}$ portion lying lateral to the levator arcus palatini. The position of the Grammatidae in the Perciformes remains uncertain. Contrary to recent studies, its traditional placement with the percoid "disjunct lateral-line serranoids" (Opistognathidae, Plesiopidae and Pseudochromidae) is not corroborated by present evidence. Monophyly of the Notograptidae, containing only *Notograptus* Günther, is supported by numerous autapomorphies, including: anterior expansion of the median ethmoid; a large section of the adductor mandibulae that originates broadly on the skull, preopercle, and suspensorium; and a highly reduced gill-arch skeleton. Of several competing hypotheses, current evidence favors a relationship of notograptids to acanthocline plesiopids.

This study developed from our independent attempts to determine outgroups to the perciform families Plesiopidae (Mooi, 1993) and Pseudochromidae (Gill, 1990). We began with the traditional alignment of these families within the Percoidei, in a group that has been termed the "disjunct lateral-line serranoids" (Böhlke, 1960). It soon became apparent that this placement was itself problematical as neither the Percoidei, nor the "disjunct lateral-line serranoids," are demonstrably monophyletic. Hence, there is no justification for restricting our search for possible relatives of plesiopids and pseudochromids to the Percoidei. Our initial studies of the position of these families have therefore expanded into a more general, long-term investigation of the subordinal and familial relationships of the Perciformes. As an introductory contribution, we examine the position and monophyly of two small perciform families: the Grammatidae, a poorly defined family that has traditionally been placed with the disjunct lateral-line serranoids, and the Notograptidae, a family that has been suggested as a relative of the pseudochromid subfamily Congrogadinae (Gosline, 1968) or of the acanthocline plesiopids (Smith-Vaniz and Johnson, 1990).

METHODS AND MATERIALS

Cladistic methodology was adopted to generate hypotheses of relationship (see Wiley, 1981 for an outline). Osteological observations were made from specimens that were cleared and stained by various techniques (Taylor, 1967; Dingerkus and Uhler, 1977; Taylor and Van Dyke, 1985). Muscle terminology follows Winterbottom (1974). Egg surface morphology was studied using the techniques outlined by Mooi (1990) and Mooi et al. (1990).

We examined a large number of perciform and other percomorph fishes, including the extensive AMS, ROM, and USNM cleared and stained collections. Some of this material, particularly preparations of plesiopids and pseudochromids, is listed separately in Mooi (1993) and Gill (1990). Our observations on grammatids and notograptids were from the following specimens (institutional abbreviations follow Leviton et al., 1985; other abbreviations: CS—cleared and stained; E—ovarian eggs examined; M—myological dissection):

* Order of authorship is alphabetical.

GRAMMATIDAE. *Gramma linki*, AMNH 35776, 11: 24.3–45.5 mm (CS, E, M). *G. loreto*, AMNH 29257, 2: 32.2–43.5 mm (E); AMNH 27351, 45 mm (E); AMS I.26250-002, 35.7 mm (CS); ANSP 81268, 44.0 mm (E); ANSP 94667, 40.6 mm (E); ANSP 94678, 34.7 mm (E); ROM uncat., 62.5 mm (M); ROM 749CS, 6: 31.0–52.0 mm (CS); ROM 997CS, 4: 39.6–43.5 mm (CS, E); ROM 31324, 44.8 mm (M); USNM 199487, 3: 28.5–46.5 mm (CS); USNM 267803, 5: 18.1–54.0 mm (M); USNM 306572, 34.0 mm (CS). *G. melacara*, AMNH 24740, 34.6–36.5 mm (E); ANSP 117359, 55.7 mm (M); ANSP 136610, 37.9 mm (CS); ROM 1006CS, 50.0 mm (CS, M). *Lipogramma anabantoides*, AMNH 33061, 9: 13.0–21.0 mm (M); ANSP 111405, 16.6 mm (CS); USNM 216405, 2: 16.6–17.0 mm (CS). *L. klayi*, ANSP 127671, 2: 23.8–27.3 mm (CS, M). *L. roseum*, AMNH 98255, 10.1 mm. *L. trilineatum*, ANSP 114024, 26.8 mm (CS); USNM 179004, 24.7 mm (holotype); USNM 317479, 20.0 mm (E).

NOTOGRAPTIDAE. *Notograptus* sp., AMS I.20780-056, 74.0 mm (CS); ROM 38369, 2: 87.5–101.0 mm (E); ROM 717CS, 82.2 mm (CS); USNM uncat., 170.0 mm; USNM 173796, 3: 78.0–152.0 mm (M); USNM 173797, 6: 46.0–180.0 mm (M); USNM 173798, 13: 82.0–168.5 mm (CS, E, M); USNM 222134, 4: 88.5–120.0 mm.

GRAMMATIDAE

Composition.—We follow Johnson (1984: 465) in including only *Gramma* Poey (with three species, Starck and Colin, 1978) and *Lipogramma* Böhlke (with seven species, Gilmore and Jones, 1988) in the Grammatidae. Previous authors have included considerably more genera. Böhlke (1960) defined the family to include “serranoid” fishes with disjunct (including multiple and posteriorly truncated) lateral lines, 11–13 dorsal-fin spines and 1,5 pelvic-fin rays. He placed the Stigmatonotidae as a junior synonym of the Grammatidae and included six genera: *Gramma*, *Stigmatonotus* Peters, *Grammatonotus* Gilbert, *Pseudochromichthys* Schmidt, *Fraudella* Whitley, and his new genus *Lipogramma*. He also stated (p. 5): “It is possible that I have erred in combining the Stigmatonotidae with the Grammatidae, and that the former should be retained for *Stigmatonotus*, *Grammatonotus* and *Lipogramma*, the latter to include *Gramma*, *Fraudella* (*Pseudochromichthys* uncertain) and the genera with disjunct lateral lines currently considered anthiid—*Callanthias* Lowe, *Xenanthias* Regan, *Pteranthias* Weber, *Anogramma* Ogilby.” Kharin (1983) added his new genus and species, *Pacificogramma stepanenkoi*, to the Grammatidae.

Pseudochromichthys is a synonym of the plesiopid *Plesiops* Cuvier (Aoyagi, 1941: 428). *Fraudella* has also been assigned to the Plesiopidae (Springer, 1982: 42; Hoese and Kuitert, 1984). *Plesiops* and *Fraudella* share several myological and osteological synapomorphies with the other plesiopid genera, in addition to various apomorphies that nest them well within the Plesiopidae (Mooi, 1993); these characters do not occur in either *Gramma* or *Lipogramma*. The inclusion of either *Fraudella* or *Plesiops* in the Grammatidae is therefore not justified.

Several of the genera included in the Grammatidae by previous authors are referable to the Serranidae: Randall (1980) considered *Xenanthias* and *Pteranthias* as synonyms of the anthiine genus *Plectranthias* Bleeker; the identity of *Stigmatonotus* is questionable, as there is no extant type material, but it appears to be based on a juvenile anthiine (Johnson, 1984: 465); and Anderson (1989) has shown *Pacificogramma stepanenkoi* to be a junior synonym of the anthiine *Pronotogrammus multifasciatus* Gill. The monophyly of the Serranidae is supported by four synapomorphies: loss or fusion of the posterior pair of uroneurals; absence of a procurrent spur; absence of preural radial cartilages (=interneural- and interhemal-spine cartilages of pu4, following the terminology of Fujita, 1989); and presence of three opercular spines (Johnson, 1983). Although *Gramma* and *Lipogramma* share the first two of these synapomorphies, both characters are reductive and relatively labile in perciforms, and neither genus possesses the single innovative serranid autapomorphy (presence of three opercular spines).

Anogramma is a synonym of *Callanthias* (Jordan, 1920: 487). *Callanthias* and *Grammatonotus* were excluded from the Grammatidae and placed as sole members of the Callanthiidae by Johnson (1984: 364; see also Anderson and Johnson, 1984: 949). Johnson used three synapomorphies to hypothesize monophyly of the Callanthiidae: nasal organ flat, without lamellae; lateral line running along dorsal-fin base and terminating near base of last ray, or continuing onto dorsal portion of caudal peduncle; and midlateral body scales modified with "unique ornamentation" (each with a series of pits and/or grooves). All three characters occur in other perciform fishes. We have observed that nasal organ lamellae are absent in some zoarcoids and in the congrogadine pseudochromid genus *Congrogadus* Günther. The remaining two proposed callanthiid synapomorphies appear to be related; we hypothesize that the dorsally positioned lateral line and the peculiar midlateral scales are derived from a disjunct lateral-line condition. Firstly, in its relatively dorsal position, the lateral line of callanthiids resembles the anterodorsal lateral line of taxa with disjunct lateral lines (e.g., primitive pseudochromids, plesiopids and *Gramma*), possibly differing only in the slightly more posterior termination (reaching to base of last dorsal ray or continuing onto caudal base, vs. usually reaching to middle to posterior third of dorsal-fin base in most other taxa with disjunct lateral lines). Secondly, the pitted and/or grooved scales of callanthiids occupy a similar position to the posterior lateral line of other taxa with disjunct lateral lines, and the pits and grooves are associated with free neuromasts; this is evidence that the pitted/grooved scales are modified lateral-line scales. We have observed similarly modified midlateral scales in various other taxa that lack tubed scales in the peduncular lateral line (e.g., the plesiopid *Steeneichthys*, anisochromine and pseudoplesiopine pseudochromids, and the grammatid *Lipogramma*). We also note that at least some cepolids have a dorsal lateral line and series of peduncular scales that closely approach those of callanthiids in general morphology. Despite the equivocal nature of the synapomorphies used to unite *Callanthias* and *Grammatonotus*, we agree with Johnson that they are sister taxa, and offer an additional synapomorphy: presence of a well-developed median frontal crest, with an associated elongation of the ossified sensory canal that serves the median posterior interorbital pore.

Monophyly. — Although a sister-group relationship has not been previously demonstrated for *Gramma* and *Lipogramma*, we believe that the two genera form a monophyletic group, which is defined by a single synapomorphy: presence of a medial $A_{1\beta}$ section of the adductor mandibulae that originates from the lateral surfaces of the metapterygoid, quadrate and levator arcus palatini (LAP) and inserts onto the medial surface of the maxilla via a tendon. The typical position of the adductor mandibulae is occupied by a lateral ($A_{1\alpha}$) section that originates from the preopercle (*Lipogramma*) or the preopercle and sphenotic (*Gramma*) and inserts onto the ligamentum primordium and lower jaw (via fascia) (Fig. 1A–D).

Mok et al. (1990) treated the occurrence of separate $A_{1\alpha}$ and $A_{1\beta}$ sections of the adductor mandibulae as a synapomorphy linking the Grammatidae with the Opistognathidae. However, there is evidence that the conditions found in these two families are nonhomologous. Although opistognathids do possess separate $A_{1\alpha}$ and $A_{1\beta}$ sections, $A_{1\beta}$ originates medial rather than lateral to LAP (Fig. 1E, F). The path of ramus mandibularis V might also indicate nonhomology of the $A_{1\beta}$ sections of opistognathids and grammatids. Ramus mandibularis V passes lateral to $A_{1\beta}$ in most opistognathids (Fig. 1F), while the nerve passes medial to $A_{1\beta}$ in most grammatids (Fig. 1B, D). In a few species of *Opistognathus* the nerve passes

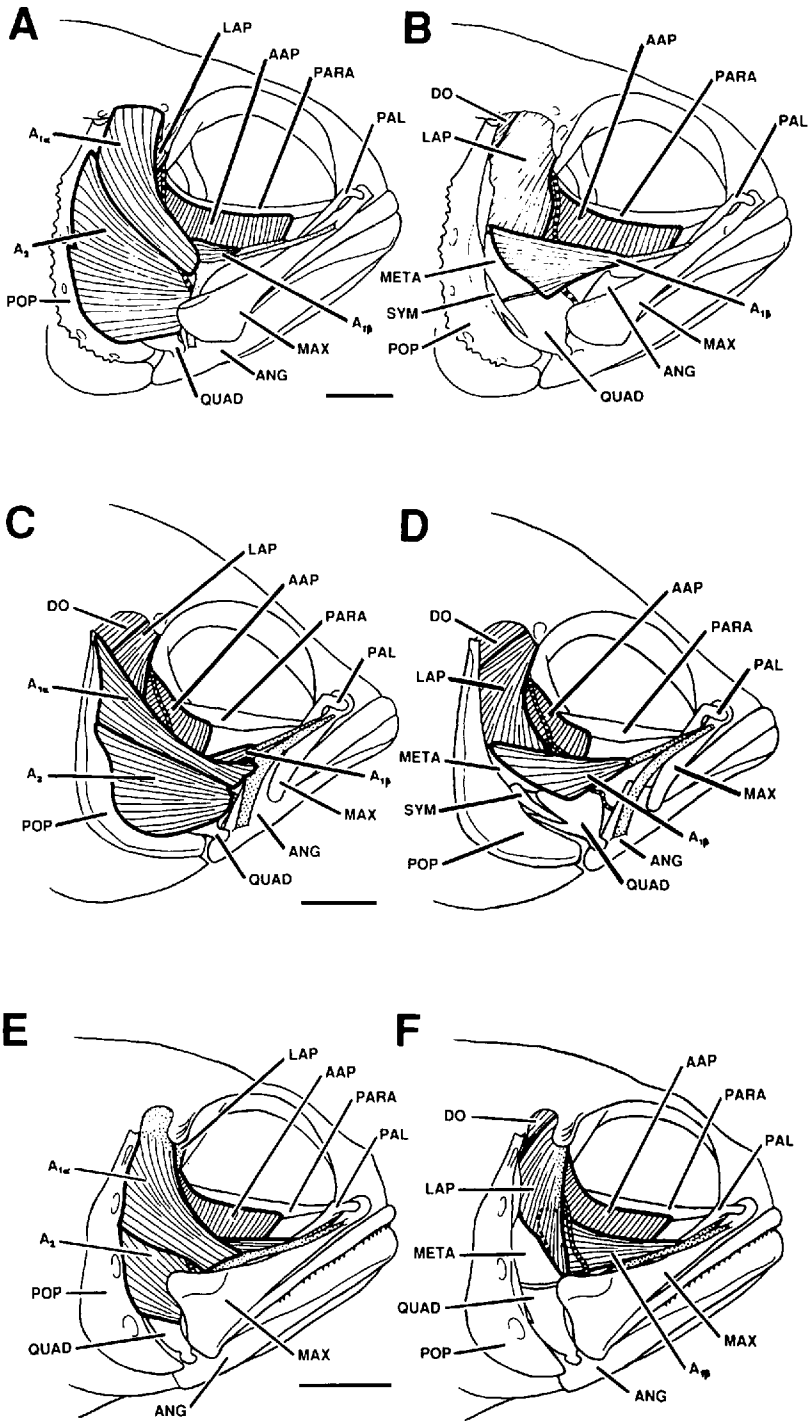


Figure 1. Right lateral view of the cheek musculature of: A, B) *Gramma linki* [AMNH 35776, 36.3 mm SL], scale bar is 2 mm; C, D) *Lipogramma anabantoides* [AMNH 33061, 17.5 mm SL], scale bar is 1 mm; E, F) *Lonchopisthus higmani* [USNM 217798, 71.0 mm SL], dotted line indicates extent of A_{1e}, scale bar is 5 mm. All superficial muscles illustrated intact in A, C, E; adductor mandibulae sections A_{1e} and A₂ removed in B, D, F. Bold lines demarcate muscles; stipple represents ligament or

medial to $A_{1\beta}$ (W. F. Smith-Vaniz, pers. comm.). In a specimen each of *Opistognathus maxillosus* and *Lipogramma klayi*, the nerve passed through $A_{1\beta}$ on one side of the head, but was lateral and medial, respectively, to $A_{1\beta}$ on the other side.

Cepolids (including owstoniids, see below) have an arrangement of the adductor mandibulae that approaches that of grammatids. The A_1 has two separate origins, a dorsolateral one from the preopercle that is lateral to the A_2 , and a ventrolateral one from the mesopterygoid medial to the A_2 and lateral to the LAP. Unlike grammatids, both of the A_1 sites of origin share fibers anteriorly and insert onto the medial and lateral surfaces of the maxilla via the same tendon.

We follow Okada and Suzuki (1956) and Springer et al. (1977: 10) in including the Owstoniidae within the Cepolidae. Springer et al. (1977) used four synapomorphies to unite the two families: last dorsal- and anal-fin pterygiophore each with a single ray, no predorsal (=supraneural) bones, first dorsal-fin pterygiophore inserting between first and second neural spines, and a single postcleithrum on each side. We add an additional synapomorphy to support monophyly of the expanded Cepolidae: presence of two rod-like, cartilage-tipped uncinat processes on epibranchial 1 (Fig. 2).

A few specializations are apparently shared by one of the grammatid genera and potentially related families (see below), but are absent in the other genus; if these specializations are homologous, they either refute monophyly of the Grammatidae, or indicate a sister-group relationship between the Grammatidae and the given family, with modification ("reversal") in one of the grammatid genera.

Lipogramma shares an apomorphy with the Opistognathidae: absence of distal radials in the spinous dorsal fin. However, the pterygiophores of opistognathids differ from those of *Lipogramma* and *Gramma* in the following: they are widely spaced (vs. closely associated), the posterodorsal tips are cartilaginous (vs. bony), and the posterolateral processes are smaller and without anteriorly directed tips (Mooi, 1993: fig. 6). The morphology and arrangement of the pterygiophores in *Gramma* and *Lipogramma* are similar, excepting the absence of distal radials in the latter genus. Mooi (1993) suggested that this loss might be related to paedomorphosis. Loss of distal radials in the spinous dorsal fin occurs homoplastically in some blennioids, and most zoarcoids and gobioids.

Gramma also shares an apomorphy with opistognathids; the $A_{1\alpha}$ section of the adductor mandibulae originates from the sphenotic as well as the preopercle (Fig. 1A, E). However, A_1 also originates from the sphenotic in various other perciforms, including: some *Plesiops* species (Mooi, 1991) and *Belonepterygion* McCulloch (Smith-Vaniz and Johnson, 1990: fig. 22c) in the Plesiopidae; *Notograptus* Günther (where A_1 originates widely from the pterotic, sphenotic and preopercle, see below); the percichthyid *Gadopsis* Richardson; and some zoarcoids (including "stichaeoids," following Anderson's, 1984, cladistic definition).

As noted by Springer et al. (1977: 10), *Lipogramma* shares two characters with the Pseudochromidae (sensu Godkin and Winterbottom, 1985) and Clinidae: lack of an ossified infrapharygobranchial 1, and presence of a cord-like ligament extending from the lateral surface of the anterior ceratohyal to the anterior portion of the dentary. The first of these occurs widely in perciforms; moreover, it is

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tendon; checkered line is ramus mandibularis V nerve. Muscles—AAP, adductor arcus palatini; $A_{1\alpha}$, $A_{1\beta}$, A_2 , sections of adductor mandibulae; DO, dilatator operculi; LAP, levator arcus palatini. Bones—ANG, anguloarticular; MAX, maxilla; META, metapterygoid; PAL, palatine; PARA, parasphenoid; POP, preopercle; QUAD, quadrate; SYM, symplectic.

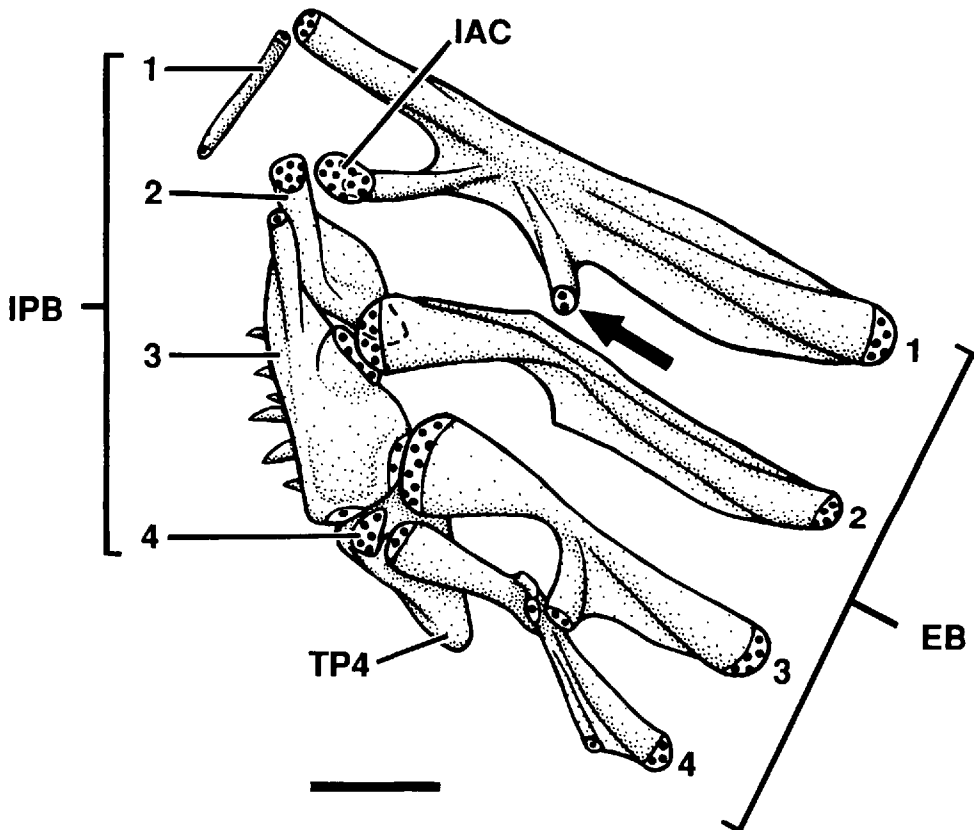


Figure 2. Right dorsal gill elements of *Cepola pauciradiata* [USNM 213502, 200.0 mm SL], dorsal view. Large stipple indicates cartilage. Arrow points to additional unciniate process on first epibranchial. EB1–4, epibranchials 1–4; IAC, interarcual cartilage; IPB1–4, infrapharyngobranchials 1–4; TP4, tooth plate of infrapharyngobranchial 4. Scale bar is 1 mm.

intraspecifically variable in both *Lipogramma* and pseudochromids (some specimens had an ossified infrapharyngobranchial 1 on one side and a cartilaginous infrapharyngobranchial 1 on the other). The second character is also widely distributed, and is associated with the relative development of a connective tissue sheath that dorsally lines the protractor hyoidei. In taxa with a “cord-like ligament” the connective tissue is well developed and robust. Cord-like development of this tissue also occurs in some zoarcoids and some serranids, and moderate development occurs in some plesiopids and many gobioids. We further dismiss a close relationship between *Lipogramma* and the Clinidae because *Lipogramma* lacks various synapomorphies that place clinids within the Blennioidei (Springer, 1993).

Phylogenetic Position.—Böhlke (1960) placed the Grammatidae among a series of “serranoid” families with disjunct lateral lines: Acanthoclinidae, Anisochromidae, Plesiopidae, Pseudochromidae, Pseudogrammidae, and Pseudoplesiopidae. The Pseudogrammidae have been incorporated subsequently into the Serranidae (Kendall, 1976: fig. 1). Springer et al. (1977) noted that the Acanthoclinidae, Grammatidae, Plesiopidae, and newly defined Pseudochromidae share several

specializations (in addition to modification of the lateral line): fewer than seven branchiostegal rays, anterior and posterior ceratohyals sutured together, hypurals 1 and 2 fused together, and hypurals 3 and 4 fused to each other and to the urostyle. They also noted that these same specializations are shared by opistognathids and some cepolids (primitive cepolids have autogenous hypurals 3 and 4). Notograftids, almost all blennioids (one specialized labrisomid, *Paraclinus walkeri* Hubbs, has seven branchiostegals, Springer, 1993), pholidichthyids, and most labrids (sensu Kaufman and Liem, 1982) also share these specializations.

Mok et al. (1990) hypothesized that the Grammatidae are the sister group of the Opistognathidae, that these families form the sister group of the Pseudochromidae, and that all three taxa form the sister group of an assemblage consisting of the Acanthoclinidae and its sister group, the Plesiopidae. Mok et al. (1990) listed two synapomorphies linking the Grammatidae with the Opistognathidae. We hypothesize that the first of these (presence of separate $A_{1\alpha}$ and $A_{1\beta}$ sections of the adductor mandibulae) is nonhomologous in the two families (see above). The second proposed synapomorphy, epaxialis muscles attach to dorsal-fin pterygiophores, is relatively widespread in perciform fishes, occurring, for example, in serranids, pseudochromids, tripterygiids, notograftids, and *Siniperca*, as well as opistognathids and grammatids. A broad survey of epaxial muscle-ptyerygiophore attachments in perciforms is in progress by the present authors.

Mok et al. (1990) identified a single synapomorphy of the Grammatidae, Opistognathidae, and Pseudochromidae: anterior tip of ceratobranchial 5 sharply pointed, not framed with cartilage. We confirm the presence of this character in these three families, but note that it also occurs in labrids and at least some blennioids. The character appears to be associated with truncation of the anteriorly projecting, cartilage-tipped process of ceratobranchial 5, and elongation and anteroventral curving (in grammatids, labrids, opistognathids, and pseudochromids) or ventral curving (in blennioids) of the ventrolateral keel that normally extends beneath the cartilage-tipped process (Fig. 3).

Mooi (1993) discussed the characters used by Mok et al. (1990) to support a sister-group relationship between the Acanthoclinidae and Plesiopidae. He also provided evidence for inclusion of the Acanthoclinidae within the Plesiopidae.

Mok et al. (1990) used two characters to unite the Acanthoclinidae, Grammatidae, Opistognathidae, Plesiopidae, and Pseudochromidae (collectively termed "pseudochromoids" by Mooi, 1990): reduced number of olfactory lamellae, and lateroventral spur on cleithrum. Both characters are widely distributed among perciforms. Taxa with reduced olfactory lamellae include zoarcoids, blennioids, callanthiids, and some serranids. A lateroventral spur on the cleithrum occurs in, for example, blennioids, many serranids, most gobioids, and some trachinoids (sensu Pietsch, 1989).

Johnson (1984: 485) suggested that the egg morphology and parental care exhibited by pseudochromids (sensu Godkin and Winterbottom, 1985) and plesiopids (sensu Mooi, 1993) is unusual within the Percoidei, and might be indicative of a close relationship. Mooi (1990) examined egg surface morphology of these and several other perciform taxa with demersal eggs: apogonids, grammatids, opistognathids, and pomacentrids. Among the taxa Mooi examined, only opistognathids, *Plesiops* (Plesiopidae), apogonids, pomacentrids, and *Gramma loreto* (Grammatidae) have chorionic filaments that are arranged around the micropyle (Mooi, 1990: figs. 3, 4, 5). However, differences in filament attachment and other egg surface characteristics suggest that conditions among these taxa could be nonhomologous. Considering that there is no evidence for a monophyletic Per-

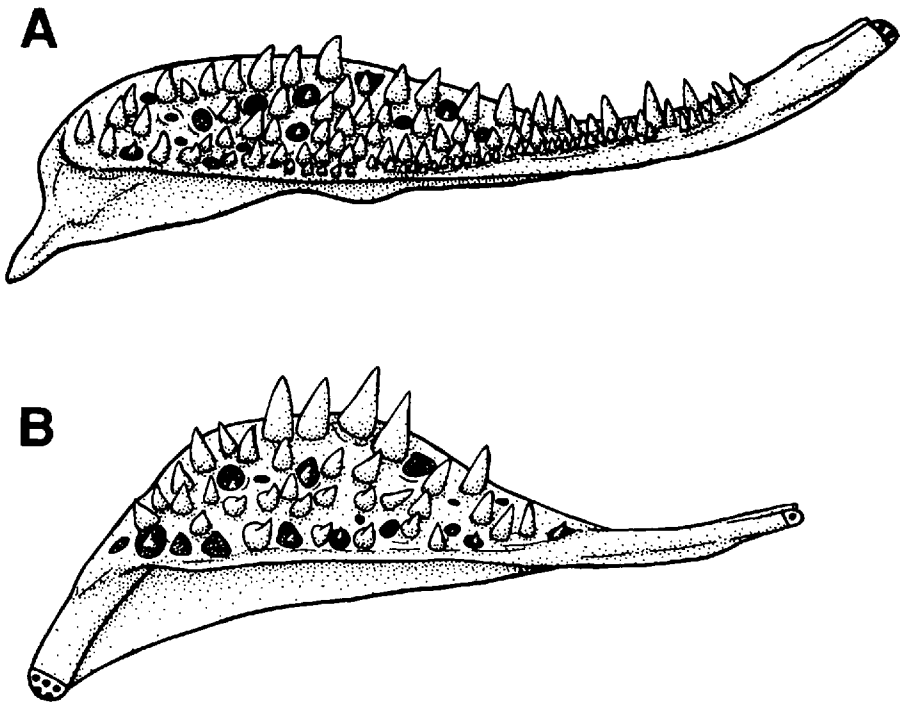


Figure 3. Dorsolateral views of the fifth ceratobranchial from the left side of: A) *Gramma loreto* [USNM 199487, 46.5 mm SL]; B) *Plesiops coeruleolineatus* [USNM 211304, 30.3 mm SL]. Note the absence of cartilage on the anterior tip of A). Scale bar is 1 mm.

coidei, other perciforms that are known to possess demersal eggs with filaments, such as blennioids and gobioids, might be possible relatives.

Gramma (all three species) is characterized by eggs with a loose cluster of filaments arising from small protrusions that surround the micropyle, and by button-like knobs that are distributed evenly over the remaining egg surface (Mooi, 1990: fig. 4). The egg morphology of *Lipogramma trilineatum*, the only species of *Lipogramma* for which eggs are available, is unlike that of *Gramma*. In *L. trilineatum* the filaments have unmodified bases, attach directly to the chorion, and are distributed evenly over the egg surface; there are no button-like knobs. Presently, egg morphology provides no evidence for either the phylogenetic position or the monophyly of the Grammatidae.

Smith-Vaniz and Johnson (1990) described the presence of a notch in the branchiostegal membrane between the third and fourth branchiostegal rays as a potential autapomorphy of the family Plesiopidae. Mooi (1993) reported a similar, though less pronounced, condition in *Gramma*, commenting that the notch in these two taxa is associated with the third ray being relatively straight rather than curved, and therefore diverging distally from the curved fourth ray. Mooi dismissed the condition as nonhomologous because, unlike plesiopids, the third branchiostegal ray of *Gramma* is not wider than its neighboring rays. *Lipogramma* lacks the notch, but possesses the straight, diverging third ray that is not wider than its neighboring rays. Gobioids with six branchiostegal rays also possess a notch between the third and fourth rays; gobioids with five rays have the notch

between the second and third rays, but the notch has not shifted position—an anterior ray has been lost.

Summary and Comments.—A redefined Grammatidae consisting of only *Gramma* and *Lipogramma* is demonstrably monophyletic. Böhlke's (1960) original group of serranoids with disjunct lateral lines has gradually been modified over the past 30 years to include only the pseudochromoids of Mooi (1990) (Grammatidae, Opistognathidae, Plesiopidae, Pseudochromidae), and possibly the Notograptidae (see below). We have considered the possible relationships of grammatids with these taxa, and cannot corroborate the hypotheses advanced by Mok et al. (1990). We can neither corroborate nor falsify monophyly of the pseudochromoids, and without evidence to unite these taxa, the sister taxon of the Grammatidae could even lie outside the Percioidei. For example, blennioids have demersal eggs with filaments that are reminiscent of those of grammatids, and at least some labrids and blennioids lack an anterior cartilage tip on ceratobranchial 5.

NOTOGRAPTIDAE

Composition.—The family Notograptidae contains one genus, *Notograptus* Günther (*Blanchardia* Castelnau is a synonym; see Ogilby, 1912), and five nominal species, which are known only from northern Australia and New Guinea: *N. gregoryi* Whitley (1941), *N. guttatus* Günther (1867), *N. kauffmani* Tyler and Smith (1970), *N. livingstonei* Whitley (1931), and *Blanchardia maculata* Castelnau (1875). The family is being revised by G. R. Allen and D. F. Hoese. Pending completion of this revision, we have not identified our specimens of Notograptidae to species.

Monophyly.—In this section, we summarize apomorphic features possessed by notograptids that are either unique to the family or are known from few other perciforms. Depending on the placement of the Notograptidae, these specializations may be autapomorphies that corroborate monophyly of the family, or they may be synapomorphies that link the family with other taxa (see Phylogenetic Position below).

SKULL (Fig. 4). A striking feature of the skull of *Notograptus* is the laterally compressed and plate-like median ethmoid that extends far anteriorly. Associated with this, the vomer bears an anterodorsal process to the anteroventral surface of the median ethmoid, and the rostral cartilage, nasal bones and the ascending processes of the premaxillae are aligned more-or-less perpendicularly, rather than obliquely, to the longitudinal axis of the body. Other features that depart from the generalized perciform condition include: vomer edentate; ascending processes of parasphenoid contact frontals, excluding the prootic from the posterior margin of the orbit; basisphenoid reduced to a small crescent-shaped bone; and sphenotics large, each with a ventrally projecting shelf for attachment of the levator arcus palatini.

SUSPENSORIUM, JAWS AND SUPERFICIAL BONES OF HEAD. The suspensorium and jaws of *Notograptus* differ from generalized perciforms in the following details: most of the bones are more horizontally elongate; the palatine extends far posteriorly beneath the ectopterygoid; the coronoid process on the anguloarticular is either reduced or absent; the palatine and jaws have broad toothed surfaces, bearing short conical teeth; and the hyomandibula is weakly associated with the remainder of the suspensorium (Fig. 5).

Notograptids have four infraorbital bones, fewer than generalized perciforms (Fig. 6). Infraorbital 1 (lacrimal) is more-or-less tubular without a ventral lamina,

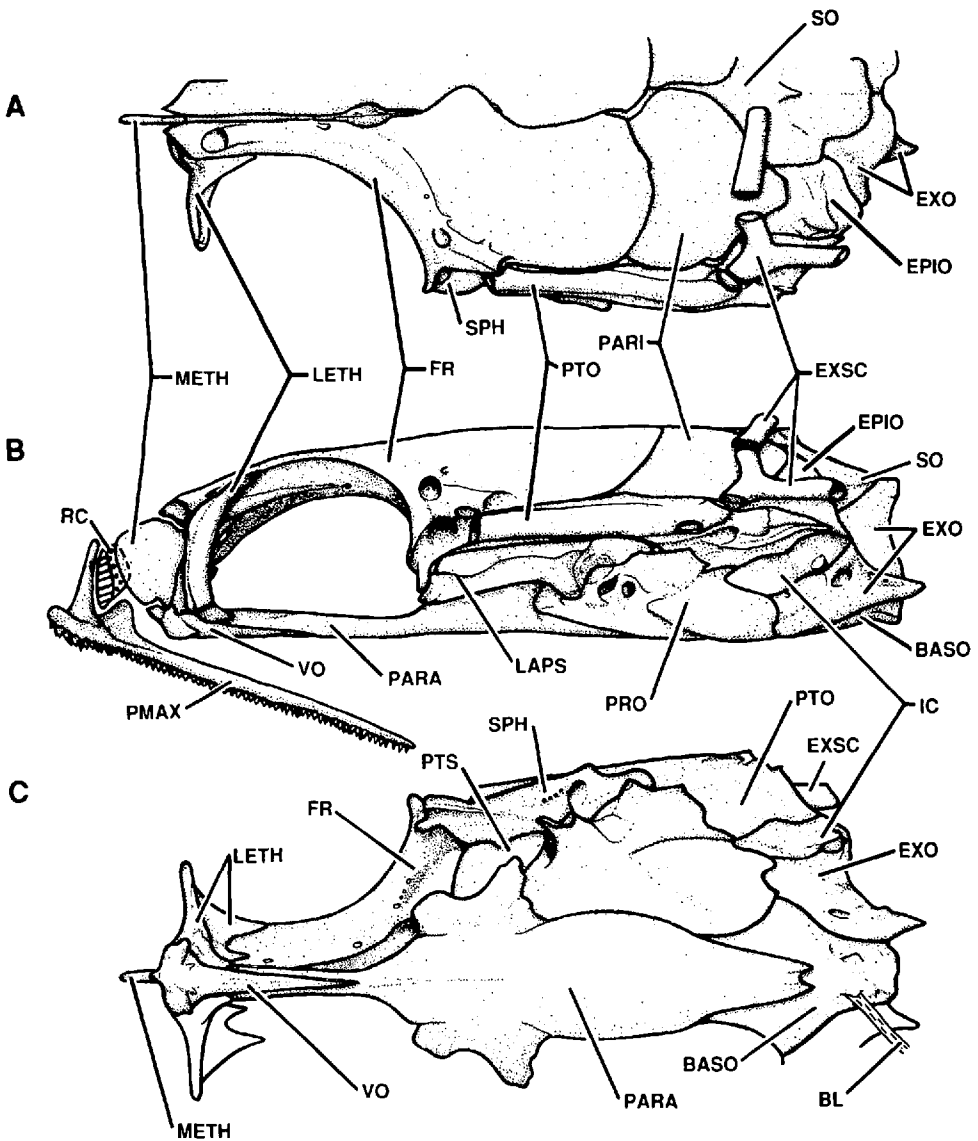


Figure 4. Skull bones of *Notograptus* [ROM 717CS, 82.2 mm SL]: A) dorsal view, left side; B) lateral view, left side, with position of right premaxilla and rostral cartilage shown in medial view; C) ventral view, left side. Large stipple indicates cartilage. Hatched area denotes cut median surface of rostral cartilage. Dotted line shows extent of rostral cartilage behind median ethmoid. Dashed lines represent ligament. BASO, basioccipital; BL, Baudelot's ligament; EPIO, epioccipital; EXO, exoccipital; EXSC, extrascapular; FR, frontal; IC, intercalar; LAPS, shelf on sphenotic for levator arcus palatini; LETH, lateral ethmoid; METH, median ethmoid; PARA, parasphenoid; PARI, parietal; PMAX, premaxilla; PRO, prootic; PTO, pterotic; PTS, pterosphenoid; RC, rostral cartilage; SO, supraoccipital; SPH, sphenotic; VO, vomer. Note that a tiny, crescent-shaped basisphenoid is present, but is obscured in lateral view by the sphenotic and parasphenoid. Scale bar is 1 mm.

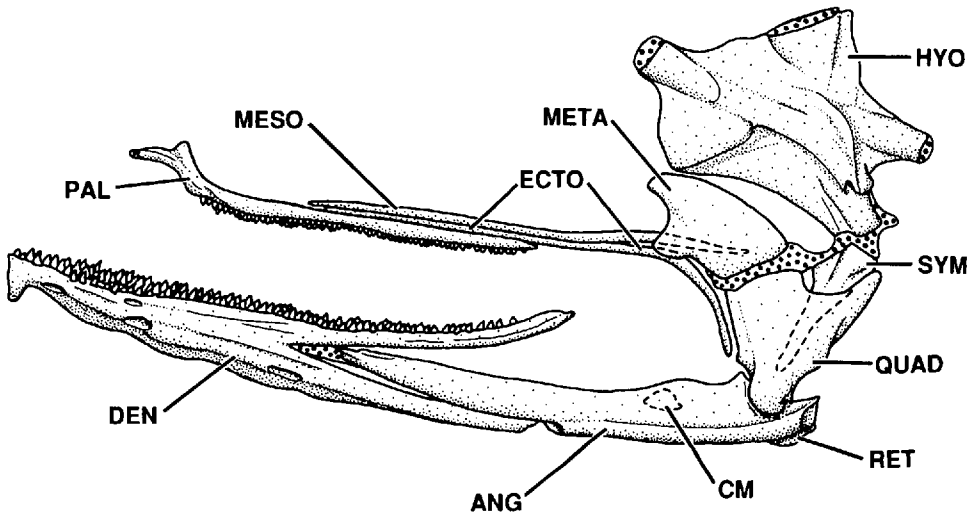


Figure 5. Lower jaw and suspensorium of *Notograptus* [ROM 717, 82.2 mm SL], left lateral view. Note that the mesopterygoid has a thin, medially projecting lamina that is not apparent in this view. Dotted lines show outlines of bones otherwise obscured. Large stipple represents cartilage. CM, coronomeckelian; DEN, dentary; ECTO, ectopterygoid; HYO, hyomandibular; MESO, mesopterygoid; RET, retroarticular. Other abbreviations as in Figure 1. Scale bar is 1 mm.

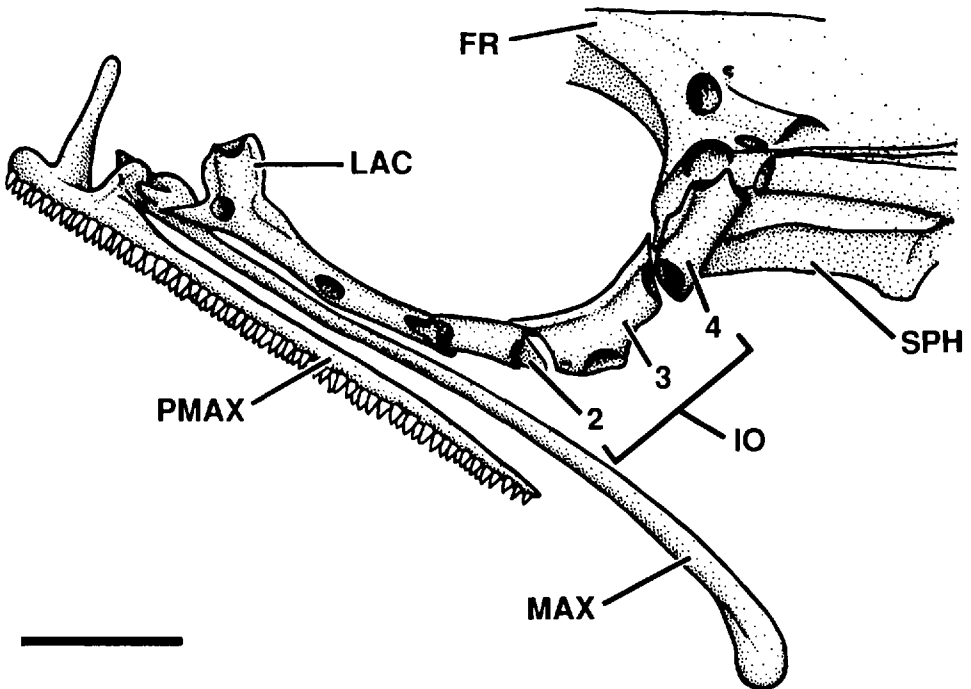


Figure 6. Infraorbital bones of *Notograptus* [ROM 717, 82.2 mm SL], left lateral view, with position relative to skull and upper jaw bones. LAC, lacrimal; IO2-4, other infraorbital bones. Other abbreviations as in Figures 1 and 4. Scale bar is 1 mm.

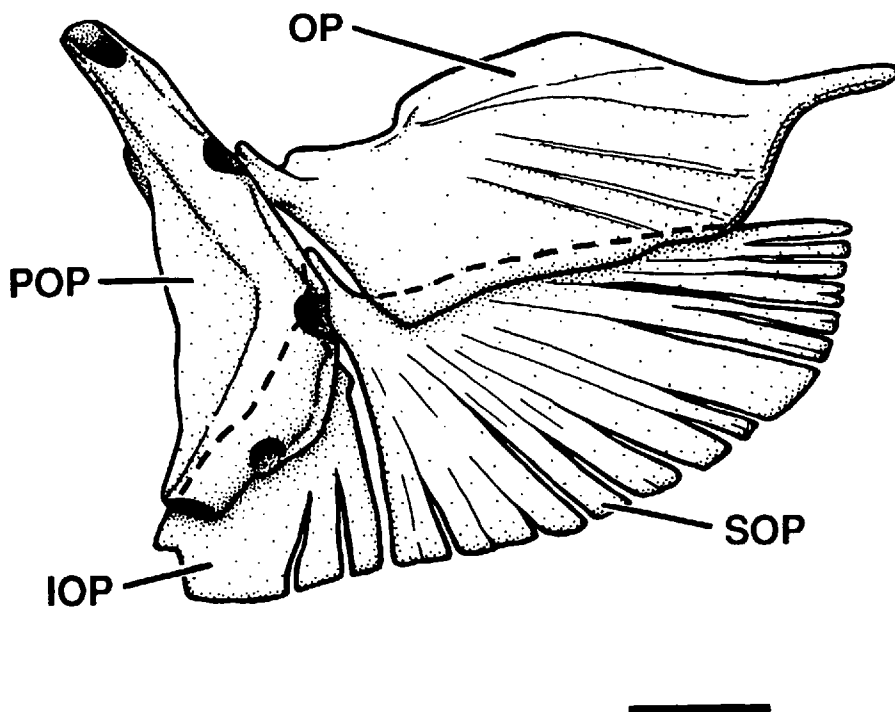


Figure 7. Opercular bones of *Notograptus* [ROM 717CS, 82.2 mm SL], left lateral view. IOP, interopercle; OP, opercle; POP, preopercle; SOP, subopercle. Scale bar is 1 mm.

and with a well-developed anteriorly projecting spine at its anteroventral corner. Infraorbital 4 (dermosphenotic?) is relatively large, posteriorly displaced, and not tightly bound to the sphenotic.

Unusual features of the opercular bones include (Fig. 7): an interopercle that is higher than it is broad; fimbriate margins on the opercle, subopercle, and interopercle; and a lateral as well as medial attachment of the levator operculi on the opercle (Fig. 8).

CHEEK MUSCULATURE. The adductor mandibulae is unusual in that it consists largely of a massive section that lies lateral to the ramus mandibularis V. It originates from the preopercle, pterotic, and sphenotic, and inserts anteriorly onto the maxilla via tendons, and anteroventrally onto the coronoid process of the dentary (Fig. 8A). This large muscle is perhaps a composite of the A_1 and A_2 sections that are usually separate in perciforms. The remaining section lying medial to the ramus mandibularis V is small; it originates from the metapterygoid and quadrate, and inserts onto the coronomeckelian bone. This portion is interpreted as A_3 (Fig. 8B).

GILL ARCHES (Fig. 9). *Notograptus* differs from generalized perciforms in lacking an interarcual cartilage, infrapharyngobranchial 1, basibranchials 3 and 4, gill rakers (including rudiments), and uncinat processes on epibranchials 1 and 2. In addition: infrapharyngobranchial 2 is rod-like and edentate (versus toothed and broadly triangular); infrapharyngobranchial 3 is greatly enlarged; the teeth on infrapharyngobranchials 3 and 4 and ceratobranchial 5 are short and granular; and the median portion of epibranchial 4 is oriented more-or-less perpendicularly to the longitudinal axis, extending medially beyond the edge of the infrapharyngobranchial 4 toothplate.

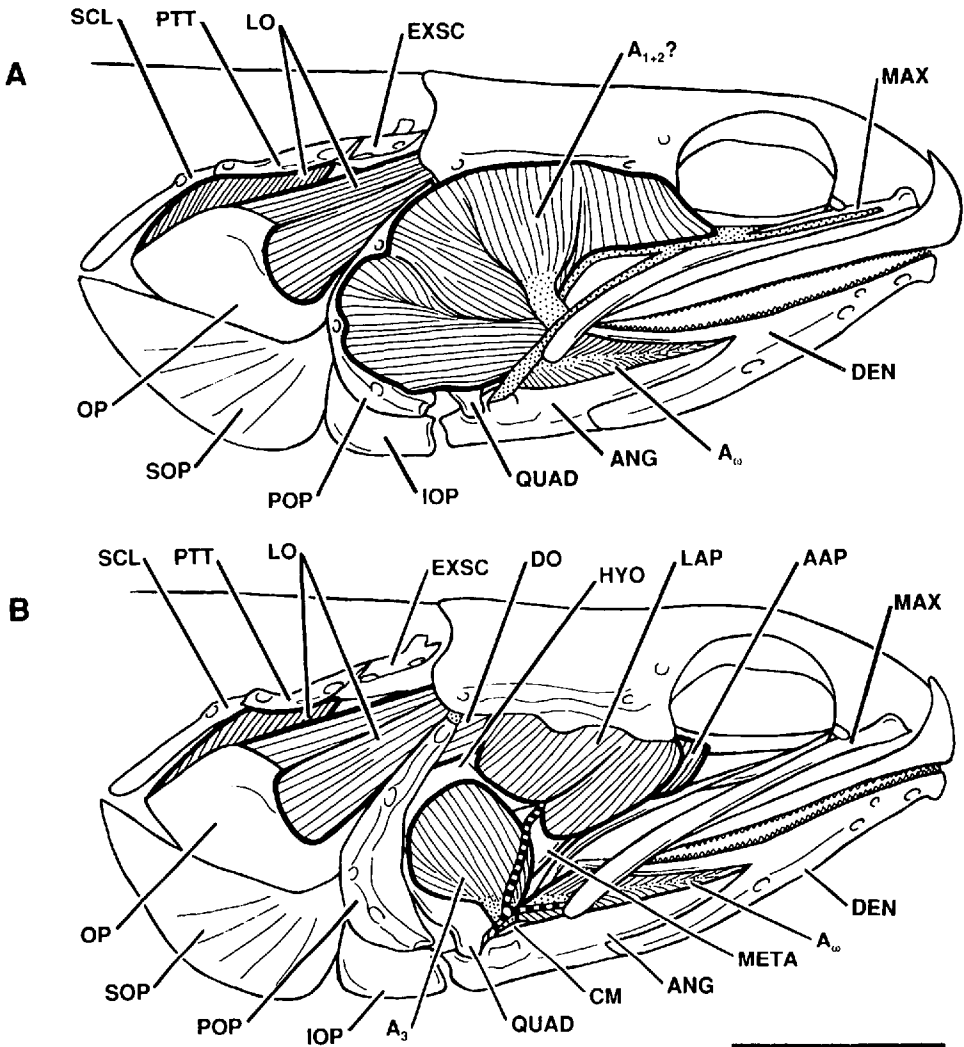


Figure 8. Cheek musculature of *Notograptus* [USNM 173796, 152.0 mm SL]. Bold lines demarcate muscles. Checkered line is ramus mandibularis V nerve and associated branches. Stipple represents tendons and ligaments. $A_{1+2?}$, A_3 , A_{10} , sections of adductor mandibulae; LO, levator operculi; PTT, posttemporal; SCL, supracleithrum. Other abbreviations as in Figures 1, 4, and 7. Scale bar is 5 mm.

PAIRED FINS. The pectoral girdle (Fig. 10) is distinctive in that: the cleithrum is strongly curved, extending far anteroventrally; the ventral tips of each cleithrum do not contact each other in the midline; the cleithrum lacks a posterodorsal lamina over the dorsal face of the scapula; and only a single (ventral) postcleithrum is present. The pelvic girdle (Figs. 11, 12) is reduced from the generalized perciform condition in the following: pelvic-fin rays 1,2 (not a single bifid ray as reported by some authors), with segmented rays unbranched (one specimen had the first ray branched on the left side only); basipterygia rod-like, widely separated anteriorly, and associated posteriorly only at the bases of the posterior pelvic processes; no ventral pelvic processes; spine- and ray-associated musculature restricted to posterior half of basipterygia; and extensor proprius absent.

VERTEBRAL COLUMN AND UNPAIRED FINS. The dorsal- and anal-fins are dis-

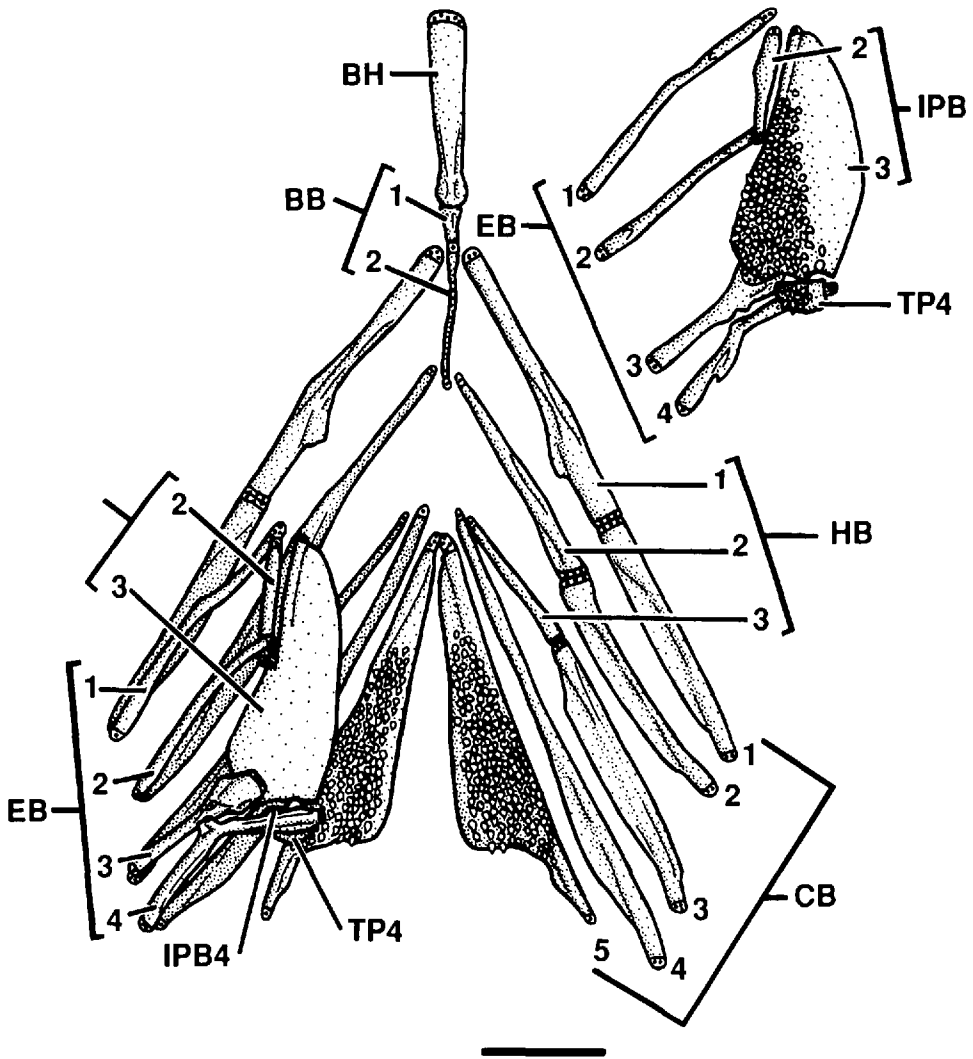


Figure 9. Gill arches of *Notograptus* [ROM 717CS, 82.2 mm SL], dorsal view. Right dorsal elements removed and shown in ventral view. Large stipple represents cartilage. BB1-2, basibranchials 1-2; BH, basihyal; CB1-5, ceratobranchials 1-5; HB1-3, hypobranchials 1-3. Other abbreviations as in Figure 2. Scale bar is 1 mm.

tinctive in the following: supraneural (predorsal) bones are absent; all dorsal-fin pterygiophores insert in a 1:1 ratio with interneural spaces; dorsal-fin rays LXII-LXIX, 1-2; anal-fin rays XXXVII-XLIII, 1-2; dorsal- and anal-fin spines increase in stoutness posteriorly; all spine-bearing dorsal- and anal-fin pterygiophores articulate with the secondarily associated spine by a complete, interlocking, bony ring, probably resulting from fusion of the distal radial with the secondarily associated proximal + middle radial (Fig. 13); and penultimate segmented dorsal- and anal-fin ray articulates closely with ultimate pterygiophore (Fig. 13). Regarding the latter character, we have only examined specimens of *Notograptus* with two segmented rays in the dorsal and anal fins, but some specimens are known to

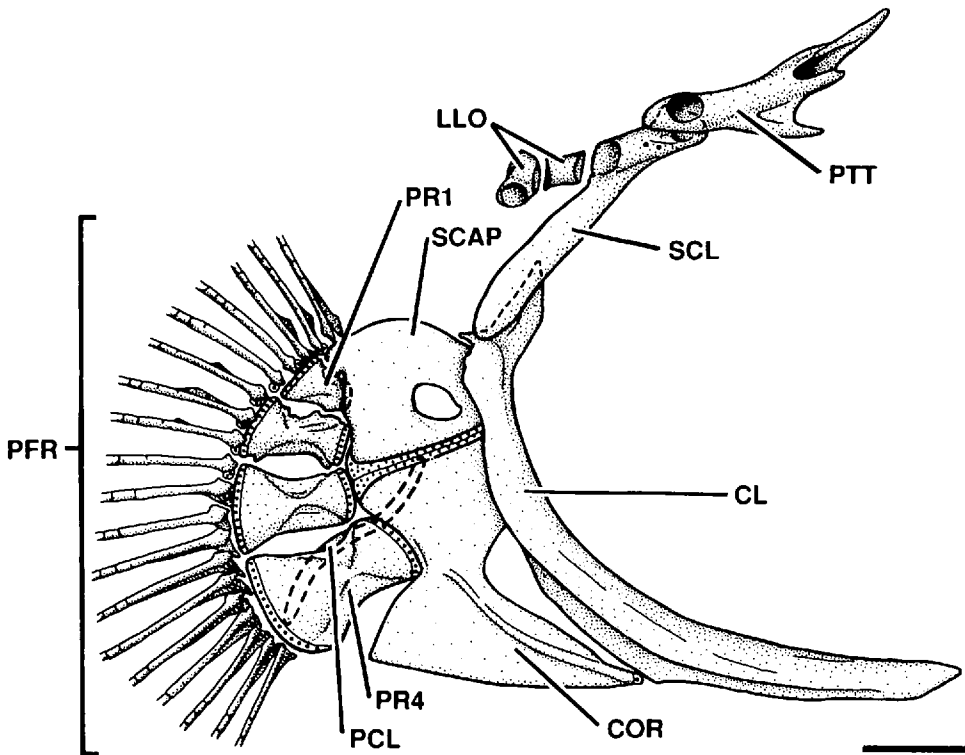


Figure 10. Right pectoral girdle and first two lateral-line ossicles of *Notograptus* [USNM 173798, 102.7 mm SL], lateral view. Large stipple represents cartilage. Dashed lines show outlines of bones otherwise obscured. CL, cleithrum; COR, coracoid; LLO, lateral-line ossicles; PCL, postcleithrum; PFR, pectoral-fin rays; PR1, 4, proximal radials 1 and 4; PTT, posttemporal; SCAP, scapula; SCL, supracleithrum. Scale bar is 1 mm.

have a single segmented ray in these fins (McCulloch, 1918: 94); the configuration of the fin rays and pterygiophores may differ in the specimens with a single segmented dorsal- and/or anal-fin ray.

The vertebral column is distinctive in that there is a large number of vertebrae (28–29 + 44–46 = 73–75 in our material, 71–75 total vertebrae given by Tyler and Smith, 1970: table 1), the epipleural ribs are confined to the first three vertebrae, and the pleural ribs are usually confined to vertebrae 3 to 6 (sometimes present on vertebra 7).

The number of free caudal skeleton elements is reduced from the generalized perciform condition: the parhypural and hypurals 1 and 2 are fused into a single element, without a hypurapophysis; hypurals 3 and 4 are fused to each other and to the urostylar complex; there are no free uroneurals (possibly fused to urostylar complex); a free hypural 5 is absent; epurals are absent (one possibly represented by the elongate pu2 neural spine); free caudal cartilages are absent; the pu2 and pu3 hemal spines are fused to their centra; and the caudal-fin rays are reduced in number to a single unsegmented ray dorsally and ventrally, and six dorsal and five ventral segmented rays (Fig. 13; see also Tyler and Smith, 1970: fig. 3).

MISCELLANEOUS. The upper and lower lips are complete (rather than interrupted at the symphysis), each with a median lobe, the lower of which is elongate and

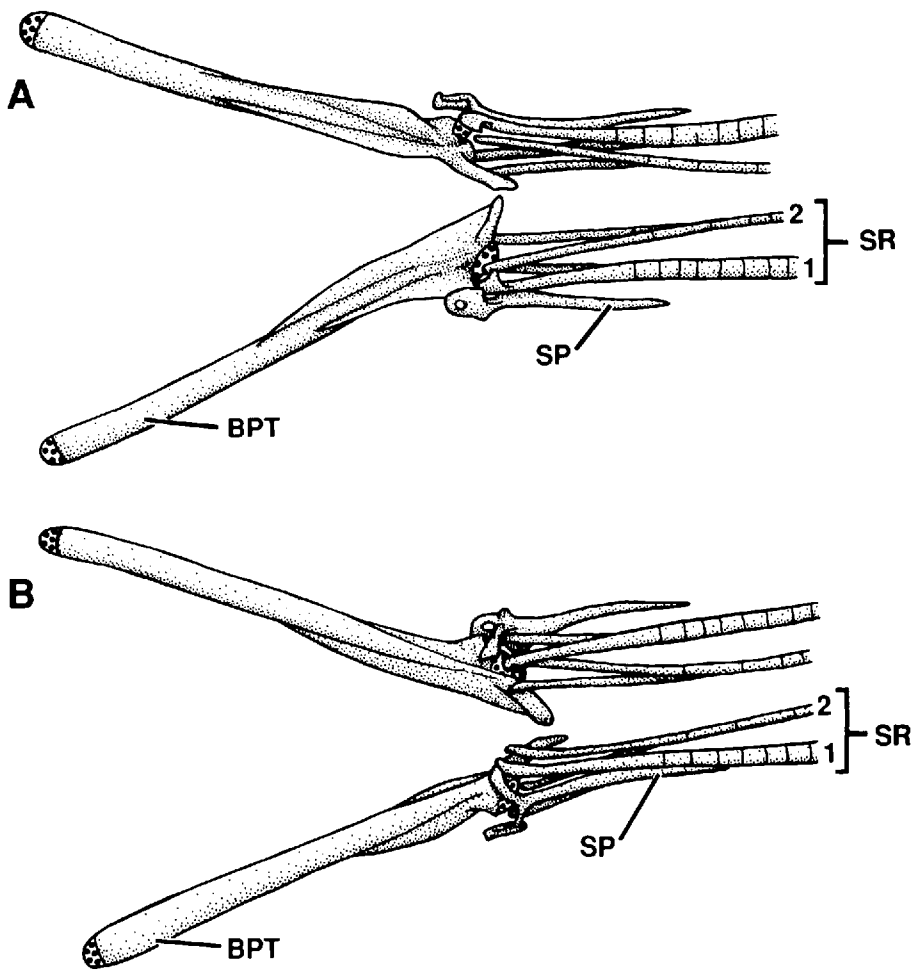


Figure 11. Pelvic girdle of *Notograptus* [USNM 173798, 102.7 mm SL]: A) dorsal view; B) ventral view. Left basipterygium is slightly dorsomedial in A) and ventrolateral in B). Large stipple represents cartilage. BPT, basipterygium; SP, spine; SR1-2, segmented rays 1-2. Scale bar is 1 mm.

barbel-like. The lateral line is represented by a series of enlarged dermal ossicles (Fig. 10), the remainder of the body being covered with small, deeply embedded cycloid scales. The alimentary tract is a straight, simple tube.

Notograptus eggs are relatively large (ovarian eggs up to 3.4 mm across), and are unusual in that they possess chorionic projections bearing filaments (Fig. 14A, B). There are usually 29-35 projections that are raised above the chorion by a central pedicel. Most projections (22-29) are roughly cruciform, giving rise to two to five filaments; two to three of these filaments are greatly elongate. The remaining five to nine projections are oblong, bearing a filament from each end. The projections are arranged in a ring closer to one pole of the egg than the other; we were unable to determine the relative location of the micropyle.

Phylogenetic Position.—Notograptids traditionally have been placed in the blennioidei. For example: Günther (1867) originally placed *Notograptus* in the Blen-

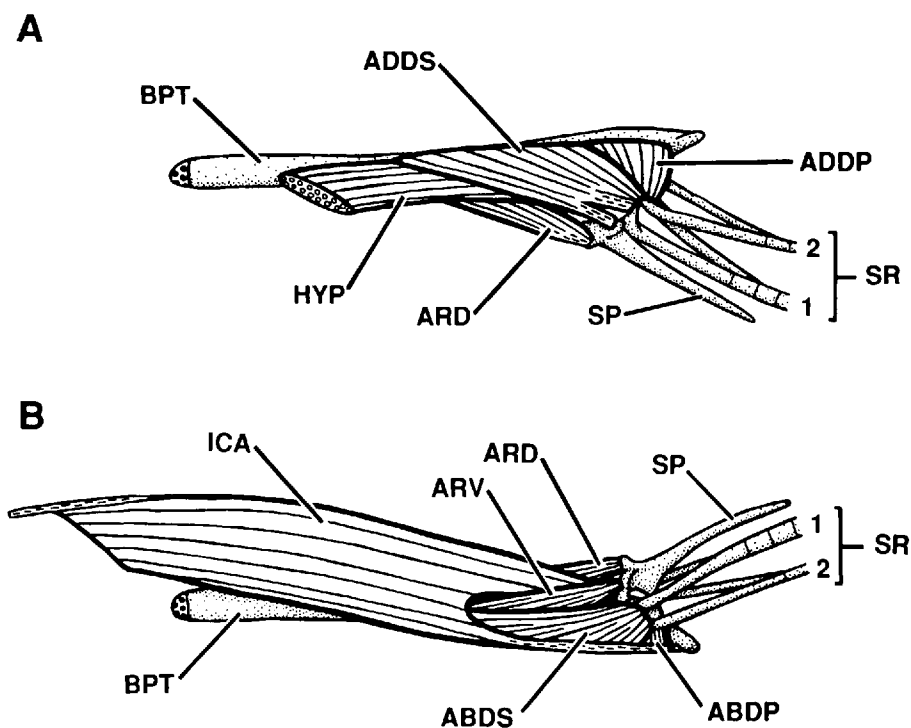


Figure 12. Pelvic musculature of *Notograptus* [USNM 173797, 180.0 mm SL]: A) dorsal view of left side; B) ventral view of left side. Bold lines demarcate muscles. Dashed areas are tendons. Small stipple indicates bone. Large stipple represents cartilage. Open circles indicate cut muscle fibers. ABDP, abductor profundus; ABDS, abductor superficialis; ADDP, adductor profundus; ADDS, adductor superficialis; ARD, arrector dorsalis; ARV, arrector ventralis; HYP, hypaxial musculature; ICA, infracranialis anterior. Other abbreviations follow Figure 11. Scale bar is 1 mm.

niidae, as did McCulloch (1918); Regan (1912) included it in his Division I (Blenniiformes) of the Blennioidei, along with the Blenniidae, Anarrhichadidae, and Congrogadidae; and de Beaufort (1951) included it in the Blennioidei, along with blenniids, congrogadids, clinids, brotulids, ophidiids, pholidichthyids (including the gobioid *Gunnellichthys*), and carapids. However, the Blennioidei of these authors variously included taxa now assigned to the Zoarcoidei, Ophidiiformes, Gobioidae, Pholidichthyidae, and Pseudochromidae, in addition to the true blennioids (*sensu* Springer, 1993).

Gosline (1968) suggested a possible relationship of notograptids to congrogadids, and less certainly to peronydiids (*sic*), placing the three families in his blennioid superfamily Congrogadoidei. More recently, Smith-Vaniz and Johnson (1990) suggested a possible relationship between notograptids and acanthocline pleysiopids.

BLENNIIDS. Of the array of apomorphic characters used by Springer (1993) to define the Blennioidei, *Notograptus* shares the following: absence of infrapharyngobranchial 1, uncinat process on epibranchial 1, and interarcual cartilage; a highly reduced (fused) caudal skeleton (although differing from blennioids in lack-

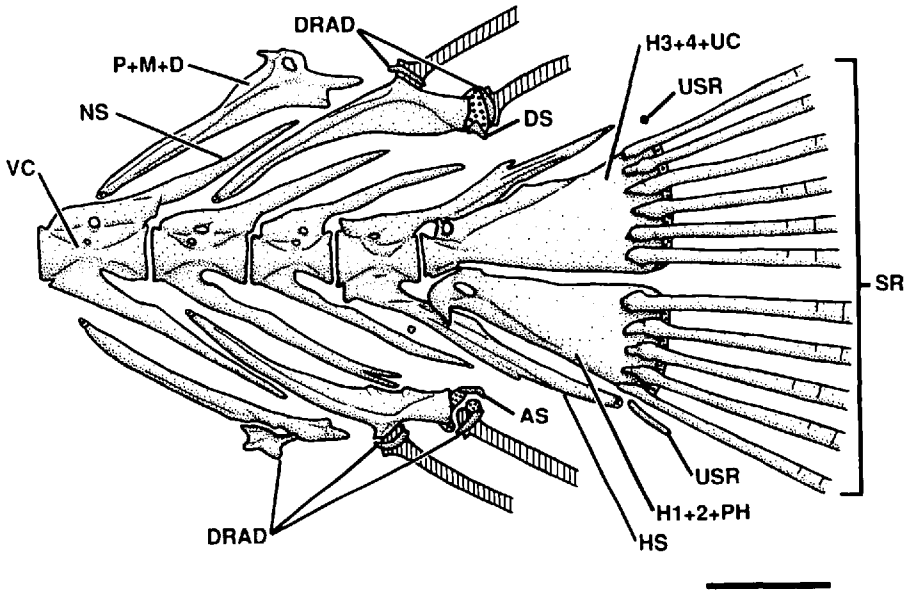


Figure 13. Posterior axial skeleton of *Notograptus* [USNM 173798, 102.7 mm SL]. Dorsal- and anal-fin spines removed. Large stipple represents cartilage. Hatched areas indicate right halves of dorsal and ventral segmented rays. Note that free distal radial of last spine-bearing pterygiophore of anal fin is fused to proximal + middle radial in most specimens. Dorsalmost (unsegmented) caudal-fin ray is elongate (rather than a nubbin) in most specimens. AS, anal stay; DRAD, distal radial; DS, dorsal stay; H1+2+PH, fused hypurals 1 and 2 and parhypural; H3+4+UC, fused hypurals 3 and 4 (and 5?) and ural centrum; HS, hemal spine on preural centrum 2; NS, neural spine; P+M+D, fused proximal, middle and distal radials of pterygiophore; SR, segmented caudal-fin rays; USR, unsegmented caudal-fin ray; VC, vertebral centrum. Scale bar is 1 mm.

ing a free hypural 5 and epurals); anteriorly positioned pelvic fins; fewer than five segmented pelvic-fin rays; a 1:1 relationship between the dorsal-fin pterygiophores and the interneural spaces; absence of supraneural bones; distal radials of spine-bearing pterygiophores, when present, fused to secondarily associated proximal + middle radial to form a complete bony ring; and presence of fewer than six infraorbital bones (Springer, 1993). However, most of these characters are relatively widely distributed among perciforms, especially among elongate forms. *Notograptus* is less specialized than blennioids in lacking the strikingly modified basipterygia that uniquely characterize the Blennioidei (Springer, 1993); however, *Notograptus* has an extremely reduced pelvic girdle that could be secondarily derived from the blennioid condition. *Notograptus* is also less specialized than the members of this suborder in the following (Springer, 1993): there are more than two anal-fin spines (3 in generalized perciforms, and 37–43 in *Notograptus*); infrapharyngobranchials 4 (including the toothplate) and 2 are present; and the proximal radials of the pectoral girdle are not longer than the width of the scapula or coracoid.

CONGROGADINE PSEUDOCROMIDS. Of the three families included by Gosline (1968: 60) in his Congrogadoidei, the Peronedysidae was not examined by him, and has been since assigned to the blennioid clinid tribe Ophiclinini by George and Springer (1980). Gosline used the following characters to link his remaining two congrogadoid taxa, *Notograptus* and Congrogadidae: an eel-like body form; subocular shelf present on "second" infraorbital (actually the third; Gosline did not include the lacrimal in his count); branched dorsal- and anal-fin rays subdivide

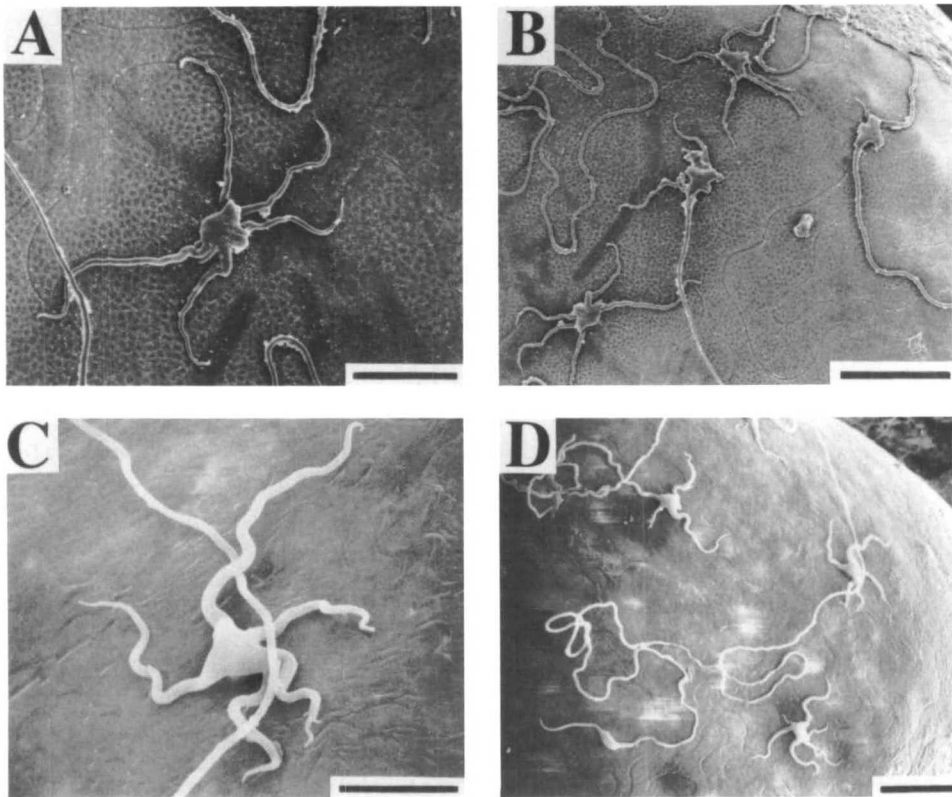


Figure 14. Scanning electron micrographs of ovarian egg surface morphology of: A, B) *Notograptus guttatus* [ROM 38369, 101.0 mm SL], scale bars are 100 μm (A) and 200 μm (B); C, D) *Belonepterygion fasciolatum* [WAM P.25851-010, 46.8 mm SL], scale bars are 25 μm (C) and 50 μm (D).

only on posterior branch; and anterior portion of the suspensorium weakly connected to the posterior portion. Godkin and Winterbottom (1985: 636) placed the Congrogadidae as a subfamily of the Pseudochromidae, and noted that none of the characters used by Gosline to align the Notograptidae with the Congrogadinae was truly synapomorphic: an eel-like body form occurs widely in perci-forms; the presence of a subocular shelf on infraorbital 3 is plesiomorphic; the branching pattern of the dorsal- and anal-fins is relatively widely distributed (and may be associated with developmental truncation); and the nature of the disassociation of the suspensorium is nonhomologous (although we further note that the condition in congrogadines is nonhomologous with that of other pseudochromids). However, notograptids and congrogadines do share several specializations (some of which are more generally shared with one or more pseudochromid taxa): absence of a free hypural 5 (although present as cartilage in congrogadines during early ontogeny; Gill, 1990); absence of free caudal-fin cartilages; an elongate pu2 neural spine; pu2 and pu3 hemal spines fused to their centra; parhypural and hypurals 1 and 2 fused together; hypurals 3 and 4 fused to each other and to the urostylar complex; no autogenous uroneurals; a relatively high number of dorsal-fin, anal-fin, and vertebral elements; fewer than five segmented pelvic-fin rays, with at least one unbranched; a 1:1 relationship between the dorsal-fin pterygiophores and the interneural spaces (although two pterygiophores insert between the third and fourth neural spines in congrogadines); relatively small, embedded

cycloid scales; a complete lower lip; absence of an interarcual cartilage; and eggs with multi-armed projections raised above the chorion on central pedicels, with arms bearing filaments (Fig. 14A, B and Mooi et al., 1990: figs. 1–5). Although not necessarily in combination with each other, all but the last three characters are variously found in many elongate fishes (e.g., zoarcoids, pholidichthyids, ophidioids, and elongate blennioids). We also doubt the homology of the egg projections in congrogadines and *Notograptus*. In congrogadines, relatively few of the projections possess filaments, and none have more than one filament from a given projection. By contrast, *Notograptus* has filaments from almost all projections, and these number as many as five per projection.

Notograptus lacks various synapomorphies that either place the Congrogadinae within the Pseudochromidae, or nest the Congrogadinae as the sister group of the Anisochrominae: fewer than three dorsal-fin spines (although Gill, 1990, argues that the two spines primitively present in congrogadines are the homologues of the first two segmented rays of three-spined pseudochromids; *Notograptus* has 62–69 dorsal-fin spines); penultimate branchiostegal ray articulates either with the anterior ceratohyal or across the anterior/posterior ceratohyal junction (versus with the posterior ceratohyal in *Notograptus* and generalized perciforms; Fig. 15); absence of an anterior cartilage on ceratobranchial 5; presence of a strap-like, lateral A₁ section of the adductor mandibulae (Godkin and Winterbottom, 1985: figs. 1, 2); absence of palatine teeth; fewer than 16 pectoral-fin rays; fewer than two anal-fin spines; upper and lower lips constricted anteriorly; and sphenotic with an enclosed sensory canal (Godkin and Winterbottom, 1985; Gill, 1990).

ACANTHOCLININE PLESIOPIDS. Smith-Vaniz and Johnson (1990: 220) noted that notograptids share several apomorphies with acanthoclinine plesiopids: proximal, middle, and distal radials of spine-bearing dorsal- and anal-fin pterygiophores fused together (i.e., distal radials have lost the articulation with serially associated proximal-middle radials, and have completely fused to their secondarily associated proximal-middle radial, each forming a closed bony ring that interlocks with the articulating spine); a high number of dorsal- and anal-fin spines; I₂ pelvic-fin rays; and lower lip with a continuous free ventral margin. In addition to these characters, notograptids and acanthoclinines share the following apomorphies (some are more generally shared with other plesiopids; Mooi, 1993): extensor proprius muscle absent; fewer than three branches on first segmented pelvic-fin ray; dorsal process for muscle attachment large only on first segmented pelvic-fin ray; a low number of caudal-fin rays; absence of lateral processes on the posterior (middle radial) portion of the proximal + middle radial of the dorsal spine-bearing pterygiophores (Mooi, 1993: figs. 23c, 24b); posterior infraorbital (dermosphenotic?) large and not tightly bound to the sphenotic; eggs with multi-armed projections raised above the chorion by a central pedicle, each projection bearing numerous filaments (Fig. 14A, B with Fig. 14C, D and Mooi, 1990: fig. 7); and possibly the relatively weak association between metapterygoid and hyomandibula (Smith-Vaniz and Johnson, 1990: fig. 16).

Some of the apomorphies of the pelvic girdle might be attributable to convergent reduction of this complex in notograptids and acanthoclinines. For example, the extensor proprius muscle is absent in other taxa that have a reduced number of pelvic-fin rays (e.g., pholidichthyids and some zoarcoids); this is also the case for a reduced number of branches on the first segmented pelvic-fin ray.

Notograptids lack various synapomorphies listed by Mooi (1993) that unite plesiopids, or that define nodes that place the acanthoclinines as a sister group to *Plesiops*: posterior subpelvic concavity; subpelvic shelf; extensor proprius inserting onto second segmented ray; parasphenoid keel; pronounced notch on the

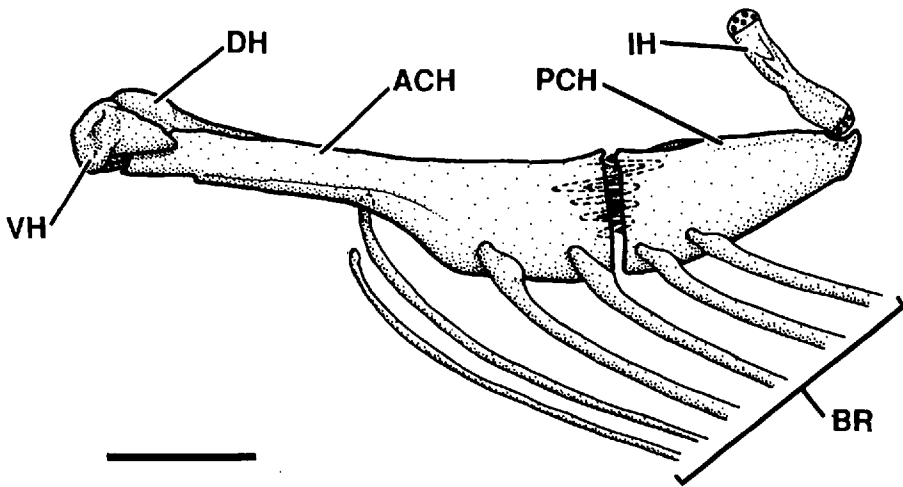


Figure 15. Left hyoid bar of *Notograptus* [ROM 717CS, 82.2 mm SL], lateral view. Large stipple represents cartilage. Dotted lines indicate medial interdigitation of anterior and posterior ceratohyals. ACH, anterior ceratohyal; BR, branchiostegal rays; DH, dorsal hypohyal; IH, interhyal; PCH, posterior ceratohyal; VH, ventral hypohyal. Scale bar is 2 mm.

posterolateral margin of the branchiostegal membranes; small basioccipital/parasphenoid foramen for dorsal aorta; posterior parasphenoid deeply bifurcate; posteroventral attachment of Baudelot's ligament to the basioccipital; posterior sphenotic spur widely separated from the anterior spur; adductor superficialis pelvius muscle inserting onto only the spine and first segmented pelvic-fin ray; abductor superficialis pelvius does not overlie the arrector ventralis pelvius; open preopercular sensory canal; expanded and ventrally positioned zygopophysis on second vertebra; incised membranes between dorsal-fin spines; three anteriormost vertebrae with smooth ventral surfaces. The first three of these features might be lacking in notograptids due to the extreme reduction of the pelvic girdle; the extensor proprius, as noted previously, is also presumed to have been lost in acanthoclinines. The last four characters are known to reverse among some derived acanthocline genera, and their absence in notograptids might only be indicative of a relationship within the Acanthoclininae.

ZOARCOIDS. Some zoarcoids resemble notograptids in the following: elongate body form, with a high number of vertebral and dorsal- and anal-fin elements (often of mostly segmented rays, although the Scytalinidae have dorsal and anal fins with all rays spinous); 1:1 association between dorsal-fin pterygiophores and interneural spaces; lack of an interarcual cartilage; reduced pelvic girdle, including reduced number of rays and loss of extensor proprius muscle; body scales small, cycloid, and deeply embedded; and ascending processes of parasphenoid that extend to frontals. Most, if not all, of these features are exhibited by other elongate, non-zoarcoid taxa. Notograptids do not share the characters presently used to unite zoarcoids, the single nostril and absence of the basisphenoid, nor a potentially derived cheek muscle arrangement (Mooi, in prep.). We therefore reject a relationship between *Notograptus* and the subgroup of elongate zoarcoids.

PHOLIDICHTHYIDS. The enigmatic, monotypic family Pholidichthyidae shares several specializations with notograptids: an elongate body form, with a high number of vertebral and dorsal- and anal-fin elements; 1:1 association between dorsal-fin pterygiophores and interneural spaces; a highly reduced (fused) caudal skeleton (including absence of free epurals, absence of free caudal cartilages, re-

duced number of caudal-fin rays, variable elongation of the pu2 neural spine, and hypural elements fused to each other and to the urostylar complex); lack of an interarcual cartilage; a reduced number of pelvic-fin rays and associated loss of extensor proprius muscle; and reduced basipterygia with the anterior tips widely separated. Almost all of these characters are widely distributed among elongate fishes, with the possible exception of the basipterygia separation. However, as the pholidichthyids have not been convincingly placed with any other fishes (Springer and Freihof, 1976, suggested possible relationships to either blennioids or labrids), there is no evidence to reject a relationship with notograptids.

Summary and Comments.—The Notograptidae possess a variety of autapomorphies that essentially ensure monophyly (e.g., anterior expansion of the median ethmoid; a large section of the adductor mandibulae that originates broadly on the skull, preopercle and suspensorium; highly reduced gill-arch skeleton). Notograptids share numerous features with other taxa that are probably associated with elongation. Considering specializations that are not obviously associated with elongation, we believe that present evidence (e.g., egg morphology; dorsal- and anal-fin pterygiophore construction; high numbers of dorsal- and anal-fin spines) favors a relationship between notograptids and acanthoclinine plesiopids. However, we do not advocate expansion of the Acanthoclininae to include *Notograptus*, pending discovery of more conclusive corroborative evidence.

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