Notograptidae, sister to *Acanthoplesiops* Regan (Teleostei: Plesiopidae: Acanthoclininae), with comments on biogeography, diet and morphological convergence with Congrogadinae (Teleostei: Pseudochromidae)

RANDALL D. MOOI* and ANTHONY C. GILL†

1Milwaukee Public Museum, 800 West Wells Street, Milwaukee, Wisconsin 53233–1478, USA
2Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

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The Notograptidae contains one genus, *Notograptus* Günther, and five nominal species from northern Australia and southern New Guinea. Morphological evidence places *Notograptus* among acanthoclinine plesiopids (continuous free margin of lower lip; head naked; dorsal and anal fins with many spines and few segmented rays; no extensor proprius; reduced number of caudal-fin rays) and supports a sister relationship with *Acanthoplesiops* (symphyseal flap on lower lip; reduced hypural 5; reduced hypurapophysis). This hypothesis resolves the relationships within *Acanthoplesiops*, clarifying the polarity of autogenous middle radials of dorsal- and anal-fin pterygiophores. The proposed relationships among acanthoclinines are: *Acanthocinus (Belonepterygion (Beliops (Notograptus (Acanthoplesiops hiatti (A. indicus (A. psilogaster (A. echinatus)))))))). The distribution of *Notograptus* compliments that of its proposed sister clade in that *Acanthoplesiops* is unknown from northern Australia or southern New Guinea. There are repeated geographical patterns among several groups suggesting that Australia is a basal area to a broader Indo-Pacific region. Similarity between the Congrogadinae (Pseudochromidae) and *Notograptus* has long been noted, both having a loosely connected suspensorium and elongate body which were mistakenly considered indicators of relationship; we add reduced branchial arches, straight, tube-like gut and highly expandable anus. We examine these similarities as an indication of a shared specialized feeding habit. *Notograptus* is an alpheid shrimp predator, able to swallow its large prey whole. Most species of congrogadines eat whole, large crustaceans. This is probably an example of convergent adaptation to a particular selective regime. © 2004 The Linnean Society of London, Zoological Journal of the Linnean Society, 2004, 141, 179–205.


*... in acanthomorphs as a whole there are about 280 families. Many of these families seem to have come down like the tablets, unblemished by analysis since their names were inscribed on stone in the days of Günther or Gill or Regan* (Patterson, 1993: 29).

INTRODUCTION

The Notograptidae, bearded eel-blennies or dirkfishes, comprises small (<200 mm SL), elongate, shallow-water fishes (Fig. 1). There is one recognized genus, *Notograptus* Günther, and five nominal species restricted to the northern coast of Australia and southern coast of New Guinea (Gill & Mooi, 1993; Mooi, 1999). The family is in need of revision.

The phylogenetic position of the family has long been in question. Günther (1867) originally described the genus in the Blenniidae, a placement followed by McCulloch (1918). Regan (1912) erected a (then) monotypic family Notograptidae for this unusual fish and since that time, it has predominantly remained with the Blennioidae (e.g. Jordan, 1923; de Beaufort, 1951; Greenwood *et al*., 1966; Norman, 1966; see review by Gill & Mooi, 1993). However, in addition to

the true blennioids (*sensu* Springer, 1993), the Blennioidei of these authors variously included taxa now assigned to the perciform suborders Percoidae, Gobioidae, Trachinoidei and Zoarcoidei, and to the paracanthopterygian order Ophidiiformes.

Greenwood et al. (1966: 401) included the Notogrammatidae in the Blennioidei, listing without comment the Stichariidae (classified in the cliniid subfamily Ophichlininae by George & Springer, 1980) as a synonym. Gosline (1968: 60), following the lead of Regan (1912), suggested a relationship of notogrammatids to congrogadids and less certainly to peronedyids [sic], placing the three taxa in his blennioid superfamily Congrogadoidea. However, Godkin & Winterbottom (1985) provided evidence for the inclusion of the Congrogadidae as a subfamily of the percoid Pseudochromidae, and George & Springer (1980) assigned peronedyids to the blennioid cliniid tribe Ophichlinini. Nelson (1984), without evidence, placed notogrammatids among the trachinoids; Mooi & Johnson (1997) provided arguments to dismantle the Trachinoidei, making inclusion of the notogrammatids in this unnatural ‘group’ uninformative.

Gill & Mooi (1993) listed apomorphic features of *Notogramma* and considered its phylogenetic position. We noted that it shared numerous features with other elongate perciforms (in particular, elongate blennioids, zoarcoïds, pholidichthyids and congrogadine pseudochromids) but concluded that many of these features are a consequence of elongation (e.g. numerous vertebrae and dorsal- and anal-fin rays; highly fused caudal skeleton; reduced pelvic fins and girdle) and thus, not necessarily indicative of close relationship. Considering characters that are not obviously associated with elongation (e.g. egg morphology; dorsal- and anal-fin spine-bearing pterygiophore construction; dorsal and anal fins comprising almost entirely spiny rays), we concluded that available evidence best supported a relationship with acanthoclinine plesiopids, a proposal first made by Smith-Vaniz & Johnson (1990). However, we elected not to place *Notogramma* in the Acanthoclininae, pending the discovery of additional corroborating evidence.

The purposes of this paper are to test the possibility of an acanthoclinine relationship by including *Notogramma* in a parsimony analysis that combines characters and taxa employed by Smith-Vaniz & Johnson (1990) in their examination of relationships within the Acanthoclininae, and by Mooi (1993) in his analysis of plesiopid monophyly and relationships among nonacanthoclinine plesiopid genera. We also examine the biogeographical implication of this formalization of our hypothesis that *Notogramma* has its closest relatives among acanthoclinine plesiopids. Lastly, we suggest that the convergence in morphology of *Notogramma* and congrogadine pseudochromids is due to a specific selective regime (similar specialized feeding behaviour) and provides an example of adaptation in the historical sense of Coddington (1988) and Larson & Losos (1996).

**MATERIAL AND METHODS**

External and myological characters were scored by examination of alcohol-preserved specimens. Osteological characters were examined using cleared and stained and X-radiographed material. Character states of nonacanthoclinine plesiopids were obtained from the literature (Smith-Vaniz & Johnson, 1990; Mooi, 1993). Character states of acanthoclinine plesiopids were obtained from specimens where available and taken from the literature when not (Smith-Vaniz & Johnson, 1990). *Acanthoplesiops naka* Mooi & Gill from Tonga (USNM 327794), known only from one small ethanol specimen (9.9 mm SL), was excluded from the phylogenetic analysis as it would not impact the placement of *Notogramma* and, having only external characters available for analysis, would introduce a series of unknowns to the data table.

**Figure 1.** *Notogramma* sp., BMNH 2002.1.2.1–2, 100.5 mm SL. Scale bar = 50 mm.
Character analysis was performed using PAUP* Version 4.0 beta10 (Swofford, 2001) and results explored using MacClade 4.05 (Maddison & Maddison, 2001). An initial branch-and-bound search was undertaken, with all characters unordered excepting characters 3, 10, 11, 19, 38 and 40, following previously published interpretations. Equally parsimonious trees were combined using strict consensus methods. The data matrix (Table 1) differentiates those characters for which taxa had no observations and were unknown (?) from those that were inapplicable (n). Two analyses were performed to deal with inapplicable characters. One used the suggestion of Maddison (1993) that inapplicable states be included as part of an unordered multistate character (composite coding as described in Strong & Lipscomb, 1999). The other used reductive coding where taxa for which a character is inapplicable are coded the same as if the state were unknown (using ‘?’) (recommended by Strong & Lipscomb, 1999). The other used supermatrix analysis of three remaining characters (10, 13 and 24) that still exhibited unknown values in a few taxa. All analyses were repeated with all characters unordered to examine any effects on topology. Finally, the tree was constrained to have Notograptus as sister to the Plesiopidae and effects on tree length noted. Tree statistics reported are length (number of steps), consistency index (CI), rescaled consistency index (RC) and retention index (RI) (Farris, 1989).

Distributional records were taken from the literature, examined specimens and museum catalogue records, the latter focusing on the collections of BMNH, MPM, USNM and AMS.

Gut contents were examined chiefly using X-radiographs (X-ray) and cleared and stained (CS) preserved (EtOH) specimens as noted above. Occasionally, ethanol-preserved (EtOH) specimens were dissected.

Institutional abbreviations follow Leviton et al. (1985).

Table 1. Data matrix for examining the phylogenetic position of Notograptus among the Plesiopidae. ? – not examined; n – not applicable due to modification.

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(EtOH, X-ray), Little Hope Is., Queensland, 26 January 1969; ANSP 165418, 98 mm (EtOH, X-ray), Cape Arnhem, Northern Australia, 14 July 1948; BMNH 1867.5.13.16 + 1867.6.6.42, 2: 114–153.5 mm, Cape York, Queensland (syntypes of *N. guttatus* Günther, 1867); BMNH 2002.1.19.16, 128.5 mm (CS), Clarence Strait, East Vernon Is., Northern Territory; BMNH 2002.1.2.1–2, 2: 65–99 mm (EtOH, X-ray), Burnside Is., Western Australia, 19 May 1996; MPM 32586, 29: 44–112 mm (EtOH, X-ray), Locker Is., Western Australia, 16 May 1996; ROM 38369, 8: 58–101 mm, Wonga Beach just south of Daintree R., Queensland, 25 September 1981; ROM 717CS, 82.2 mm (CS), Wonga Beach just south of Daintree R., Queensland, 25 September 1981; USNM 173796, 3: 77–159 mm (EtOH, X-ray), Groot Eylandt, Northern Territory, 19–25 April 1948; USNM 173797, 6: 45–178 mm (EtOH, X-ray), Groot Eylandt, Northern Territory, 7 June 1948; USNM 173798, 11: 81–170 mm (EtOH, X-ray), Cape Arnhem, Northern Territory, 14 July 1948; USNM 222134, 4: 87–120 mm (EtOH, X-ray), 31 May 1979, Clarence Strait, East Vernon Is., Northern Territory; USNM 257875, 31: 12–36 mm; USNM 257876, 9: 15–38 mm.

**OTHER PLESIOPIDAE (ALL REMAINING MATERIALS X-RADIOGRAPHS UNLESS OTHERWISE NOTED)**

*Acanthoclinus fuscus* Jenyns (5 lots, 68 specimens: 28–220 mm SL): ANSP 165085, 2: 46–47 mm (CS); MPM 32616, 3: 160–220 (EtOH); USNM 200547, 4: 55–84 mm; USNM 200548, 6: 53–95 mm; USNM 339246, 53: 28–99 mm.  
*A. littoreus* Forster (2 lots, 7 specimens: 56–119 mm): ANSP 165089, 2: 56–78 mm (CS); USNM 339230, 5: 98–119 mm.  
*A. marilynae* Hardy: ANSP 134947, 2: 90–95 mm (CS).  
*A. matti* Hardy: ANSP 165088, 52 mm (EtOH, suspensorium CS, X-ray).  
*A. rua* Hardy: ANSP 165087, 46 mm (CS, gutted).  
*Acanthoplesiops echinatus* Smith-Vaniz & Johnson: ANSP 166316, 21 mm (EtOH, gill arches and suspensorium CS, X-ray).  
*A. hiatti* Schultz (3 lots, 10 specimens: 15–20 mm SL): ANSP 165421, 20 mm (CS, gutted); USNM 135783, 2: 15–16 mm; USNM 257874, 7: 15–20 mm.  
*A. indicus* (Day) (5 lots, 5 specimens: 19–27 mm SL): ANSP 122483, 27 mm (CS); ANSP 165570, 22 mm (CS, gutted); BMNH 1889.8.17.5, 19 mm (holotype); RUSI 17291, 22 mm (CS); RUSI 17293, 22 mm (EtOH).

*A. psilogaster* Hardy (3 lots, 4 specimens: 12–22 mm SL): USNM 288813, 12 mm; USNM 318027, 22 mm; USNM 326763, 2: 15–16 mm.

*A. naka* Mooi & Gill: USNM 327794, 9.9 mm (holotype) (EtOH).  
*Assessor flavissimus* Allen & Kuiter: MPM 40273, 36.0 mm (CS).  
*A. macneilli* Whitley: MPM 40268, 39.0 mm (EtOH).  
*Belios xanthokrossos* Hardy: ANSP 165557, 26 mm (EtOH, X-ray), 26 mm (CS, gutted).  
*Belonepterygion fasciolatum* (Ogilby) (4 lots, 43 specimens: 12–42 mm SL): ANSP 142690, 42 mm (EtOH, X-ray); BMNH 1914.12.28.1–2, 2: 30–39 mm; MPM 40265, 2: 47–48 mm (EtOH); USNM 257875, 31: 12–36 mm; USNM 257876, 9: 15–38 mm.

**PSEUDOCHROMIDAE**

*Anisochromis kenyae* Smith: (10 lots, 46 specimens: 13.8–25.6 mm SL): AMS I.28113–064, 2: 13.9–22.1 mm; ANSP 134469, 25.6 mm; ROM 56501, 2: 22.1–23.0 mm; ROM 56502, 9: 13.8–22.7 mm; ROM 56711, 21.6 mm; RUSI 149, 21.3 mm (holotype); RUSI 854, 14: 17.5–25.0 mm (paratypes); RUSI 4905, 3: 22.3–23.9 mm; RUSI 4906, 7: 21.6–25.0 mm (23.3 mm, CS); USNM 216415, 6: 21.7–24.5 mm (paratypes).  
*A. mascarenensis* Gill & Fricke (7 lots, 11 specimens: 13.3–25.5 mm SL): BMNH 1976.8.24.1–10, 10: 16.8–25.4 mm SL (paratypes; 21.5 mm CS); CAS 37640, 14: 16.1–24.9 mm (paratypes); USNM 215859, 26: 18.7–26.1 mm (paratypes); USNM 216462, 23.9 mm (holotype); USNM 216463, 19: 16.2–27.0 mm (paratypes); USNM 216464, 26.8 mm (paratype);  

USNM 216465, 3: 22.6–23.9 mm (paratypes); USNM 216466, 2: 26.5–28.3 mm (paratypes).

_Blennoedus scapularis_ Günther (15 lots, 120 specimens: 28.5–87 mm SL): AMS I.A. 606–8, 7: 41–77 mm; AMS I.7072–4, 7076, 8: 45–71.6 mm; AMS I.17445–151, 13: 47–87 mm. AMS I.20200–029, 19: 34–87 mm; BPBM 17412, 6: 57–85 mm; MPM field no. RDM96-20, 6: 28.5–60 mm; MPM field no. RDM96-28, 10: 30–73 mm; ROM 43211, 9: 45–85 mm; ROM 432127, 2: 46.4–48.6 mm; ROM RW93-12, 5: 46.4–55.6 mm; ROM RW93-16, 6: 42–55 mm; ROM RW93-21, 53 mm; USNM 205026, 26: 38–53 mm; WAM P.25112–014, 74 mm; WAM P.4645, 57.6 mm.

_Congrogadus hierchthys_ Jordan & Richardson (9 lots, 30 specimens: 50–159 mm SL): BMNH 1993.3.11: 727–728, 2: 101–102 mm; CAS 40138, 125 mm; CAS SU20208, 108 mm (holotype); CAS SU34113, 159 mm; CAS SU33664, 8: 74–102 mm; CAS SU33665, 3: 100–123 mm; ROM 46818, 12: 50–68 mm; SOSC SP 1978–17, 70.5 mm; USNM 61684, 92 mm (paratype).

_C. malayanus_ (Weber) (3 lots, 12 specimens: 30.8–70.0 mm SL): AMS I.20828–018, 2: 38.2–62.5 mm; QM I.17705, 2: 61–63 mm; ZMA 112.577, 8: 30.8–70.0 mm (syntypes).

_C. spinifer_ Borodin (11 lots, 34 specimens: 35.5–121 mm SL): AMS IA.839, 6: 55–70 mm; AMS IA.4239, 5: 37–100 mm; AMS IA.4266, 3: 35.5–84.3 mm; AMS IA.4675, 81 mm; AMS I.15557–215, 3: 72–130 mm; AMS I.21842–011, 6: 49.2–121 mm; AMS I.21943, 121 mm; BMNH 1911.1.4: 3–4, 116 mm; BMNH 1933.8.14: 18–21, 5: 57–89 mm; SAMA F.1494, 2: 44–63.5 mm; WAM P.5520, 83 mm.

_C. subducens_ (Richardson) (25 lots, 75 specimens: 31–340 mm SL): BPBM 14415, 2: 38–62 mm; CAS SU 7120, 100 mm; CAS SU 33860, 2: 97.5–116; MNHN 6716, 171 mm; MPM 32613, 340 mm (EtOH); MPM 32617, 205 mm (EtOH); MPM field no. RDM96-10, 65 mm; ORI 333144, 1; RMNH 6720, 2: 146–332 mm; RMNH 6721, 342 mm; ROM 3911, 281 mm; SOSC ref. no. BBC 1676 A, 2: 170–191 mm; SOSC ref. no. BBC 1679, 10: 158–210 mm; SOSC SP 78, 71.3; USNM 122460, 102.2 mm; USNM 173804, 10: 150–302 mm; USNM 212291, 7: 31–156 mm; USNM 287587, 12: 92–320 mm; USNM 287588, 10: 227–314 mm; USNM 287589, 3: 107–279 mm; WAM P.10070, 108.5 mm; WAM P.22454, 31.2 mm; WAM P.25532–005, 75 mm; WAM P.22670, 101.3 mm; WAM P.31013–025, 183 mm.

_C. winterbottomi_ Gill, Mooi & Hutchins (15 lots, 31 specimens: 61.3–119 mm SL): AMS I.39770–001, 2: 66.9–74.3 mm; BMNH 1999.9.21.1–3, 3: 77.6–115.4 mm; BMNH 1999.9.21.4–5, 2: 71.5–84.5 mm; CSIRO H5237-01, 92.5 mm; MPM 32574, 5: 61.3–101.8 mm; NTM S.14970–001, 80.9 mm; QM I.31415, 107.3 mm; ROM 71992, 2: 85.3–107.0 mm; SAMA F9302, 81.5 mm; USNM 356035, 97.5 mm; WAM P.31013–046, 2: 66.1–111.5 mm; WAM P.31017–022, 3: 71.8–115.7 mm; WAM P.31018–012, 4: 66.8–119.0 mm; (all preceding are paratypes); WAM P.31582–001, 85.1 mm (holotype); WAM P.31582–002, 2: 68.5–80.0 mm (paratypes).

_Halidesmus polytretus_ Winterbottom (2 lots, 2 specimens: 57.0–57.3 mm SL): LACM 30695–13, 57.3 mm (holotype); LACM 30695–29, 57.0 mm (paratype).

_H. scapularis_ Günther: RUSI 11057, 20: 45.5–97.5 mm.

_H. socotraensis_ Gill & Zajonz (4 lots, 6 specimens: 39.6–69.5 mm SL): BMNH 2002.1.19.3, 63.3 mm SL (paratype); ROM 72697, 60.0 mm (paratype); SMF 29223, 64.3 mm (holotype); SMF 29293, 3: 39.6–69.5 mm (paratype).

_H. thomaseni_ (Nielsen) (4 lots, 78 specimens: 29–134 mm SL): USNM SSOC ref. no. 145, 5: 22.5–51.0 mm.

_H. shakai_ Winterbottom (16 lots, 57 specimens: 22–55 mm): BPBM 21709, 48 mm; ROM 56788, 36 mm; ROM 56789, 2: 25–44 mm; ROM 56790, 11: 22–47 mm; ROM 76–10, 7: 42–50 mm; ROM 76–11, 54.8 mm; ROM 76–12, 3: 42–50; ROM 76–15, 9: 35–52 mm; ROM 76–24, 3: 42–46 mm; RUSI 8955, 2: 43–48 mm; RUSI 8994, 2: 37–52 mm; RUSI 9199, 3: 46–52 mm; RUSI 9333, 3: 38–48 mm; RUSI 9415, 2: 44–54 mm; RUSI 9451, 3: 45–47 mm; RUSI 9800, 4: 35–55 mm.


_Haliophis aethiopus_ (Richardson) (25 lots, 85 specimens: 65–294 mm): BMNH 1911.1.4: 22–47 mm; BMHN 1933.8.14: 18–21, 5: 57–89 mm; SAMA F.1494, 2: 44–63.5 mm; WAM P.5520, 83 mm.

16, 14: 30–50 mm; ROM 38245, 102 mm; ROM 38346, 9: 20.7–57 mm; ROM X-ray C4, 13: 43.7–93.5 mm; ROM X-ray C15, 56 mm; ROM X-ray plate no. 3, 3: 34–80 mm; RUSI 5402, 38.1 mm; RUSI 5414, 4: 70–78 mm; RUSI 5427, 10: 50–104 mm; RUSI 5585, 28 mm; RUSI uncat., 17: 56–82 mm; SMF 29198, 14: 38–79.5 mm; SMF 29224, 64.8 mm; SOSC acc. no. 54, 12: 63–84 mm; SOSC ref. no. 142, 86 mm; SOSC ref. no. 145, 10: 50–104 mm; SOSC ref. no. 145, 16: 23–100 mm; SOSC ref. no. 170, 10: 61–78 mm; SOSC ref. no. 540, 125.4 mm; SOSC ref. no. 540, 3: 45–58 mm; SOSC ref. no. 540, 3: 80–91 mm; SOSC ref. no. 540, 4: 80–127 mm; SOSC ref. no. 540, 13: 30–93 mm; TAU P3744, 52.7; TAU P4911, 4: 39.2–77.5 mm; USNM 212290, 35: 24–84 mm; USNM 273294, 24: 29–110 mm; USNM 279889, 16: 23–100 mm; USNM 285199, 10: 60–75 mm; USNM 308028, 10: 62–98 mm; USNM 310402, 16: 23–100 mm; USNM uncat., Tulear, 87 mm; USNM uncat., Israel, 15: 35–98 mm; WAM P.4912, 4: 39–77 mm.

*Natalichthys leptus* Winterbottom (2 lots, 2 specimens: 52–56.4 mm SL): SAM 28938, 56.4 mm (holotype); SAM 28939, 52.0 mm (paratype).

*N. ori* Winterbottom (2 lots, 2 specimens: 54–60.5 mm SL): SAM 17340, 60.5 mm (holotype); SAM 28993, 54.0 mm (paratype).

*N. sam* Winterbottom (2 lots, 2 specimens: 40.4–43.2 mm SL): SAM 21915, 43.2 mm (holotype); SAM 28940, 40.4 mm (paratype).

*Rusichthys explicitus* Winterbottom (3 lots, 3 specimens: 39.8–52 mm): BPBM 35886, 52 mm (holotype); ROM 68794, 39.8 mm (paratype); ROM 1555CS, 44.4 mm (paratype).

*R. plesiomorphus* Winterbottom: USNM 218164, 39.7 mm (paratype).

**CHARACTER ANALYSIS**

Characters are numbered 1–59, but are referenced to those as numbered in earlier papers using the designation RDM for Mooi (1993) and SVJ for Smith-Vaniz & Johnson (1990) (e.g. character 3 here is the same as character 3 in Mooi, 1993 and character 4 in Smith-Vaniz & Johnson, 1990). Figures of the states of many of these characters can be found in Mooi (1993) and Smith-Vaniz & Johnson (1990), and are referenced after the character number of the appropriate abbreviation. Interpretation for conditions of these characters in plesiospid and acanthoclinines are also found in these publications. Some character conditions have been reinterpreted with respect to those of RDM and SVJ, and have been recoded to reflect our current interpretation. Any such changes are noted under the character description. After reference to literature character numbering, the relevant nodes (as lettered in Fig. 2) or taxa are noted. If only a single node is listed, the character exhibits no homoplasy. Reference to nodes or taxa that show reversals or independent acquisitions for particular characters could vary from those listed below, depending on optimization.

Character 1 (RDM 1, fig. 2; node A). Subpelvic cavity on pelvic girdle: absent (state 0); present (state 1). The pelvic girdle of *Notograptus* lacks a posterior subpelvic cavity, but the girdle is very reduced (Gill & Mooi, 1993: figs 11, 12) and the absence may be secondary. We therefore coded the character as inapplicable (n) for *Notograptus*.

Character 2 (RDM 2, fig. 2; node A). Subpelvic shelf on pelvic girdle: absent (state 0); present (state 1). The pelvic girdle of *Notograptus* lacks a subpelvic shelf but, as noted in the previous character, the girdle is very reduced and the absence may be secondary. We therefore coded the character as inapplicable (n) for *Notograptus*.

Character 3 (RDM 3, SVJ 4; node A state 1, node H state 2). Number of pelvic-fin rays: I,5 (state 0); I,4 (state 1); I,2 (state 2). *Notograptus* has 1,2 pelvic-fin rays (Gill & Mooi, 1993: 339, figs 11, 12). This character was originally interpreted as an ordered transformation series and we see no reason to alter this interpretation.

Character 4 (RDM 4; node A state 1, node H state 2). Extensor proprius insertion: on one or two of innermost rays (state 0); on second, third and fourth rays (state 1); muscle absent (state 2). *Notograptus* and acanthoclinines lack an extensor proprius. The original interpretation did not include state 2, treating the absence of the muscle as an autapomorphy of the Acanthoclininae. With the addition of state 2 as potentially informative, we have opted to run this character as unordered.

Character 5 (RDM 5, figs 3, 5; node A). Distal radials of spine-bearing dorsal pterygiophores: autogenous (state 0); associated with the following proximal-middle pterygiophore to form a complete bony ring that interlocks with the articulating spine (state 1). *Notograptus* has the derived state for this character (Fig. 3; Gill & Mooi, 1993: 340, fig. 13). A similar morphology appears in some other taxa (e.g. blennioids, labrids) (Gill & Mooi, 1993; Mooi, 1993), although we have interpreted it as nonhomologous.

Character 6 (RDM 6, fig. 10; node A, reversal in *Notograptus* and *Acanthoplesiops echinatus*). Paraphenoid keel: absent (state 0); present (state 1). *Notograptus* lacks a paraphenoid keel (Gill & Mooi, 1993: 346, fig. 4) and we could not find one in *Acanthoplesiops echinatus* (although the specimen was damaged); these are interpreted as reversals.

Figure 2. Strict consensus cladogram from two equally parsimonious trees from a branch-and-bound search using composite coding of the data set in Table 1 (no. of steps = 123; CI = 0.642; RC = 0.547; RI = 0.852). Nodes are lettered as in the text. Characters supporting each node, those without homoplasy in bold, are: A – 1, 2, 3, 4(1), 5, 6, 7, 8; B – 9, 10(1), 11(1); C – 12, 13, 14, 15, 16; D – 17; E – 18, 19(1), 20; F – 21, 22, 23; G – 10(2), 24, 25, 26; H – 4(2), 18, 19(1), 28, 29, 30, 31(1); I – 32(1), 33; J – 46, 58; K – 34, 35, 36, 37, 38(1); L – 19(2), 39, 40(1), 41, 42, 46, 47; M – 43, 44, 45; N – 31(2), 48, 50, 51, 53; O – 32(3), 49, 52, 54, 55, 56, 57, 59; P – 47; Q – 36, 38(2). Numbers below nodes are decay indices.

Figure 3. *Notograptus* sp., BMNH 2002.1.19.16, 128.5 mm SL, first seven vertebrae and associated dorsal-fin structures in left lateral view. Abbreviations: d4 + pm5, fourth distal radial fused with fifth proximal and middle radials; ds1, first dorsal spine; e1, first epineural; e3, third epineural; li, ligament; r1, first rib; r4, fourth rib; v1, first vertebra; v7, seventh vertebra. Scale bar = 5 mm.
Character 7 [RDM 7, fig. 11 (SVJ, fig. 1); node A, reversal in *Notograptus*. Notch or rounded projection on posterolateral margin of branchiostegal membrane: absent (state 0); present (state 1). *Notograptus* lacks a notch or rounded projection on the posterolateral margin of the branchiostegal membrane (Fig. 4, Gill & Mooi, 1993: 346); this is interpreted as a reversal.

Character 8 [RDM 8, fig. 12 (SVJ 17, fig. 16); nodes A, reversal at L]. Posterior border of preopercular sensory canal: closed (state 0); open (state 1). The posterior border of the preopercular canal is closed in *Notograptus* (Gill & Mooi, 1993: fig. 7). Derived acanthoclines exhibit a similar apparent reversal from the derived condition.

Character 9 (RDM 9, fig. 14; node B). Basioccipital/parasphenoid foramen: large (state 0); small (state 1). The foramen is very small in *Notograptus*, providing evidence of higher plesiopid affinity.

Character 10 (RDM 10, fig. 15; node B state 1, node G state 2, independent acquisition of state 2 in Steeneichthys, reversal to state 1 in *Notograptus*). Adductor superficialis pelvicus inserts: on spine and first three or more segmented rays (state 0); on spine and first one or two segmented rays (state 1); on spine and first ray only (state 2). *Notograptus* has this muscle inserting on the spine and first two segmented rays (state 1), but the reduced pelvic girdle supports only two rays (Gill & Mooi, 1993: fig. 12). Hence, *Notograptus* may exhibit state 1 only as a result of reducing the number of pelvic-fin rays and the associated muscle insertions. If *Notograptus* is an acanthocline, its condition must be interpreted as independently acquired or reversed to a condition of inserting on both segmented pelvic-fin rays. Treated as ordered as originally interpreted by Mooi (1993).

Character 11 (RDM 11; node B state 1, independent acquisition of state 2 in Steeneichthys and *Notograptus*). Branches on first segmented pelvic-fin ray: three or more (state 0); two (state 1); one (state 2). This was originally interpreted as an ordered transformation series, which seems a reasonable interpretation so is maintained here. *Notograptus* has an unbranched first pelvic-fin ray (Gill & Mooi, 1993: 339), which is shared with *Steeneichthys*, but is considered an independent derivation.

Character 12 (node C). Swim bladder: present (state 0); absent (state 1). *Notograptus* and all plesiopids other than *Trachinops* and *Assessor* do not have swim bladders.

Character 13 [RDM 12, fig. 16 (SVJ fig. 18); node C, reversal in *Notograptus*]. Zygapophysis on second vertebra: small and dorsally placed (state 0); expanded and displaced ventrally (state 1). Dorsally placed in *Notograptus*, requiring interpretation as an apparent reversal (Fig. 5).

Character 14 (RDM 13, fig. 14; node C). Posterior tip of parasphenoid: not bifurcate (state 0); deeply bifurcate (state 1). Deeply bifurcate in *Notograptus* (Fig. 5) placing the taxon among higher plesiopids. Note this is a correction to the observations of Gill & Mooi (1993: fig. 4c).

Character 15 (RDM 14, fig. 17; node C, reversal in Callopleisiops). Base of fourth segmented pelvic-fin ray: square-shaped with sharp angles forming the articulation with the pelvic girdle and providing sites for muscle attachment (state 0); not angular (state 1). *Notograptus* has only two segmented pelvic-fin rays, so this character was considered inapplicable (n) for the genus, as it is for acanthoclines.

Character 16 (RDM 15; node C, reversals in Callopleisiops, Fraudella, *Notograptus*). Spinous dorsal-fin membranes: not incised (state 0); incised (state 1). The spinous dorsal fin of *Notograptus* is not incised.

Character 17 (RDM 16, fig. 18; node D). Posterodistal portion of first proximal-middle radial of first anal pterygiophore: does not contact second pterygiophore (state 0); contacts second anal pterygiophore (state 1). Notograptids exhibit state 0 (Fig. 6).

Character 18 (RDM 17, SVJ 1, fig. 2; node E, independently derived at node H). Lower lip configuration: interrupted by isthmus (state 0); continuous (state 1). The lower lip is continuous in *Notograptus* (Gill & Mooi, 1993: 341), which supports a position among the Acanthoclininae. An independent occurrence of this condition is shared by Callopleisiops and Steeneichthys. Mooi (1993) was hesitant to include this character due to its variability and polymorphism in pseudochromid taxa reported by Gill (1990). Such polymorphism has not been observed among plesiopids.

Character 19 (RDM 18, SVJ 6; node E state 1, independently derived at node H, node L state 2, state 3 autapomorphic for *Notograptus*). Number of total caudal-fin rays: 27–29 (state 0); 24 (state 1); 18–22 (state 2); 13 (state 3). *Notograptus* has 13 caudal-fin rays (Gill & Mooi, 1993: 341, fig. 13). This character was run ordered in the analysis to be consistent with the interpretations of RDM and SVJ.

Character 20 (RDM 19, fig. 13; node E). Base of pu2 haemal spine: broad (state 0); constricted (state 1). *Notograptus* has a relatively broad base on the pu2 haemal spine (Gill & Mooi, 1993: 13).

Character 21 [RDM 20, fig. 19 (SVJ fig. 18); node F, reversal at node L]. Ventral surface of anterior second and third vertebrae: ridged (state 0); smooth.
Figure 4. *Notograptus* sp., BMNH 2002.1.2.1–2, 100.5 mm SL, dorsal, left lateral and ventral views of head. Mechanical stippling is branchiostegal membranes. Abbreviations: aip, anterior interorbital pores; atp, anterior temporal pore; bf, barbel-like flap; dp, dentary pores; itp, intertemporal pore; llp, lateral-line pores; np, nasal pores; pip, posterior interorbital pore; pop, preopercular pores; popt, posterior otic pore; pp, parietal pores; ptp, posttemporal pore; scp, supracleithral pore; sobp, suborbital pore; solt, supraotic pore. Scale bar = 5 mm.

Figure 5. *Notograptus* sp., ANSP 109653, 63 mm SL, ventral view of parasphenoid. Anterior to left. Parasphenoid stippled. Scale bar = 1 mm.

Figure 6. *Notograptus* sp., BMNH 2002.1.19.16, 128.5 mm SL, first three anal-fin spines and their pterygiophores in left lateral view. Abbreviations: as1, first anal spine; as3, third anal spine; d2 + pm3, second distal radial fused to third proximal and middle radials; hs1, first haemal spine; hs3, third haemal spine; li, ligament. Scale bar = 2 mm.
(state 1). Ridged in Notograptus (Fig. 7). This apparent reversal also occurs in Beliops and Acanthoplesiops and serves to unite these taxa.

Character 22 (RDM 21, fig. 14; node F, reversal at node L). Attachment sight on basioccipital for Baudelot’s ligament: on lateral fossa (state 0); on medial, triangular, slightly raised process (state 1). Raised processes occur in Notograptus, but from lateral fossa (Gill & Mooi, 1993: fig. 4). A similar apparent reversal occurs in the derived acanthoclinines Beliops and Acanthoplesiops.

Character 23 (RDM 22, fig. 20; node F, reversal in Notograptus). Posterior sphenotic spur: small and closely applied to anterior spur (state 0); large and widely separated from anterior spur (state 1). Sphenotic spur absent or perhaps closely applied in Notograptus making this a reversal.

Character 24 (RDM 23, fig. 21; node G, reversal in Notograptus). Abductor superficialis pelvicus: overlies arrector ventralis pelvicus posterior to the infracarinalis anterior (state 0); does not overlie arrector ventralis pelvicus posterior to the infracarinalis anterior (state 1). In Notograptus the abductor superficialis pelvicus overlies the arrector ventralis pelvicus posterior to the infracarinalis anterior (Gill & Mooi, 1993: 347, fig. 12), making this an apparent reversal.

Character 25 (RDM 24, fig. 22; node G, reversal at node O, independent acquisition in Steeneichthys). Dorsal process for muscle attachment on segmented pelvic-fin rays: large on first two or more rays (state 0); large on first ray only (state 1). In Notograptus only the first segmented ray bears a large dorsal attachment for muscle attachment (Gill & Mooi, 1993: 346, fig. 11a). This places the genus among higher pleisopids. The character reverses in Acanthoplesiops, the hypothesized sister taxon of Notograptus.

Character 26 (RDM 25, figs 23, 24; node G, independent loss in Trachinops, reversal in Beliops xanthokrossos). Lateral process on posterior (middle radial) portion of proximal-middle radial of spine-bearing pterygiophores: present (state 0); absent (state 1). The lateral processes are absent in Notograptus (Fig. 3; Gill & Mooi, 1993: fig. 13). Beliops xantho-

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**Figure 7.** Notograptus sp., BMNH 2002.1.19.16, 128.5 mm SL, first five vertebrae in ventral view. Abbreviations: e1, first epineural; e3, third epineural; r1, first rib; r3, third rib; v1, first vertebra; v5, fifth vertebra. Scale bar = 1 mm.

krossos has very small lateral processes on the first two pterygiophores, but they are absent on remaining posterior spine-bearing pterygiophores; we have coded the species conservatively as showing a reversal.

Character 27 (RDM 26, figs 23, 24; independent acquisitions in Plesiops and Steeneichthys). Anterior process on distal-radial portion of spine-bearing dorsal pterygiophores: present (state 0); absent (state 1). Notograptus has an anterior process on all dorsal-fin pterygiophores (Fig. 3).

Character 28 (SVJ 2; node H). Squamation: head scaled (state 0); head naked (state 1). The head is naked in Notograptus.

Character 29 (SVJ 3; node H). Number of dorsal- and anal-fin rays: low number of spines (7–16 dorsal and 3 anal) and high number of segmented rays (6–21 dorsal and 7–23 anal) (state 0); high number of spines (17–26 dorsal and 7–16 anal) and low number of segmented rays (2–6 dorsal and 2–6 anal) (state 1). Notograptus has a high number of dorsal and anal-fin spines (62–69 and 37–43, respectively) and low number of segmented rays (1–2 in each fin) (Gill & Mooi, 1993: 340). This provides evidence for Notograptus as an acanthoclinine.

Character 30 (SVJ 5; node H). Number of branched caudal-fin rays: 15–17 (state 0); 14 or fewer (state 1). Notograptus has 11 branched caudal-fin rays and is coded as state 1. As acanthoclinines have 12 or 14, the condition in Notograptus could be interpreted as autapomorphic. Here we have chosen to interpret the reduced number of branched rays as homologous, i.e. assuming homology in the absence of contrary evidence (Hennig’s Auxiliary Principle).

Character 31 (SVJ 7; nodes H state 1, reversal at node L, node N state 2, Steeneichthys state 3). Number of lateral lines: two (state 0); three (state 1); one (state 2); none (state 3). Notograptus has a single lateral line consisting of enlarged ossicles (Gill & Mooi, 1993: 342, fig. 10). This character was run as unordered as there is no evidence that the defined states form an ordered transformation series.

Character 32 (SVJ 8, fig. 13; node I state 1, Notograptus state 2, node O state 3, independent acquisition of state 3 in Steeneichthys). Infraorbital bones: five (state 0); six (state 1); four (state 2); one (state 3). Notograptus has four infraorbital bones (Gill & Mooi, 1993: fig. 6). The character was run unordered, there being no clear polarity demonstrated and homology among retained infraorbital elements unknown. It could be interpreted as providing weak evidence of a Notograptus + Acanthoplesiops clade, if polarized as a reduction in number of elements among acanthoclinines being derived.

Character 33 (SVJ 9, fig. 13; node I). Suborbital shelf: present (state 0); absent (1). Notograptus has a suborbital shelf on infraorbital 3. The character is not applicable to Acanthoplesiops so provides no data regarding possible affinities with Notograptus.

Character 34 (SVJ 10, fig. 2; node K). Gill membranes: separate (state 0); united (state 1). Notograptus has the gill membranes united to each other and, additionally, has them fused to the isthmus (Fig. 4). The character supports Notograptus as a derived acanthoclinine.

Character 35 (SVJ 11, fig. 14; node K, independent acquisitions in Trachinops, Assessor and Steeneichthys, reversal in Beliops xanthokrossos). Supramaxilla: present (state 0); absent (state 1). Notograptus lacks a supramaxilla (Gill & Mooi, 1993: fig. 6), supporting its placement among higher acanthoclinines.

Character 36 (SVJ 12, fig. 15; node K, reversal at node Q). Teeth on infrapharyngobranchial 2: present (state 0); absent (state 1). Notograptus lacks teeth on infrapharyngobranchial 2 (Gill & Mooi, 1993: 338, fig. 9) like its hypothesized relatives among acanthoclinines.

Character 37 [SVJ 13, fig. 17 (RDM, fig. 13); node K, independent acquisitions in Steeneichthys and Acanthoclinus fuscus]. Haemal spine of pu2: autogenous (state 0); united with vertebral centrum (state 1). Notograptus has the haemal spine of pu2 united with the vertebral centrum (Gill & Mooi, 1993: 341, fig. 13). Although exhibiting some homoplasy, the character supports a position of Notograptus among higher acanthoclinines.

Character 38 (SVJ 14, fig. 2; node K state 1, node Q state 2, independent acquisitions of state 1 in Acanthoclinus rua and state 2 in Steeneichthys). Number of dentary pore positions: five (state 0); four (state 1); three (state 2). Notograptus has four dentary pore positions (Fig. 4). This character was treated as ordered.

Character 39 (SVJ 16, fig. 16; node L, reversal in Notograptus). Primary opercular spine: plate-like or fimbriate (state 0); pungent (state 1). Notograptus has a fimbriate opercular margin, an apparent reversal (Gill & Mooi, 1993: fig. 7).

Character 40 (SVJ 18, fig. 15; node L state 1, state 2 autapomorphic for Notograptus). Interarcual cartilage size: relatively long, almost as long as or longer than pharyngobranchial 1 (state 0); relatively short, less than half as long as pharyngobranchial 1 (1); absent (2). Notograptus lacks an interarcual cartilage (Gill & Mooi, 1993: 338, fig. 9). This character was treated as ordered.

Character 41 (SVJ 19, fig. 17; node L). Second and third epurals: separate (state 0); fused (state 1). *Notograptus* lacks epurals (Gill & Mooi, 1993: 341, fig. 13), a state considered inapplicable (n) for this character.

Character 42 (SVJ 20, fig. 18; node L). First neural spine: autogenous (state 0); joined to centrum (state 1). As noted under Character 40, *Notograptus* lacks an interarcual cartilage (Gill & Mooi, 1993: fig. 13), a state considered inapplicable (n) for this feature.

Character 43 (SVJ 21, fig. 15; node M). Intercarcal cartilage shape: rod-shaped (state 0); cone-shaped (1). *Notograptus* has a smooth joint between the metapterygoid and the quadrate (Gill & Mooi, 1993: fig. 5).

Character 44 (SVJ 22, fig. 16; node M). Metapterygoid-quadratojugal joint: smooth (state 0); interdigitated (state 1). *Notograptus* has a smooth joint between the metapterygoid and the quadrate (Gill & Mooi, 1993: fig. 5).

Character 45 (SVJ 23, fig. 19; node M). Scapulocoracoid joint: smooth (state 0); interdigitated (state 1). *Notograptus* lacks a secondary spine on the opercle, which, in combination with the other characters, places it among higher acanthoclinines (Fig. 6).

Character 46 (SVJ 24; nodes J, independently acquired at node L, reversal at node O). Supernumerary spines on first anal-fin pterygiophore: two (state 0); one (state 1). *Notograptus* has one supernumerary spine, which, in combination with the other characters, places it among higher acanthoclinines (Fig. 6).

Character 47 (SVJ 25; nodes L, reversal at node P). Middle radials of segmented-ray-bearing dorsal- and anal-fin pterygiophores: autogenous (state 0); united with proximal radials (state 1). The middle radials of segmented-ray-bearing dorsal- and anal-fin pterygiophores of *Notograptus* form a single element with the proximal radials (Figs 3 and 6; Gill & Mooi, 1993: fig. 13), as they are in *Beliopterus* and *Acanthoplesiops hiatti*. Remaining species of *Acanthoplesiops* form a clade on the basis of a reversal to autogenous middle radials in median fins. This resolves the polytomy among *Acanthoplesiops* presented in the original analysis of Smith-Yaniz & Johnson, 1990).

Character 48 (SVJ 27, figs 1, 11; node N, independent acquisition in *Steeneichthys*). Symphyseal flap on lower lip: absent (state 0); present (state 1). *Notograptus* has an elongate, barbel-like flap on the lower lip (Figs 1 and 4; Gill & Mooi, 1993: 341), which is interpreted as a modified symphyseal flap as exhibited by *Acanthoplesiops*, which in some individuals can be quite long.

Character 49 (SVJ 28, fig. 15; node O). Uncinate process on epibranchial 1: not parallel to main arm, so that junction between two arms is 'V'-shaped (state 0); parallel to main arm, so that junction between two arms is 'U'-shaped (state 1). *Notograptus* lacks an uncinate process on epibranchial 1 (Gill & Mooi, 1993: 338, fig. 9), so the character states are inapplicable (n) for this feature.

Character 50 (SVJ 29, fig. 17; node N). Size of hypural 5: large to moderate (state 0); very small or absent (state 1). *Notograptus* lacks hypural 5 (Gill & Mooi, 1993: 341, fig. 13). It is suggested here that the loss of hypural 5 in this taxon is a direct modification of the condition in *Acanthoplesiops* of a reduced element.

Character 51 (SVJ 30, fig. 17; node N). Hypurapophysis: present (state 0); absent (state 1). *Notograptus* lacks a hypurapophysis (Gill & Mooi, 1993: 341, fig. 13), sharing this condition with *Acanthoplesiops*.

Character 52 (SVJ 31, fig. 16; node O). Secondary opercular spine: absent (state 0); present (state 1). *Notograptus* lacks a secondary spine on the opercle, although it does bear a slight expansion in this region of the bone (Gill & Mooi, 1993: fig. 7). Smith-Yaniz & Johnson (1990: 249) incorrectly reported that “... *Fraudella* has a series of prominent spines on the posterior margin of the opercle”; *Fraudella* exhibits a typical perciform condition with a single primary opercular spine.

Character 53 (SVJ 32, fig. 19; Node N). Ventral arm of coracoid: moderately slender (state 0); robust (state 1). The ventral arm of the coracoid of *Notograptus* is relatively robust (Gill & Mooi, 1993: fig. 10), suggesting a relationship to *Acanthoplesiops*, although the general shape of these elements differs among these taxa (cf. SVJ, fig. 19d, e).

Character 54 (SVJ 33, fig. 19; node O). Pectoral radial formula: 2-1-1 (state 0); 3-0-1 (state 1). *Notograptus* has a 2-1-1 radial formula (Gill & Mooi, 1993: fig. 10).

Character 55 (SVJ 34; node O). Supracleithral lateral-line canal: present (state 0); absent (state 1). *Notograptus* has a lateral-line canal in the supracleithrum (Gill & Mooi, 1993: fig. 10).

Character 56 (SVJ 35; node O). Anterior-posterior ceratohyal suturing: medial only (state 0); on both medial and lateral surfaces (state 1). *Notograptus* has the anterior and posterior ceratohyals sutured on the medial surface only (Gill & Mooi, 1993: fig. 15).
Character 57 (SVJ 36, fig. 20; node O). Scales in mid-lateral series: not bilobed (state 0); bilobed (state 1). The mid-lateral series of scales of Notograptus are not bilobed.

Character 58 (SVJ 37, fig. 21; node J, independent acquisition in Notograptus). Body scales: some ctenoid (state 0); cycloid (state 1). Notograptus has cycloid scales (Gill & Mooi, 1993: 342), apparently an autapomorphy among higher acanthoclines.

Character 59 (SVJ 38, fig. 22; node O, independent acquisition in Belonepterygion). Adductor mandibulae A1 section: laterally exposed (state 0); covered by A2 laterally (state 1). The adductor mandibulae of Notograptus is modified, lacking distinct A1 and A2 sections (Gill & Mooi, 1993: 338, fig. 8); this character was therefore considered inapplicable (n) for Notograptus and uninformative regarding its phylogenetic position among acanthoclines.

**Excluded characters from previous studies**

SVJ 15. Maximum standard length: c. 46–200 mm (state 0); <27 mm (state 1). Notograptus exceeds 46 mm standard length (largest specimen examined 178 mm; 185 mm SL reported by Taylor, 1964), suggesting a reversal to larger size. This is a questionable character; it is difficult to use SL as an index of size when plesiopids vary so much in body shape. The change in maximum size is not a particularly convincing characteristic for building phylogenies, with substantial changes in size notable among many percomorph groups as well as within the Plesiopidae (e.g. Plesiopinae, Paraplesiopinae).

SVJ 26. Pale spot on pectoral-fin base: absent (state 0); present (state 1). Smith-Vaniz & Johnson (1990) proposed that a pale spot on the pectoral-fin base is an autapomorphy of the acanthocline genus Acanthoplesiops, but noted (p. 249) that the spot ‘is difficult to discern in preserved specimens, but in fresh material it is usually conspicuous’. Our survey indicates that the derived state is more widely distributed, though we acknowledge that we had difficulty in determining its presence in some taxa. It is present in at least Beliops xanthokrossos (see Hardy, 1994: fig. 496), all four species of Acanthoclinus (Paulin & Roberts, 1992: pl. 8A–D), possibly Beliops batanensis (see Smith-Vaniz & Johnson, 1990: fig. 7), and several species of Plesiops (e.g. P. cephalataenia, P. coralicola, P. coeruleolineatus, P. ocycephalus; see Masuda et al., 1984: pl. 126I–M; Mooi, 1995: figs 11–13, 15 and 29). Notograptus lacks a pale spot on the pectoral-fin (Fig. 1). However, because of our difficulty in determining its distribution, this character was not included in the analysis.

**Phylogenetic analysis**

Of the 61 characters surveyed for Notograptus and plesiopids, two were excluded from the analysis and seven could not be scored for Notograptus (Table 1). Characters 1, 2 and 15 were not applicable due to modification and autapomorphic reduction of the pelvic girdle in Notograptus. Character 41 could not be scored because of the lack of epurals in Notograptus, and 43 and 49 were inapplicable due to absence of particular dorsal gill elements. The adductor mandibulae of Notograptus is autapomorphically modified and obscures its interpretation for Character 59.

Several other characters have no direct bearing on the position of Notograptus among plesiopids (17, 20, 27, 44, 45, 52, 54–57) but have been retained in this analysis to maintain the structure of the original plesiopid tree of Mooi (1993) and acanthocline topology of Smith-Vaniz & Johnson (1990). Hence, 42 characters are potentially informative regarding the relationships of Notograptus among plesiopids.

Analysis using all 59 characters (79 steps minimum) with composite coding for inapplicable characters and six characters ordered resulted in two equally parsimonious trees (no. of steps = 123; Cl = 0.642; RC = 0.547; RI = 0.852). Both trees placed Notograptus as the sister taxon to Acanthoplesiops among the Acanthoclininae as defined by Mooi (1993) and Smith-Vaniz & Johnson (1990). Topology changes involved only the relationships among species of Acanthoclinus, shown as a polytomy in the strict consensus tree (Fig. 2). This is a relatively robust tree, particularly at nodes A, H, L and O (note decay indices on Fig. 2). With such decay values, strict consensus of trees even six steps longer than the most parsimonious topology retained these nodes and left Notograptus among a polytomy of the derived acanthoclines Beliops xanthokrossos, B. batanensis and Acanthoplesiops. Various analytical manipulations (e.g. unordering all characters, deleting characters with unknown inapplicable states) resulted in identical strict consensus topologies (excepting collapse of node I and loss of Acanthoclinus monophyly due to character deletion) and only slight decreases in CI, RC and RI. Constraining the placement of Notograptus as sister of the Plesiopidae lengthened the tree by 20 steps. Reductive coding of inapplicable states (Strong & Lipscomb, 1999) resulted in the same two most parsimonious trees and strict consensus result as the initial composite coding, with slightly different tree statistics as a consequence of treating inapplicable states as unknowns rather than as a new state (no. of steps = 112; Cl = 0.625; RC = 0.533; RI = 0.853). Our interpretation and coding of these characters has no affect on the conclusion that Notograptus is an acanthocline.

Of the eight characters that Mooi (1993) (Fig. 2, node A) used to define plesiopids, Notograptus shares three: a reduced number of pelvic-fin rays (3), modification or loss of the extensor proprius (4) and a bony pterygiophore ring articulating with dorsal-fin spine bases (5). Although several nonplesiopids also share these conditions (see Mooi, 1993 and Gill & Mooi, 1993), two of the eight characters cannot be scored for Notograptus (as noted above). Of the three others, a secondary loss of a parasphenoid keel (6) and open preopercular canal (8) are known to occur among higher acanthoclinine plesiopids; the absence of a branchiostegal notch (7) is a novel reversal in our hypothesis. However, convincing evidence positions Notograptus as a derived plesiopid through a series of nested characters as reviewed below.

Placing Notograptus among higher plesiopids (Fig. 2, nodes B–G) are six characters: small aortic foramen (9), two or fewer branches on the first pelvic-fin ray (11), loss of swim bladder (12), posterior end of parasphenoid deeply bifurcate (14), large dorsal process on first pelvic-fin ray only (25), loss of posterior lateral processes on dorsal-fin spine-bearing pterygiophores (26).

Notograptus also exhibits all six of the characters listed by Smith-Vaniz & Johnson (1990) as defining the Acanthoclininae (Fig. 2, node H): only two pelvic-fin rays (3), complete lower lip (18), reduced number of caudal-fin rays (19), head scaleless (28), dorsal and anal fins with high numbers of spines (29) and reduced number of branched caudal-fin rays (30). Smith-Vaniz & Johnson (1990: 220) provided a list of characters that differ between Notograptus and acanthoclinines, but all (excepting perhaps the absence of a branchiostegal notch, character 7) could be explained as a result of an autopomorphic feeding morphology and behaviour in Notograptus. Notograptus and acanthoclinines also share an absence of the extensor proprius pelvicus (4); because other plesiopids have modified this muscle, we originally interpreted its absence as ‘inapplicable’ (n) but have reinterpreted it as an autapomorphy of acanthoclinines, including Notograptus.

Notograptus can be hypothesized to be among higher acanthoclinines (Belonepterygion, Beliops, Acanthopleisiops; Fig. 2, node K) with the following five characters: fusion of gill membranes (34), loss of supramaxilla (35), no teeth on second infrapharyngobranchial (36), haemal spine of pu2 united with centrum (37) and reduced number of dentary pores (38). Although the conditions are unknown for the other taxa, Notograptus and Belonepterygion share an extraordinarily similar egg surface morphology modified by multiarmed projections raised above the chorion by a central pedicel. This might be further indication of a close relationship (Gill & Mooi, 1993: Fig. 14). However, Acanthoclinus and some other plesiopids (e.g. Assessor) have similar, although not identical, egg surface morphology. Until homologies are understood and character distribution among other acanthoclinines is determined, the character remains merely a tantalizing similarity.

Notograptus is related to Beliops and Acanthopleisiops (Fig. 2, node L) based on a further four characters: reduced or absent interarcual cartilage (40), first neural spine fused to centrum (42), one supernumerary spine on first anal-fin pterygiophore (46) and middle radials of pterygiophores supporting dorsal- and anal-fin segmented rays forming a single element with proximal radials (47). This relationship is also weakly supported by three apparent reversals in these taxa: preopercular canal no longer open (8), ventral surfaces of three anterior vertebræ no longer smooth (21) and Baudelot's ligament again originating from a lateral position on the basioccipital (22).

We have placed Notograptus as the sister taxon to the genus Acanthopleisiops based on four characters: presence of a symphysal flap (48), reduced or absent hypural 5 (50), loss of hypurapophysis (51) and robust coracoid arm (53). The presence of only one lateral line (31, state 2) can also be considered as evidence uniting Notograptus and Acanthopleisiops, although this is a relatively labile feature exhibiting several states for which homology is difficult to determine. As we note below, Notograptus and Acanthopleisiops species examined have straight guts with no bends or constrictions demarcating a stomach, an apparent additional synapomorphy for these taxa, although character distribution of this feature has not been fully explored.

Speaking against the inclusion of Notograptus in the Plesiopidae are nine characters: lack of a parasphenoid keel (6), no branchiostegal notch (7), a primitive condition of the insertion of the adductor superficialis pelvis to both segmented rays (10, state 1), dorsally positioned zygapophysis (13), dorsal fin membranes not incised (16), posterior sphenotic spur absent (23), abductor superficialis pelvis overlaps the arrector ventralis pelvisicus (24), opercular spine flattened and fimbriate (39). Among these characters, 6 and 16 are known to reverse among other acanthoclinines, so could be considered somewhat more labile and less informative. In our estimation, characters 7 and 10 provide the strongest evidence against the inclusion of Notograptus among plesiopids. We have no reasonable arguments to explain their apparent reversal to the primitive condition necessitated by our hypothesis. Character states for several others are not presently known for all acanthoclinines (13, 23, 24) and might exhibit a similar lability to 6 and 16, although unlikely. The interpretation of characters 13 and 24 is somewhat subjective; additionally, the modifications in the morphology of the pelvic girdle, and size and shape of the zygapophysis, might suggest...
that these are autapomorphic states in *Notograptus*. It could be argued that branchiostegal and opercular morphology (characters 7 and 39) has been modified as a result of a unique jaw mechanism and feeding behaviour. In any event, none of the nine homoplastic characters associated with the position of *Notograptus* as the sister to *Acanthoplesiops* provides substantial evidence to overturn the hypothesis.

**IMPACT ON CLASSIFICATION AND RELATIONSHIPS AMONG ACANTHOCLININES**

The realignment of the Notograptidae as a sister genus to the plesiopid acanthoclinine genus *Acanthoplesiops* resolves a longstanding phylogenetic enigma. After being included among a fluid ‘Blennioidea’ for over 100 years at the familial rank, and bounced to other wastepaper basket higher taxa such as the Trachinoidei, the peculiar genus *Notograptus* can settle among a growing Plesiopidae. Relationships of the Plesiopidae to other perciforms remain problematic.

As sister to *Acanthoplesiops*, *Notograptus* exhibits a condition that polarizes a previously equivocal character, middle radials of pterygiophores bearing segmented rays free or forming a single element with the proximal radials (47). In Smith-Vaniz & Johnson (1990: 248, fig. 12), the presence of trisegmented pterygiophores (free proximal, middle and distal radials) is considered primitive and the presence of united proximal-middle radials derived, occurring once in the genus *Beliops* and interpreted as independently derived in *Acanthoplesiops* *hiatti*. As Smith-Vaniz & Johnson (1990: 255) noted, it is equally parsimonious to interpret the character of having united proximal-middle radials arising in a common ancestor of *Beliops* + *Acanthoplesiops* with a reversal to a trisegmented condition in *Acanthoplesiops* indicus + (*A. echinatus* + *A. psilogaster*). With the insertion of *Notograptus* as sister to *Acanthoplesiops*, a choice can now be made between these alternative interpretations in favour of the latter. *Notograptus* has proximal-middle radials as a single element, which suggests that *Acanthoplesiops* *hiatti* is the sister to the remaining *Acanthoplesiops* species (Fig. 2). We have been unable to determine the condition of this or several other characters in the new species of *Acanthoplesiops* *naka*; its position remains equivocal (Mooi & Gill, 2004).

**BIogeography**

With the inclusion of *Notograptus*, the distribution of the Acanthoclininae expands to an area previously unrecognized as being occupied by the subfamily (Fig. 8; Smith-Vaniz & Johnson, 1990: fig. 3). In effect,
an unexplained ‘hole’ in the distribution of acanthoclinines, northern Australia, has been plugged with the addition of Notograptus. We also note that the distribution of Belonepterygion should be modified to include at least Thevenard Island of north-western Australia (MPM), Santa Cruz Islands of the Solomons (USNM), Shepherd and Erromango Islands of Vanuatu (USNM), Loyalty Islands (USNM), and Middleton and Elizabeth Reefs (AMS; Gill & Reader, 1992).

As the sister group, Notograptus provides resolution of the relationships among Acanthoplesiops through the reinterpretation of the evolution of middle/proximal radial association (character 46; described above). Within Acanthoplesiops, A. hiatti, a West Pacific species, is sister to a three species clade that is Indo-West Pacific. Within this clade, the Indian Ocean taxon, A. indicus, is sister to two allopatric West Pacific species, A. psilogaster to the north (Japan, Taiwan, Batanes) and A. echinatus to the south (southern Philippines and Moluccas) (Figs 8, 9A). This interpretation suggests that an endemic northern Australian taxon (Notograptus) is sister to a more broadly distributed Indo-West Pacific taxon (Acanthoplesiops) with a more complicated biogeographical history, perhaps influenced by some of the factors outlined by Springer & Williams (1990). Where Acanthoplesiops naka from Tonga fits into this history cannot be determined at this time (Mooi & Gill, 2004).

The basic Notograptus/Acanthoplesiops area relationships are broadly similar to those of derived pseudochromids (Gill & Hutchins, 1997; Gill & Edwards, 1999; Fig. 9B) if the Acanthoplesiops distribution pattern is viewed as a potentially repeating Western Indian Ocean versus Pacific + Eastern Indian Ocean pattern. This is the same pattern found in the Congrogadinae. Their sister group, Anisochrominae, is Western Indian; the sister to those is another repeating pattern (Lubbockichthys – Pacific/Eastern Indian Oceans ((Amsichthys + Pseudoplesiops – both Pacific/East Indian Oceans) + (Childichthys + Pectinochromis – both Western Indian Ocean))). The sister to all these is Assiculoides (Kimberley District of Western Australia) and the sister to all of these is Assicusilus (north-western Australia) (Fig. 9B). Hence, the Notograptus/Acanthoplesiops and the derived pseudochromid area relationships can be reduced to the repeating Pacific/Indian Ocean pattern with a sister relationship to northern (or perhaps north-western) Australia. This pattern is roughly equivalent to that seen in some invertebrate taxa such as marine water striders (Andersen, 1998) (Fig. 9C). Other fish taxa have an Australian (Pacific/Indian Ocean) pattern, but the Australian distribution is temperate or southern rather than northern (e.g. Pempheridae, R. Mooi, unpubl. data; other Plesiopidae, Paraplesiops + Calloplesiops + Steeneichthys). The Australian region has numerous marine endemic families (Brachionichthyidae, Pataecidae, Gnathanacanthidae, Dinoolestidae, Leptobramidae, Enoplosidae, Arripidae, Odacidae, Leptoscopidae) and genera (e.g. certain aplodactylids, gobiesocids, clinids, monacanthids, antenariids, gobiids, stygnathids etc.) that might provide similar repeated patterns (Mooi & Gill, 2002). To make strides in understanding the biogeographical history of Australia, we need to determine the relatives to these groups and search for repeated patterns of distribution.

This is in contrast to the hypothesis proposed by Santini & Winterbottom (2002) using Brook’s Parsimony Analysis (BPA). Although a ‘South Australia Basin’ is shown basal to all areas excluding New Zealand, Indian Ocean areas form a series of basal areas to several Indonesian and west and central Pacific areas that are then more closely related to independent ‘West’ and ‘North Australia’ basins (the latter encompassing the distribution of Notograptus) (Fig. 10A). Their analysis used several groups, including acanthoclinines; Notograptus was not included as

Figure 9. Area/taxon cladograms of A, Notograptus + Acanthoplesiops; B, derived Pseudochromidae; C, marine water striders (after Andersen, 1998: fig. 7e).
Figure 10. Area cladogram of the Indo-Pacific determined from a combined data set of 13 cladograms using Brooks Par-
simony Analysis (A) after Santini & Winterbottom (2002); (B) with Plesiops and acanthoclinine data corrected, single most
parsimonious tree from a branch-and-bound search (no. of steps = 283; CI = 0.601; RC = 0.382; RI = 0.635). Numbers under
nodes are decay indices.
its position was unclear. With our hypothesis that Notograptus is an acanthocline, we wanted to examine what impact adding it to this data base might have on the results. However, upon closer inspection of the Santini and Winterbottom data set, we discovered that the acanthocline and Plesiops portions have several errors in coding of internal nodes and occurrence of taxa in identified areas. In addition, two taxa are missing from the Plesiops cladogram (cf. Mooi, 1995: fig. 34 and Santini & Winterbottom, 2002: fig. 1B VIII), and their inclusion alters coding of internal nodes. With corrections, using BPA we found a single most parsimonious tree with considerable difference from that reported by Santini & Winterbottom (2002) (Fig. 10B). This corrected tree perhaps reflects more closely the general description of biogeography of the region discussed earlier, where west and north Australian areas are found farther ‘down’ the tree and are sister to a broader western Pacific and Indonesian region, although it differs in that Indian Ocean regions remain as a series of sister areas to Australian, Indonesian and West Pacific areas. Adding Notograptus to this corrected data set has no impact on the tree topology, not surprisingly given the size of the data set. However, even this corrected biogeographical tree should be treated with some scepticism because it exhibits low decay indices (Fig. 10B) and further errors or omissions might exist in the coding of the several included groups that we did not reexamine. There are also methodological questions that should be reconsidered, for example, how to delimit areas (six of the regions in the data set of Santini & Winterbottom are not defined by endemic taxa), and several listed nudibranch taxa do not occur in any of the areas (i.e. they appear in the cladograms of the analysed groups and in the data set, but occur outside of the Indo-West Pacific in the Caribbean, Atlantic and Mediterranean). There continues to be considerable discussion on how to perform BPA and whether or not it is the most appropriate method of analysis (Ebach, Humphries & Williams, 2003; van Veller, Brooks & Zandee, 2003; references therein). We have not pursued other methods with these data because of the questionable area designations and unverified coding for most taxa.

Biology of Notograptus

The largest specimen examined was 178 mm SL, although a 185 mm SL specimen was reported by Taylor (1964). Gill & Mooi (1993: 342, fig. 14a, b) described the eggs of Notograptus: 29–35 roughly cruciform chorionic projections arranged in a narrow ring closer to one pole of the egg than the other, 1–3 rows of projections wide. The projections are raised above the surface by a short pedicel, and the projection’s arms are produced into filaments, two to three greatly elongate. In other acanthoclinines, similar-looking eggs bind together via the filaments and the egg mass is guarded by the male in a burrow; similar behaviour is expected in Notograptus. In the specimen with largest ovarian eggs (USNM 173798, 170 mm SL), the eggs come in three basic size classes: very small (0.5–0.6 mm in diameter), small (0.9–1.2 mm in diameter) and large (2.5–3.4 mm in diameter). This size distribution is indicative of a cyclical breeding cycle, perhaps lunar. Gravid females ranged in size from 88 mm SL to 170 mm SL and were found in collections made in February, April, May, June and September. Because our sample is small and collections were restricted to January through September, reproduction taking place in other months cannot be precluded. The largest specimens carried the most eggs (170 mm SL, 63 right ovary + 53 left ovary = 116 mature eggs; 170 mm SL, 47 + 42 = 89; 152 mm SL, 41 + 38 = 79; 103 mm SL, 24 total; 88 mm SL, 18 + 14 = 32). Note that the right ovary always contained more eggs than the left. Males do not have a modified intromittent organ, and eggs are likely fertilized after laying.

We have examined 99 specimens of Notograptus and found 32 with identifiable gut contents (Table 2). Eighteen of these contained whole alpheid shrimp, always swallowed tail first (Fig. 11A, B). Thirteen (usually smaller) specimens contained only one or two claws, suggesting that smaller individuals are only able to obtain these parts. However, a 51 mm fish engulfed a whole 23 mm shrimp (claw tips to telson tip) that filled the entire gut from the anus to well into the buccal chamber (Fig. 11C). The largest individual examined (USNM 173797, 178 mm SL) had eaten a 24 mm SL gobiid. This apparent exception to a strict alpheid diet is likely an artefact of collection methods; rotenone collecting kills smaller fishes first that are often eaten by as yet unaffected bigger individuals that may not be piscivores under normal circumstances. Considering that the gobid was in excellent condition in the gut (scales still intact, no digestion), and that the specimen was collected with ‘barbasco root’ (J. T. Williams, pers. comm.; a source of rotenone), opportunistic feeding is a likely explanation for this anomalous food item. Our observations strongly indicate that Notograptus are alpheid shrimp specialists. Many morphological features of Notograptus appear to be adapted to accommodate their feeding speciality. The elongate body would permit entry into shrimp burrows. The extremely large gape, knobby teeth and reduced gill arches would all facilitate eating large prey whole. The gut is straight, lacking the complicated intestinal bends that would hamper ingestion of large prey. Additionally, pleated skin around the anus (reminiscent of a baleen whale throat) allows evacuation of large indigestible items (Fig. 12A). In
Table 2. Frequency of specimens with specific gut contents of *Notograptus* and selected plesiopids, anisochromines, and congrogadines. Size ranges in mm SL.

<table>
<thead>
<tr>
<th>Species</th>
<th>N : size range</th>
<th>Alpheids whole (w), parts (p)</th>
<th>Stomatopods (s) or shrimps (h)</th>
<th>Amphi/Isopods</th>
<th>UnID Crust.</th>
<th>Digested fish</th>
<th>Undigested fish</th>
<th>UnID</th>
<th>Empty</th>
<th>Other (*incidental)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Notograptus</em> 99</td>
<td>44–178</td>
<td>18w, 13p</td>
<td>–</td>
<td>–</td>
<td>2</td>
<td>–</td>
<td>1 (gobiid with scales)</td>
<td>–</td>
<td>65</td>
<td>–</td>
</tr>
<tr>
<td><em>Acanthoclinus fuscus</em></td>
<td>68 : 28–220</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>11</td>
<td>–</td>
<td>2 (1 with 3 tripterygiids)</td>
<td>5</td>
<td>48</td>
<td>1 snail, 1 limpet</td>
</tr>
<tr>
<td><em>A. littoreus</em></td>
<td>7 : 56–119</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>4</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>2</td>
<td>1 mollusc</td>
</tr>
<tr>
<td><em>A. marilynae</em></td>
<td>2 : 90–95</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><em>A. matti</em></td>
<td>1 : 52</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><em>Acanthoplesiops echinatus</em></td>
<td>1 : 21</td>
<td>1p</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><em>A. hiatti</em></td>
<td>9 : 15–20</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>6</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>3</td>
<td>–</td>
</tr>
<tr>
<td><em>A. indicus</em></td>
<td>4 : 19–27</td>
<td>1p</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>2</td>
<td>–</td>
</tr>
<tr>
<td><em>Acanthoplesiops naka</em></td>
<td>1 : 9.9</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td><em>A. psilogaster</em></td>
<td>4 : 12–22</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>4</td>
<td>–</td>
</tr>
<tr>
<td><em>Beliops xanthobrossos</em></td>
<td>1 : 26</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td><em>Belonepterygion fasciolatum</em></td>
<td>43 : 12–42</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>43</td>
<td>–</td>
</tr>
<tr>
<td><em>Anisochromis kenyae</em></td>
<td>46 : 13.8–25.6</td>
<td>27 1 s</td>
<td>–</td>
<td>9</td>
<td>–</td>
<td>–</td>
<td>2</td>
<td>28</td>
<td>3 ostracods</td>
<td>1 crab</td>
</tr>
<tr>
<td><em>A. mascarenensis</em></td>
<td>11 : 13.3–25.5</td>
<td>–</td>
<td>1 h</td>
<td>6</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>3</td>
<td>1 ostracods</td>
<td>–</td>
</tr>
<tr>
<td><em>A. straussi</em></td>
<td>82 : 16.1–28.3</td>
<td>3 s, 2 h</td>
<td>1 i</td>
<td>15</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>11</td>
<td>46</td>
<td>3 gastropods</td>
</tr>
<tr>
<td><em>Blimnodesmus scapularis</em></td>
<td>120 : 28.5–87</td>
<td>2p</td>
<td>2 s, 2 h</td>
<td>2a</td>
<td>10</td>
<td>–</td>
<td>–</td>
<td>24</td>
<td>78</td>
<td>1* mollusc</td>
</tr>
<tr>
<td><em>Congrogadus hierichthys</em></td>
<td>30 : 50–159</td>
<td>1p</td>
<td>1 h</td>
<td>1</td>
<td>5</td>
<td>1</td>
<td>–</td>
<td>4</td>
<td>17</td>
<td>–</td>
</tr>
<tr>
<td>Species</td>
<td>N</td>
<td>Size Range</td>
<td>Parts</td>
<td>Shrimps</td>
<td>Fish</td>
<td>Other</td>
<td>Crustacea</td>
<td>Undigested Fish</td>
<td>Digested Fish</td>
<td>Nature</td>
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</tr>
<tr>
<td>Congrogadus malayanus</td>
<td>12</td>
<td>31–70</td>
<td>–</td>
<td>–</td>
<td>3</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>8</td>
</tr>
<tr>
<td>C. spinifer</td>
<td>1w</td>
<td>3,2 h</td>
<td>–</td>
<td>–</td>
<td>10</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>2</td>
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<tr>
<td>C. subducens</td>
<td>4w</td>
<td>1,1 h</td>
<td>–</td>
<td>–</td>
<td>10</td>
<td>28 (a few of these with undigested fish, but often mixed with digested; 3 with Crustacea; 8 with 2–3 fish)</td>
<td>–</td>
<td>2</td>
<td>29</td>
<td>–</td>
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<tr>
<td>C. winterbottomi</td>
<td>5h</td>
<td>12a</td>
<td>–</td>
<td>–</td>
<td>2</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>3</td>
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<tr>
<td>Halidesmus polytretus</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>2</td>
<td>–</td>
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<tr>
<td>H. scapularis</td>
<td>–</td>
<td>–</td>
<td>20 (some might be shrimps)</td>
<td>–</td>
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<td>–</td>
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<tr>
<td>H. socotraensis</td>
<td>–</td>
<td>–</td>
<td>4</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>2</td>
<td>–</td>
<td>–</td>
<td>2</td>
</tr>
<tr>
<td>H. thomsoni</td>
<td>–</td>
<td>–</td>
<td>12</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>40</td>
<td>26</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Halimuraena hexagonata</td>
<td>–</td>
<td>–</td>
<td>8</td>
<td>9</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>11</td>
</tr>
<tr>
<td>H. shakai</td>
<td>1p</td>
<td>1,11 h</td>
<td>2</td>
<td>11</td>
<td>1</td>
<td>–</td>
<td>17</td>
<td>13</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Halimuroenoides isostigma</td>
<td>1w?</td>
<td>–</td>
<td>–</td>
<td>4</td>
<td>–</td>
<td>–</td>
<td>8</td>
<td>5</td>
<td>–</td>
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</tr>
<tr>
<td>Haliophis aethiopus</td>
<td>–</td>
<td>1 h</td>
<td>–</td>
<td>1</td>
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<td>–</td>
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<tr>
<td>H. guttatus</td>
<td>1w</td>
<td>2,6 h</td>
<td>24</td>
<td>105</td>
<td>2</td>
<td>6</td>
<td>30</td>
<td>132</td>
<td>2* sponge spicules</td>
<td>–</td>
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<tr>
<td>Natalichthys leptus</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<td>–</td>
<td>–</td>
<td>2</td>
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<tr>
<td>N. ori</td>
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<td>–</td>
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<td>2</td>
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<tr>
<td>N. sam</td>
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<tr>
<td>Rusichthys explicitus</td>
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<td>–</td>
<td>–</td>
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<td>3</td>
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<tr>
<td>R. plesiomorphous</td>
<td>1</td>
<td>40</td>
<td>–</td>
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</table>
comparison, *Plesiops* and *Belonepterygion* have recognizable stomachs with sharp bends, and *Acanthoclinus* has a bend apparently confined to a shorter portion of the posterior intestine in some species but substantially convoluted with two loops in *A. fuscus*. *Beliops xanthokrossos* has a straight gut with a substantial constriction that demarcates a short posterior intestine. *Acanthoplesiops* examined have a straight gut, which would serve as an additional synapomorphy with *Notograptus*. Pleated skin around the anus is found to a lesser degree in *Acanthoclinus* (Fig. 12B), and *Acanthoplesiops* has only slight anterior pleating. Such pleating does not occur in other acanthoclinines, *Plesiops* [*P. nigricans* (Rüppell), MPM 31314], *Steeneichthys* (*S. nattivatus* Allen, MPM SOL 98–32; *S. plesiopsus* Allen & Randall, WAM P30629.016) or other percoids [*e.g.* *Cephalopholis cyanostigma* (Valenciennes), MPM 31524; *Perca flavescens* (Mitchell), MPM 20093]. A reviewer pointed out what appears to be anal pleating in at least some *Ecsenius* (Springer, 1988: figs 22, 23), but this pleating is of very limited extent being only about 6% of head length compared with 30 + % of head length in *Notograptus*.

Diet of acanthoclinines other than *Notograptus* has been difficult to determine, as the guts of most specimens examined were empty (105 specimens of 141) (Table 2). Only *Acanthoclinus* and *Acanthoplesiops* had specimens with identifiable gut contents. Most *Acanthoclinus* contained unidentified crustaceans (16); remaining specimens contained various molluscs (four) and fishes (two). All of the few *Acanthoplesiops* with gut contents contained crustaceans (nine), with two of these having parts of alpheid shrimps. A further outgroup, the genus *Plesiops*, feeds mostly on small crustaceans, or parts of larger ones, and gastropods (64% crustaceans, 32% gastropods, 2% fishes, 1% pelecypods, 1% ophiuroid arms of 322 specimens with identifiable gut contents; 451 specimens had empty guts). In *Plesiops*, at least 20% of the gastropod shells contained hermit crabs, although most did not; some had opercula intact, and one gut contained an abalone, indicating that gastropods are a true portion of the diet. Overall, data are limited for plesiopids, but it appears that an alpheid diet is a specialization among derived acanthoclinines and is likely an autapomorphy of *Notograptus*.

Figure 11. X-radiographs of *Notograptus* sp., MPM 32586, showing whole alpheid shrimps in their guts. A, 73 mm SL, scale bar = 10 mm. B, Close-up of A, scale bar = 5 mm. C, 51 mm SL, scale bar = 5 mm, note claws of shrimp extend into buccal cavity.
Figure 12. Pleated anal region of A, *Notograptus* sp., USNM 173797, 148 mm SL; B, *Acanthoclinus fuscus*, MPM 32616, 190 mm SL; C, *Congrogadus subducens*, MPM 32613, 340 mm SL. Anterior to left. Note that pleated region in the *Notograptus* specimen is as large as the others’ despite being the smallest individual illustrated. Abbreviations: gp, genital papilla; a, anus; p, pleating; sr, first anal-fin element, spine in (A) and (B), ray in (C). Scale bar = 4 mm.
COMPARISON WITH CONGROGADINES: ADAPTIVE CONVERGENCE

The Congrogadinae, or eel blennies, and Notograptus share a long taxonomic history where they were regarded as potential relatives in the Blennioidae of Regan (1912) and Gosline (1968), or even the Trachinoidei (Nelson, 1984). Today, congrogadines are firmly ensconced as a derived subfamily among the Pseudochromidae by Godkin & Winterbottom (1985) with corroboration by Gill (1990), and any similarity between congrogadine and Notograptus specializations is undoubtedly a result of convergence, i.e. independent derivation from different pre-existing characters (Gill & Mooi, 1993).

Knowing this, their morphological convergence is quite extraordinary and the original hypotheses of close relationship of these taxa by Regan (1912) and Gosline (1968) are understandable. Along with the elongate body (cf. Figs 1 and 13), Gosline (1968: 45, 60) noted that both taxa have the anterior portion of the suspensorium only weakly connected to the posterior portion. However, the condition in each is clearly not homologous; in congrogadines the endopterygoid has a weak connection to the metapterygoid and no attachment to the ectopterygoid, whereas in Notograptus the loose connection is between the metapterygoid and hyomandibular (cf. Gill & Mooi, 1993: fig. 5 and Godkin & Winterbottom, 1985: fig. 6). In both, this convergence presumably permits the mouth to open widely to engulf large, whole prey. Both groups have reduced branchial elements, although to a higher degree in Notograptus. The gut of congrogadines is a straight tube except for a very small S-shaped bend just before the anus, very similar to the completely straight gut found in Notograptus. In addition, the anus and surrounding skin is pleated, presumably to permit wide expansion to ease excretion of large indigestible items (Fig. 12C). Anisochromines, the sister taxon of congrogadines, also show slight pleating around the anus that is otherwise absent in pseudochromids [e.g. Cypho purpurascens (De Vis), MPM 32315]. The remarkable convergence of derived and specialized morphology between congrogadines and Notograptus suggests that these are the result of adaptation through similar selective regimes, perhaps as evidenced through diet and behavioural data.

Data on congrogadine diets are scarce. Harmelin-Vivien (1979) reported that Haliophis guttatus of Madagascar is essentially a diurnal predator feeding primarily on shrimp (45% of diet) and brachyuran crabs (22% of diet), and secondarily on galatheid crabs, amphipods, fish eggs and hermit crabs. Only a few fishes were found in the 132 specimens examined. Maugé & Bardach (1985: 376; our translation) stated for Halimuraenoides isostigma that 'the stomach contents, visible in radiographs, chiefly are shrimps of the Alpheidae and very rarely fishes'. Our own observations of 830 congrogadine specimens using X-radiography (Table 2) indicate that most eat crustaceans (306 specimens), with stomatopods, penaeids and amphipods or isopods being the most common identifiable types (87 specimens). Evidence of alpheid shrimps was found in only 11 specimens (five whole shrimps in larger Congrogadus specimens, one whole shrimp in Haliophis guttatus, Fig. 14), although a further 208 specimens contained unidentified crustaceans. Some specimens, mostly larger Congrogadus subducens, contained fishes (40), many of which were well digested, ruling out rotenone collecting artefact. Molluscs were found only as incidental food items in five specimens, so are not generally a part of a normal congrogadine diet. One Natalichthys specimen contained what appeared to be a pycnogonid, and two Haliophis guttatus specimens had incidental sponge spicules ingested, suggesting foraging among sponges (Table 2). The diet of Rusichthys, sister to all other congrogadines (Winterbottom, 1986), is unknown. The sister group of congrogadines, the Anisochrominae, eat mostly crustaceans (shrimps, crabs, ostracods in 46 of 49 with identifiable stomach contents) and only rarely molluscs (three of 49) (Table 2).

Congrogadine morphology is well suited to a behaviour of engulfing large crustaceans from confined spaces such as burrows or narrow coral interstices. Such behaviour would likely be similar to that of Notograptus, which is inferred to involve entering alpheid shrimp burrows and eating the shrimp whole. The convergence of morphology and feeding specialization between Notograptus and basal congrogadines

Figure 13. Exemplar of the Congrogadinae, Congrogadus winterbottomi, WAM P.31582–001, 85.1 mm SL (holotype).
provides a pattern attributable to adaptation in the historical sense (Coddington, 1988; Larson & Losos, 1996). The feeding modes might have provided a common selective regime for convergence of morphology among these taxa.

Indeed, feeding behaviour of Notograptus and congrogadines might yet prove more similar than we have demonstrated here. Halimuraenoides isostigma, a basal member of the congrogadines (Winterbottom, 1986), is reported as eating mostly alpheids (Maugé & Bardach, 1985). If the diet of Rusichthys, the sister to remaining congrogadines, is found to be predominantly burrow-inhabiting alpheid shrimps, the case for convergent adaptation would be even more palatable. The congrogadine body form and other unique features would be an adaptation to this specialized diet, with a secondary broadening of food preference to other crustaceans and fishes as body size increases.

As noted by de Quieroz (1998), repeating phylogenetic patterns of morphology and behaviour might be consistent with an adaptive explanation, but alternative explanations are not falsified. For example, a straight gut might be strictly a function of being narrow-bodied, as perhaps a folded gut cannot be accommodated in the confines of an eel-like body. However, true eels (Anguilliformes) seem not to be so restricted, having a separate stomach overlying the intestine [e.g. Moringua edwardsi (Jordan & Bollman), MPM 24972; Gymnothorax moringa (Cuvier), MPM 30833]. Functional studies could be undertaken to examine the enlarged gape and whether or not reduced gill arches provide an advantage for eating large prey. We think that the loose connection in the suspensorium of congrogadines and Notograptus might function somewhat like the distensible jaws of snakes to permit the engulfing of large prey (and breaking the general rule of never eat anything larger than your head). However, if other examples of fishes with elongate body, large gape, reduced branchial arches, straight gut and stretchy anus can be correlated with eating alpheid shrimps or similarly hard-bodied, relatively large, burrow-inhabiting or otherwise confined prey, an even stronger case for convergent evolution and adaptation to a particular selective regime could be put forward.

ACKNOWLEDGEMENTS

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Figure 14. X-radiograph of Haliophis guttatus, SMF 29198, 62.5 mm SL. Note the whole alpheid shrimp in the gut.
commented on aspects of an earlier version of the manuscript. Special thanks are due to S. Raredon for X-raying hundreds of specimens. MPM and BMNH material of Notograptus was collected with the cooperation of B. Hutchins (WAM). We are grateful to D. F. Hoes for initially bringing to our attention that Notograptus is an alpheid shrimp predator. P. Hurst photographed the whole specimens in Figures 1 and 13. This work was supported, in part, by the United States National Science Foundation under grant no. DEB-9317695 to RDM.

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