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

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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: *Acanthoclinus* (*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.

ADDITIONAL KEYWORDS: adaptation – biology – classification – feeding behaviour – myology – osteology – phylogeny.

> '. . . 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 Blennioidei (e.g. Jordan, 1923; de Beaufort, 1951; Greenwood *et al.*, 1966; Norman, 1966; see review by Gill & Mooi, 1993). However, in addition to

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Figure 1. *Notograptus* sp., BMNH 2002.1.2.1–2, 100.5 mm SL. Scale bar = 50 mm.

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

Greenwood *et al*. (1966: 401) included the Notograptidae in the Blennioidei, listing without comment the Stichariidae (classified in the clinid subfamily Ophiclininae by George & Springer, 1980) as a synonym.

Gosline (1968: 60), following the lead of Regan (1912), suggested a relationship of notograptids to congrogadids and less certainly to peronedyids [sic], placing the three taxa in his blennioid superfamily Congrogadoidae. However, Godkin & Winterbottom (1985) provided evidence for the inclusion of the Congrogadidae as a subfamily of the percoid Pseudochromidae, and George & Springer (1980) assigned peronedysids to the blennioid clinid tribe Ophiclinini. Nelson (1984), without evidence, placed notograptids among the trachinoids; Mooi & Johnson (1997) provided arguments to dismantle the Trachinoidei, making inclusion of the notograptids in this unnatural 'group' uninformative.

Gill & Mooi (1993) listed apomorphic features of *Notograptus* and considered its phylogenetic position. We noted that it shared numerous features with other elongate perciforms (in particular, elongate blennioids, zoarcoids, 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 spinous 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 *Notograptus* 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 *Notograptus* 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 *Notograptus* has its closest relatives among acanthoclinine plesiopids. Lastly, we suggest that the convergence in morphology of *Notograptus* 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 *Notograptus* and, having only external characters available for analysis, would introduce a series of unknowns to the data table.

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 possible effect of these codings on the position of *Notograptus* was also examined by deleting the characters inapplicable to *Notograptus* and repeating the analysis. Additionally, the analysis was repeated with the removal of all inapplicable and unknown states in the matrix by deleting all inapplicable characters (1, 2, 15, 33, 41, 43, 49, 59), deletion of the two taxa with most unexamined (unknown) states (*Beliops batanensis* Smith-Vaniz & Johnson and *Acanthoclinus psilogaster* Hardy), along with elimination 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) specimens as noted above. Occasionally, ethanol-preserved (EtOH) specimens were dissected.

Institutional abbreviations follow Leviton *et al.* (1985).

NOTOGRAPTUS

(16 lots, 99 specimens: 44–178 mm SL): AMNH 216034, 100.5 mm, North West Cape, Western Australia, 3 April 1969; ANSP 109653, 11: 63–105 mm (EtOH, X-ray), 4: 70–90 mm (CS), Little Hope Is., Queensland, 17 January 1969; ANSP 109654, 38 mm

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

		1	11111	11112	22222	22223	33333	33334	44444	44445	55555	5555
Character number	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	6789
Outgroup	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	0000
Trachinops	11111	11100	00000	00000	00000	10000	00001	00000	00000	00000	00000	0000
Assessor	11111	11111	10000	00000	00000	00000	00001	00000	00000	00000	00000	0000
Paraplesiops	11111	11111	11111	11000	00000	00000	00000	00000	00000	00000	00000	0000
Calloplesiops	11111	11111	11110	01111	00000	00000	00000	00000	00000	00000	00000	0000
Steeneichthys	11111	11112	21111	11111	00001	01000	33n01	01200	00000	00100	00000	0000
Fraudella	11111	11111	11111	00000	11100	00000	00000	00000	00000	00000	00000	0000
Plesiops	11111	11112	11111	10000	11111	11000	00000	00000	00000	00000	00000	0000
Acanthoclinus fuscus	11221	11112	1111n	10110	11111	10111	11100	01000	00000	10000	00000	0010
A. littoreus	11221	11112	1111n	10110	11111	10111	11100	00000	00000	10000	00000	0010
A. rua	112?1	11112	1111n	10110	111?1	10111	11100	00100	00000	00000	00000	0000
A. marilynae	112?1	1111?	1111n	10110	111?1	10111	11100	00000	00000	00000	00000	0000
A. matti	11221	11112	1111n	10110	11111	10111	11100	00000	00000	00000	00000	0000
Belonepterygion	11221	11112	1111n	10110	11111	10111	10011	11100	00000	00000	00000	0001
Beliops xanthokrossos	112?1	1101?	1111n	10120	001?1	00111	00010	11111	11111	11000	00000	0000
Beliops batanensis	??2?1	?10??	1???n	00120	?????	10111	00011	11111	11111	11000	00000	0000
Notograptus	nn221	00011	2101n	00130	00001	10111	22011	11102	n1n00	111n1	10100	001n
Acanthoplesiops indicus	11221	1101?	1111n	10120	001?0	10111	23n11	11111	11000	00111	11111	1101
A. hiatti	11221	1101?	1111n	10120	001?0	10111	23n11	11111	11000	01111	11111	1101
A. psilogaster	?????	?10??	11??n	1?12?	?????	??111	23n11	01211	11000	00111	11111	1101
A. echinatus	??221	01012	11?1n	10120	00110	10111	23n11	01211	11000	00111	11111	1101

(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), Groote Eylandt, Northern Territory, 19–25 April 1948; USNM 173797, 6: 45–178 mm (EtOH, X-ray), Groote 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 325199, 14: 68–101 mm (EtOH, X-ray), Darwin, Northern Territory, 18–19 February 1988.

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).

Beliops xanthokrossos Hardy: ANSP 165557, 2: 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.

Paraplesiops poweri Ogilby: MPM 40288, 50.0 mm (EtOH).

Plesiops coeruleolineatus Rüppell: MPM SOL 98–20, 46.5 mm (EtOH).

Trachinops taeniatus Günther: MPM 40291, 48.0 mm (EtOH).

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 2001.3.8.2, 23.3 mm (paratype, CS); BPBM 16277, 13.3 mm (paratype); MNHN 2001–494, 24.1 mm (paratype); SMNS 20933, 2: 19.7–25.5 mm (paratypes); SMNS 21025, 4: 19.7–25.2 mm (partypes); SMNS 23037, 23.9 mm (holotype); USNM 364534, 19.6 mm (paratypes).

A. straussi Springer, Smith & Fraser (9 lots, 82 specimens: 16.1–28.3 mm SL): AMNH 35892, 6: 22.0–28.0 mm SL (paratypes); 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).

Blennodesmus scapularis Günther (15 lots, 120 specimens: 28.5–87 mm SL): AMS IA. 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: 57–87; 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 43212?, 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 hierichthys Jordan & Richardson (9 lots, 30 specimens: 50–159 mm SL): BMNH 1933.3.11 : 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 358035, 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 SOSC ref. 4, 40: 30–82 mm; USNM SOSC acc. no. 23, 30: 29–90 mm; USNM Cruise 4–8, 5: 66–75 mm; ZMUC P.75396–98, 3: 60–134 mm (paratypes).

Halimuraena hexagonata Smith (5 lots, 28 specimens: 22.5–60 mm SL): RUSI 863, 10: 45–60 mm; RUSI 4019, 4: 32.5–45 mm; RUSI 5326, 4: 22.4–33.5 mm; RUSI 5402, 5: 28.2–31.9 mm; USNM SOSC 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.

Halimuraenoides isostigma Maugé & Bardach (3 lots, 18 specimens: 65–242 mm): MNHN 1985–240, 242 mm (holotype); MNHN 1985–241, 15: 65–278 mm (paratypes); ROM 46134, 2: 78–117 mm (paratypes).

Haliophis aethiopus Winterbottom (2 lots, 2 specimens: 49–50 mm SL): BPBM 20920, 49 mm (holotype); ROM 38419, 50 mm (paratype).

H. guttatus (Forsskål) (38 lots, 308 specimens: 20.7–132 mm SL): BMNH 1951.1.16 : 606–608, 2: 48.6–66 mm; BMNH 1960.3.15 : 1591–1603, 13: 44–100 mm; BPBM 18361, 4: 65–132 mm; BPBM 19883, 4: 36–88 mm; BPBM 22600, 3: 34–50; LACM 30859–

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 5858, 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 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 plesiopids 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). Posterior 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 I,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*). Parasphenoid keel: absent (state 0); present (state 1). *Notograptus* lacks a parasphenoid 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.

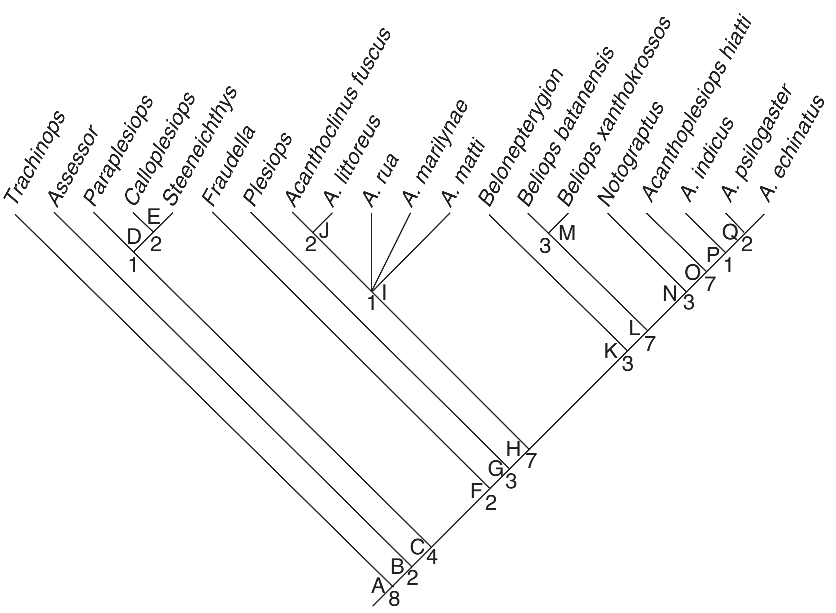

Figure 2. Strict consensus cladogram from two equally parsimonious trees from a branch-and-bound search using composite coding of the data set in Table 1 (no. of steps = 123; CI = 0.642; RC = 0.547; RI = 0.852). Nodes are lettered as in the text. Characters supporting each node, those without homoplasy 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.

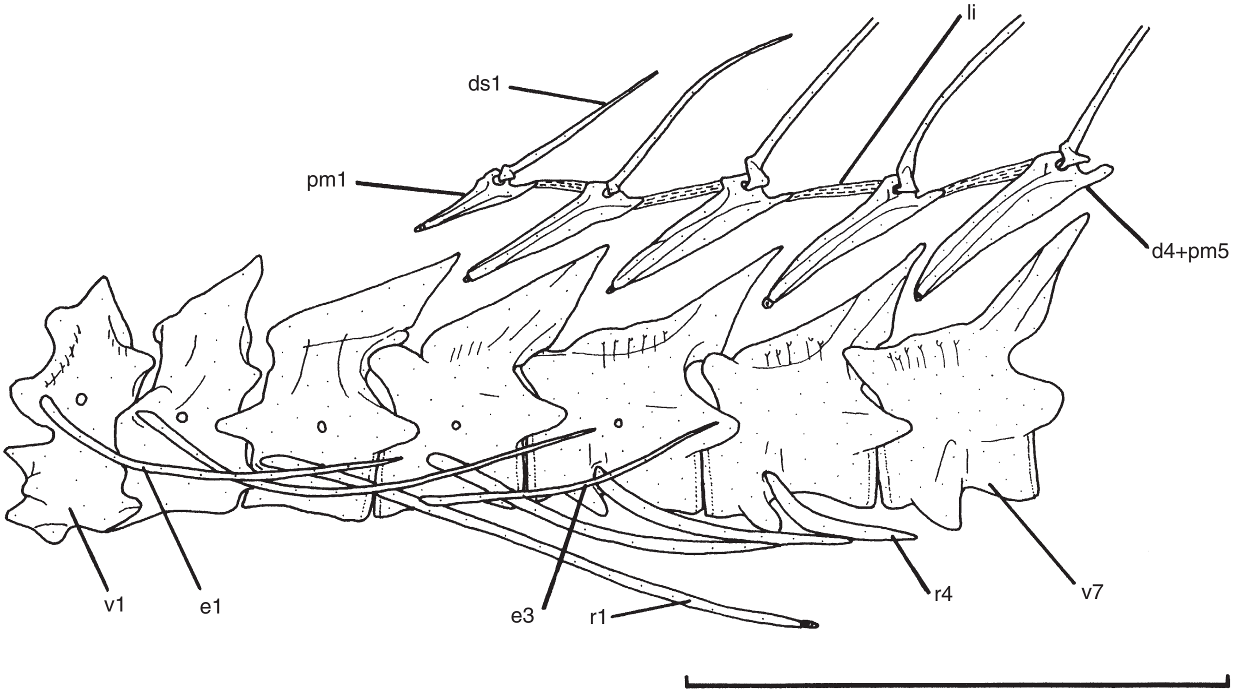

Figure 3. *Notograptus* sp., BMNH 2002.1.19.16, 128.5 mm SL, first seven vertebrae and associated dorsal-fin structures in left lateral view. Abbreviations: d4 + pm5, fourth distal radial fused with fifth proximal and middle radials; ds1, first dorsal spine; e1, first epineural; e3, third epineural; 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 acanthoclinines 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 acanthoclinine, 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. 3).

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 *Calloplesiops*). 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 acanthoclinines.

Character 16 (RDM 15; node C, reversals in *Calloplesiops, 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 *Calloplesiops* 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

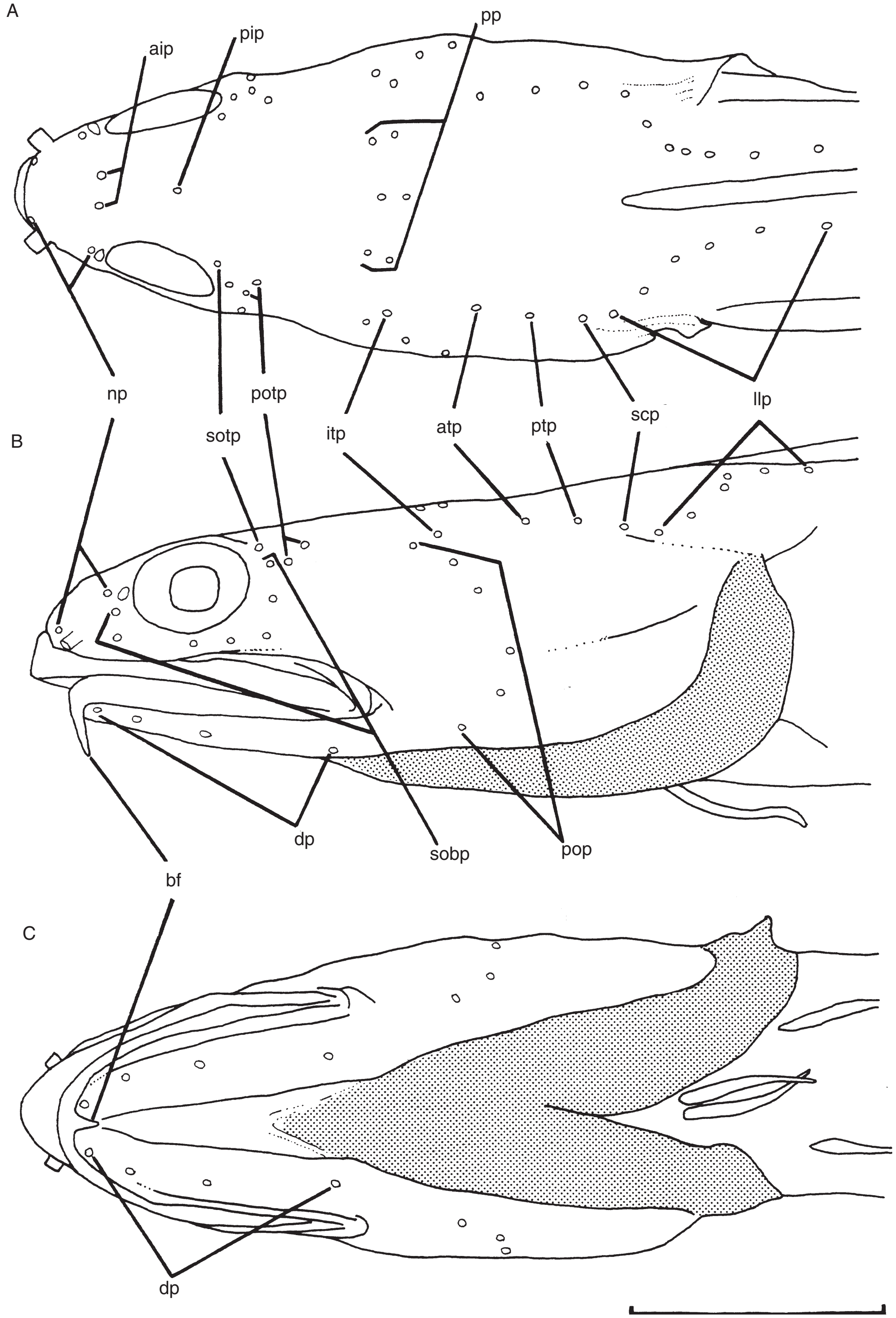

Figure 4. *Notograptus* sp., BMNH 2002.1.2.1–2, 100.5 mm SL, dorsal, left lateral and ventral views of head. Mechanical stippling is branchiostegal membranes. *Abbreviations*: aip, anterior interorbital pores; atp, anterior temporal pore; bf, barbel-like flap; dp, dentary pores; itp, intertemporal pore; 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; sotp, supraotic pore. Scale bar = 5 mm.

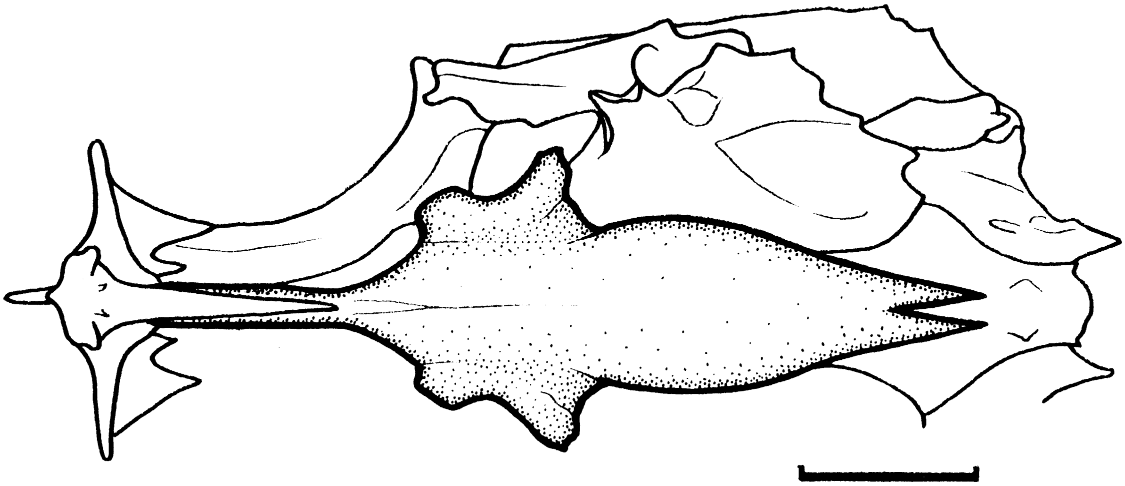

Figure 5. *Notograptus* sp., ANSP 109653, 63 mm SL, ventral view of parasphenoid. Anterior to left. Parasphenoid stippled. Scale bar = 1 mm.

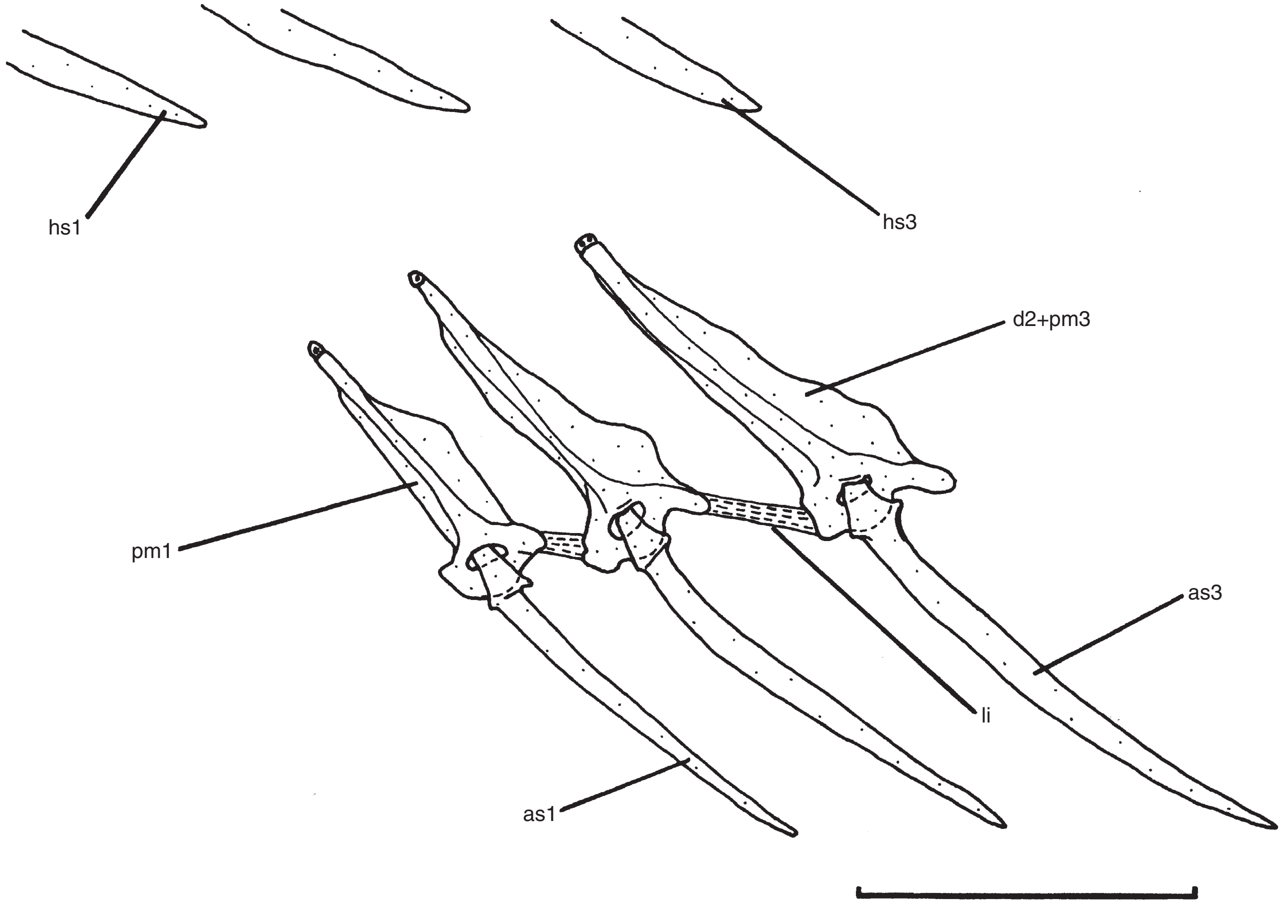

Figure 6. *Notograptus* sp., BMNH 2002.1.19.16, 128.5 mm SL, first three anal-fin spines and their pterygiophores in left lateral view. *Abbreviations:* as1, first anal spine; as3, third anal spine; d2 + pm3, second distal radial fused to third proximal and middle radials; hs1, first haemal spine; hs3, 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 plesiopids. 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-*

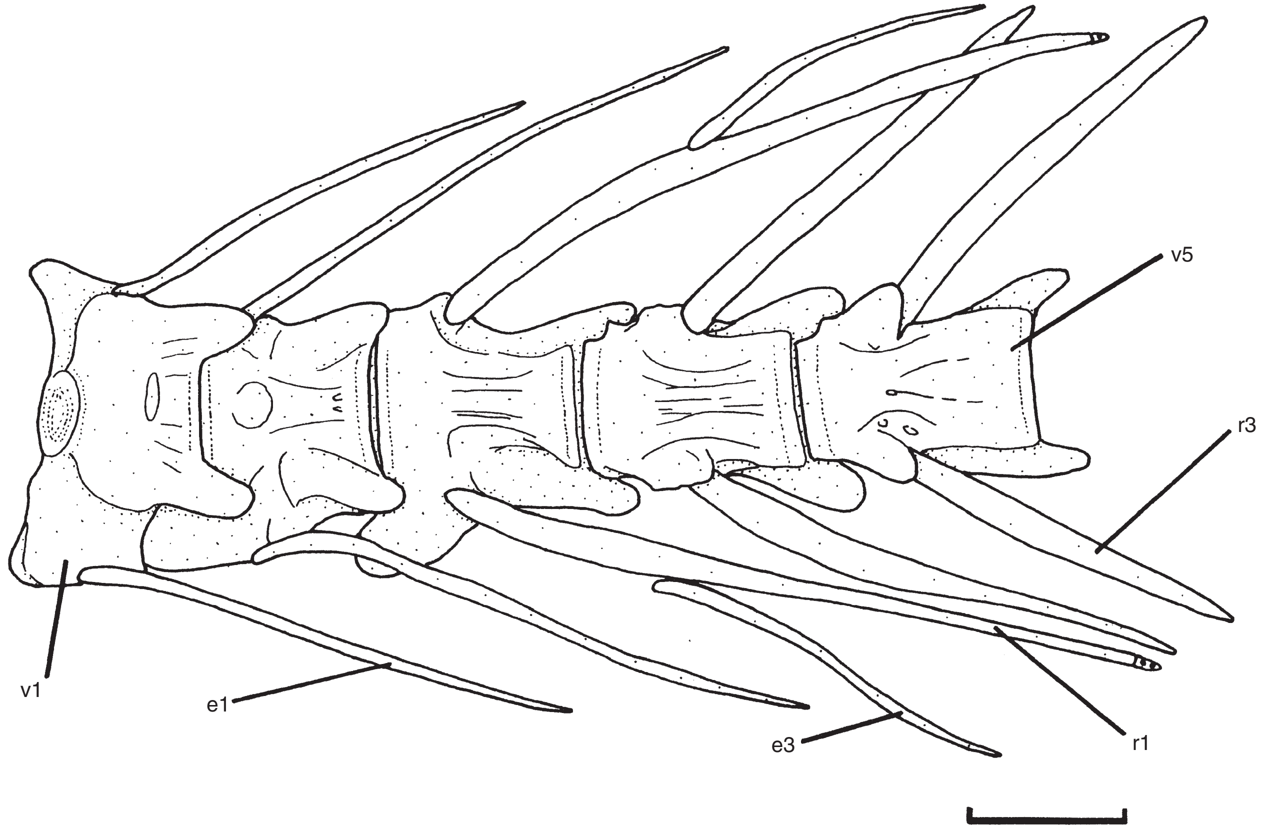

Figure 7. *Notograptus* sp., BMNH 2002.1.19.16, 128.5 mm SL, first five vertebrae in ventral view. *Abbreviations:* e1, first epineural; e3, third epineural; r1, first rib; r3, third rib; v1, first vertebra; v5, fifth vertebra. Scale bar = 1 mm.

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). The first neural spine is joined to its centrum in *Notograptus* (Fig. 3).

Character 43 (SVJ 21, fig. 15; node M). Interarcual cartilage shape: rod-shaped (state 0); cone-shaped (1). As noted under Character 40, *Notograptus* lacks an interarcual cartilage (Gill & Mooi, 1993: 338, fig. 9), and interarcual morphology characters are inapplicable (n).

Character 44 (SVJ 22, fig. 16; node M). Metapterygoid-quadrate 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* has a smooth joint between the scapula and the coracoid (Gill & Mooi, 1993: fig. 10).

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). This character exhibits considerable homoplasy among acanthoclinines, however.

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 *Beliops* species 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-Vaniz & 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-Vaniz & 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 acanthoclinines.

Character 59 (SVJ 38, fig. 22; node O, independent acquisition in *Belonepterygion*). Adductor mandibulae A_2 section: laterally exposed (state 0); covered by A_1 laterally (state 1). The adductor mandibulae of *Notograptus* is modified, lacking distinct A_1 and A_2 sections (Gill & Mooi, 1993: 338, fig. 8); this character was therefore considered inapplicable (n) for *Notograptus* and uninformative regarding its phylogenetic position among acanthoclinines.

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 perciform 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 acanthoclinine 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. cephalotaenia*, *P. corallicola*, *P. coeruleolineatus*, *P. oxycephalus*; 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 acanthoclinine 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; CI = 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 acanthoclinines *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; CI = 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 acanthoclinine.

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 autapomorphic 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*, *Acanthoplesiops*; 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 *Acanthoplesiops* (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 vertebrae 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 *Acanthoplesiops* based on four characters: presence of a symphyseal 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 *Acanthoplesiops*, although this is a relatively labile feature exhibiting several states for which homology is difficult to determine. As we note below, *Notograptus* and *Acanthoplesiops* 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 pelvicus to both segmented rays (10, state 1), dorsally positioned zygapophysis (13), dorsal fin membranes not incised (16), posterior sphenotic spur absent (23), abductor superficialis pelvicus overlies the arrector ventralis pelvicus (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,

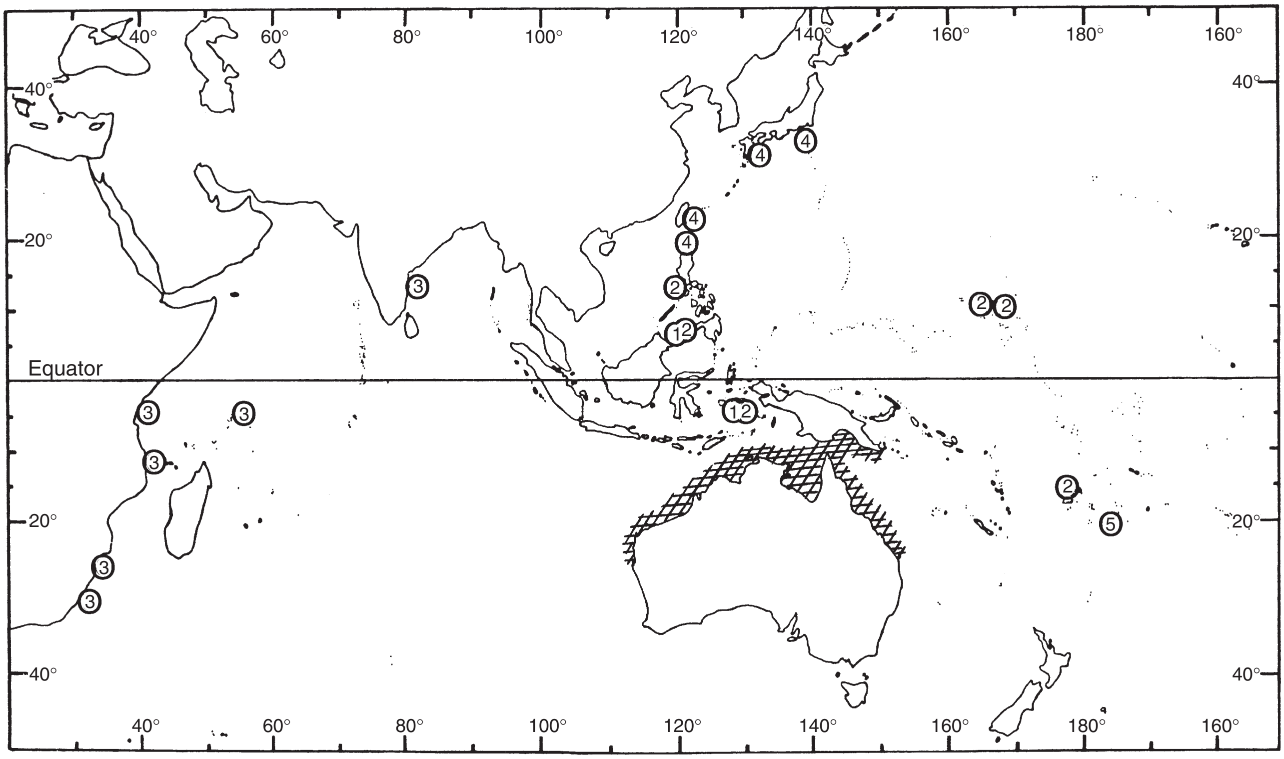

Figure 8. Distribution of *Notograptus* (hatching) and *Acanthoplesiops* (1: *A. echinatus*; 2: *A. hiatti*; 3: *A. indicus*; 4: *A. psilogaster*; 5: *A. naka*).

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).

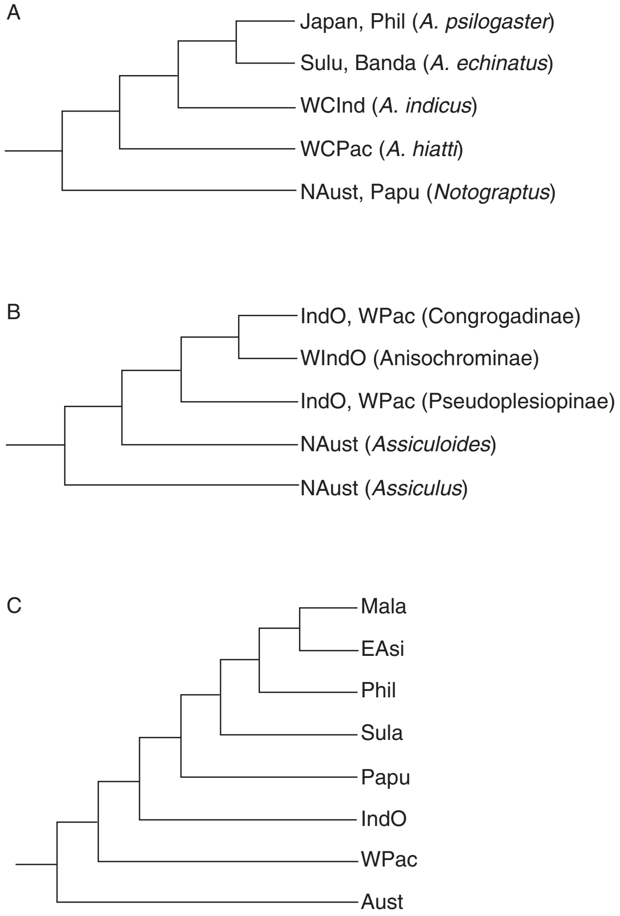

Figure 9. Area/taxon cladograms of A, *Notograptus* + *Acanthoplesiops*; B, derived Pseudochromidae; C, marine water striders (after Andersen, 1998: fig. 7e).

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) + (*Chlidichthys* + *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 *Assiculus* (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, Dinolestidae, Leptobramidae, Enoplosidae, Arripidae, Odacidae, Leptoscopidae) and genera (e.g. certain aplodactylids, gobiesocids, clinids, monacanthids, antenariids, gobiids, syngnathids 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

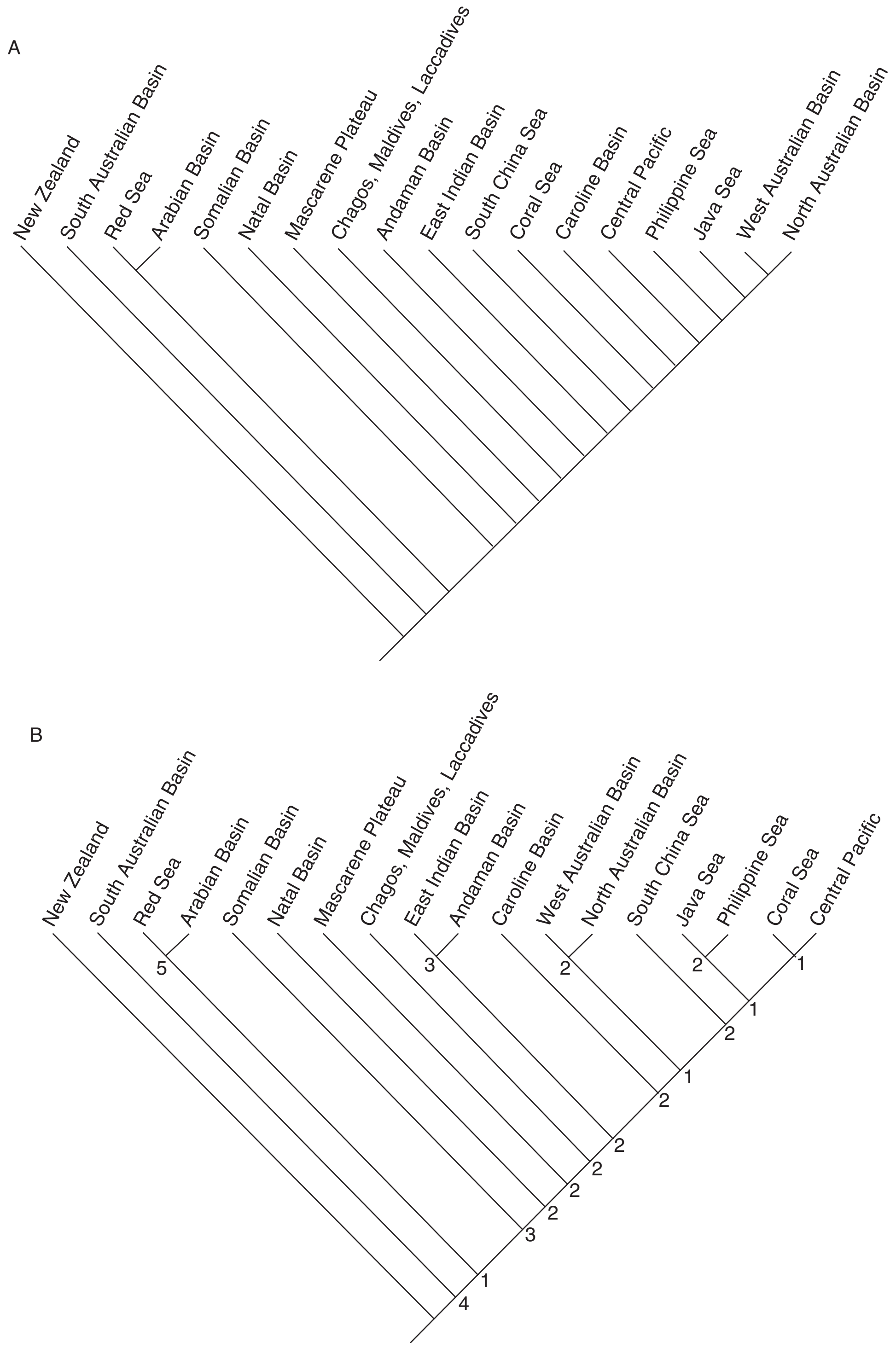

Figure 10. Area cladogram of the Indo-Pacific determined from a combined data set of 13 cladograms using Brooks Parsimony Analysis (A) after Santini & Winterbottom (2002); (B) with *Plesiops* and acanthoclinine data corrected, single most parsimonious tree from a branch-and-bound search (no. of steps = 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 acanthoclinine 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 gobiid 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, knobbly 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

Species *N* : size range	Alpheids whole (w), parts (p)	Stomatopods (s) or shrimps (h)	Amphi/Isopods	UnID Crust.	Digested fish	Undigested fish	UnID	Empty	Other (*incidental)
Notograptus 99 : 44–178	18w, 13p	–	–	2	–	1 (gobiid with scales)	–	65	–
Acanthoclinus fuscus 68 : 28–220	–	–	–	11	–	2 (1 with 3 tripterygiids)	5	48	1 snail, 1 limpet
A. littoreus 7 : 56–119	–	–	–	4	–	–	–	2	1 mollusc
A. marilynae 2 : 90–95	–	–	–	1	–	–	–	–	1 snail
A. matti 1 : 52	–	–	–	–	–	–	–	1	–
Acanthoplesiops echinatus 1 : 21	1p	–	–	–	–	–	–	–	–
A. hiatti 9 : 15–20	–	–	–	6	–	–	–	3	–
A. indicus 4 : 19–27	1p	–	–	1	–	–	–	2	–
Acanthoplesiops naka 1 : 9.9	–	–	–	–	–	–	–	1	–
A. psilogaster 4 : 12–22	–	–	–	–	–	–	–	4	–
Beliops xanthokrossos 1 : 26	–	–	–	–	–	–	–	1	–
Belonepterygion fasciolatum- 43 : 12–42	–	–	–	–	–	–	–	43	–
Anisochromis kenyae 46 : 13.8–25.6	2?	1 s	–	9	–	–	2	28	3 ostracods 1 crab
A. mascarenensis 11 : 13.3–25.5	–	1 h	–	6	–	–	–	3	1 ostracods
A. straussi 82 : 16.1–28.3	–	3 s,2 h	1i	15	–	–	11	46	3 gastropods 1 ostracod
Blennodesmus scapularis 120 : 28.5–87	2p	2 s,2 h	2a	10	–	–	24	78	1* mollusc
Congrogadus hierichthys 30 : 50–159	1p	1 h	1	5	1	–	4	17	–

Congrogadus malayanus 12 : 31–70	–	–	–	3	–	–	8	1	–
C. spinifer 33 : 36–121	1w	3 s,2 h	–	10	–	–	2	15	3* small snails
C. subducens 75 : 31–340	4w	1 s,1 h	–	10	28 (a few of these with undigested fish, but often mixed with digested; 3 with Crustacea; 8 with 2–3 fish)	2	29	–	–
C. winterbottomi 31 : 66.1–119	–	5 h	12a	2	–	–	3	8	1 mollusc
Halidesmus polytretus 2 : 57–57.3	–	–	–	2	–	–	–	–	–
H. scapularis 20 : 46–98	–	–	–	20 (some might be shrimps)	–	–	–	–	–
H. socotraensis 6 : 39.6–69.5	–	–	–	4	–	–	–	2	–
H. thomaseni 78 : 29–134	–	–	–	12	–	–	40	26	–
Halimuraena hexagonata 28 : 22–60	–	–	8	9	–	–	–	11	–
H. shakai 57 : 22–55	1p	1 s,11 h	2	11	1	–	17	13	–
Halimuraenoides isostigma 18 : 65–278	1w?	–	–	4	–	–	8	5	–
Haliophis aethiopus 2 : 49–50	–	1 h	–	1	–	–	–	–	–
H. guttatus 308 : 21–132	1w	2 s,6 h	24	105	2	6	30	132	2* sponge spicules
Natalichthys leptus 2 : 52–56	–	–	–	–	–	–	–	2	–
N. ori 2 : 54–60.5	–	–	–	–	–	–	–	2	–
N. sam 2 : 40–43	–	–	–	–	–	–	–	1	1 pycnogonid?
Rusichthys explicitus 3 : 40–52	–	–	–	–	–	–	–	3	–
R. plesiomorphus 1 : 40	–	–	–	–	–	–	–	1	–

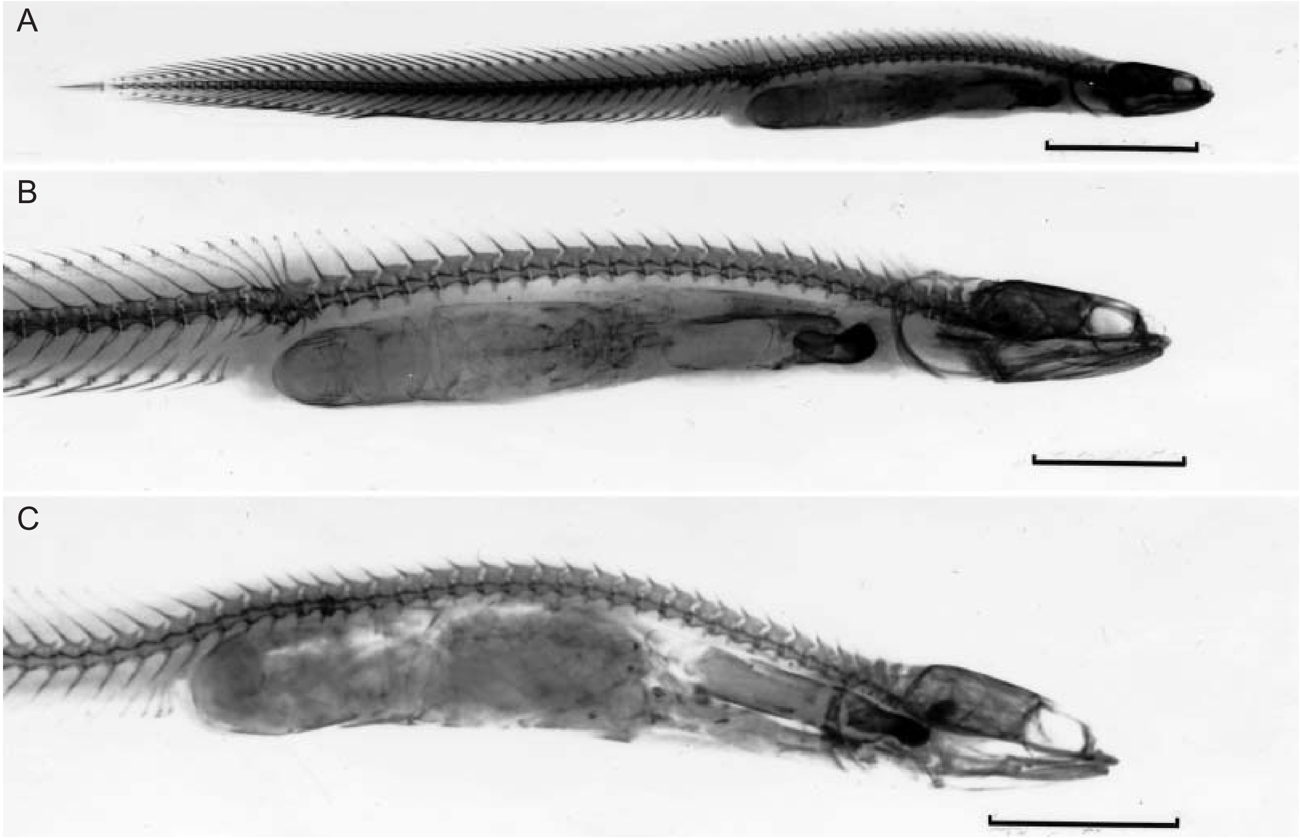

Figure 11. X-radiographs of *Notograptus* sp., MPM 32586, showing whole alpheid shrimps in their guts. A, 73 mm SL, scale bar = 10 mm. B, Close-up of A, scale bar = 5 mm. C, 51 mm SL, scale bar = 5 mm, note claws of shrimp extend into buccal cavity.

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. nativitatus* Allen, MPM SOL 98–32; *S. plesiopsus* Allen & Randall, WAM P30629.016) or other percoids [e.g. *Cephalopholis cyanostigma* (Valenciennes), MPM 31524; *Perca flavescens* (Mitchill), 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*.

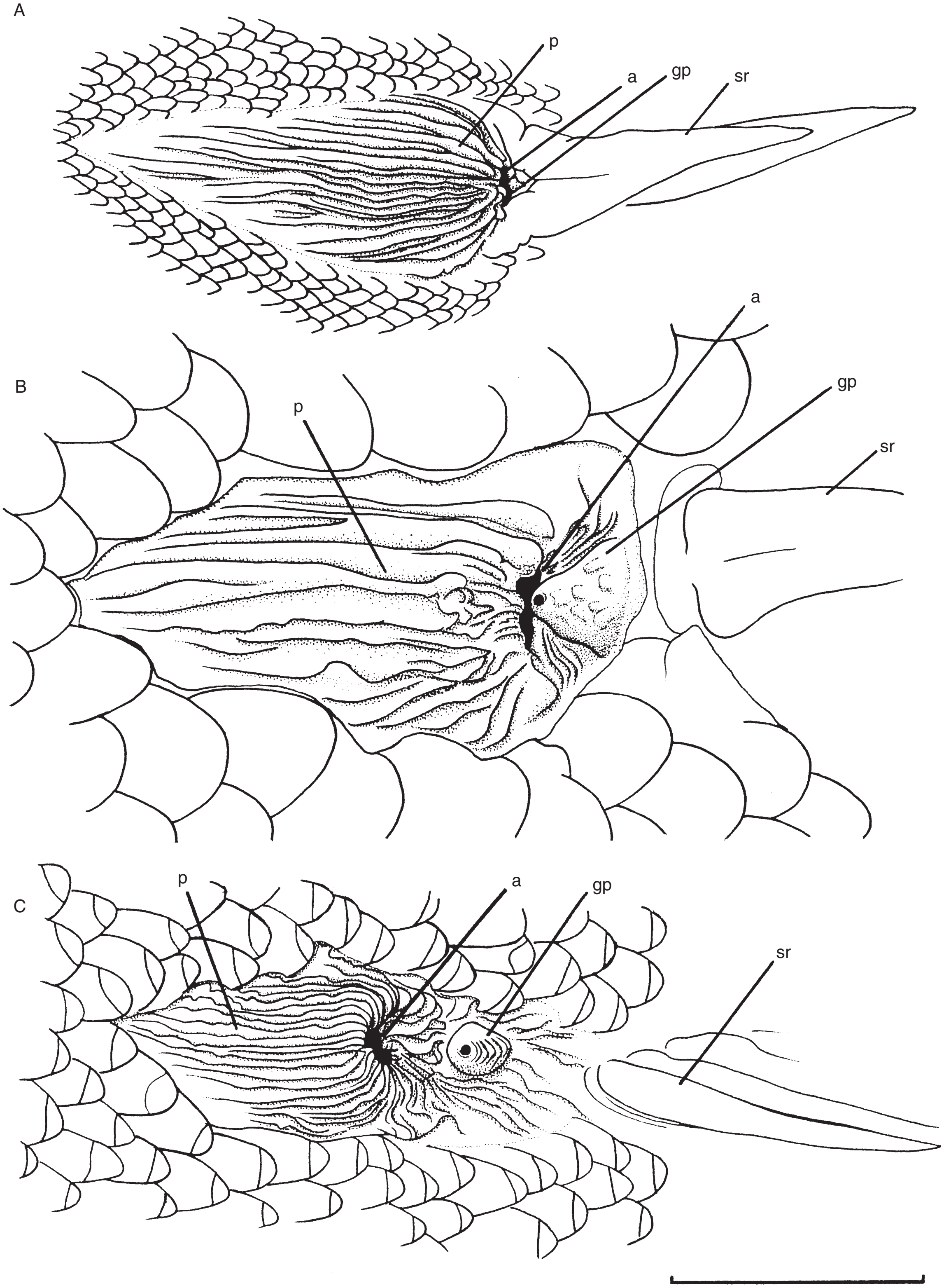

Figure 12. Pleated anal region of A, *Notograptus* sp., USNM 173797, 148 mm SL; B, *Acanthoclinus fuscus*, MPM 32616, 190 mm SL; C, *Congrogadus subducens*, MPM 32613, 340 mm SL. Anterior to left. Note that pleated region in the *Notograptus* specimen is as large as the others' despite being the smallest 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 Blennioidei 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

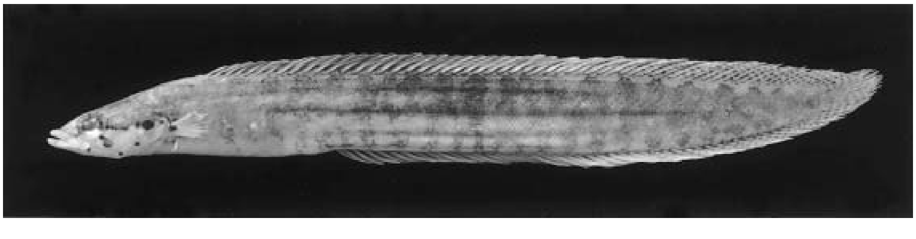

Figure 13. Exemplar of the Congrogadinae, *Congrogadus winterbottomi*, WAM P.31582–001, 85.1 mm SL (holotype).

Figure 14. X-radiograph of *Haliophis guttatus*, SMF 29198, 62.5 mm SL. Note the whole alpheid shrimp in the gut.

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.

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