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Larvae of *Enchelyurus ater* (Günther, 1877) and *E. kraussi* (Klunzinger, 1871) (Pisces: Blenniidae: Omobranchini)

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ABSTRACT The omobranchinin blenniid, *Enchelyurus ater*, ranges across the islands of the south Pacific Ocean, and *E. kraussi* ranges from the Red Sea to the Mariana Islands and eastern Australia. The planktonic larvae of these blennies were identified by establishing developmental series up to large larvae identifiable to species using morphological and meristic characters and geographic location. Larvae of both species are similar in appearance, hatch at about 1.5–2.5 mm length, and undergo notochord flexion at about 4.5–5.5 mm. *Enchelyurus ater* probably is near 12 mm, and *E. kraussi* probably nearer 15 mm, at settlement from the plankton. Larvae of both species have a rounded head, a short, coiled gut, an elongate, compressed tail, and about 34 myomeres. Small spines are present on the posterior preopercular margin at, or soon after, hatching. The spine at the preopercular angle becomes largest, reaching about 25% of head length in the postflexion stage. First the pectoral-fin rays, then principal caudal-fin rays, dorsal- and anal-fin anlagen, and pelvic-fin buds begin to form during the preflexion stage. All principal caudal rays are present by the end of the flexion stage. Pelvic-fin rays and all segmented dorsal- and anal-fin rays are present by mid-postflexion stage. Dorsal-fin spines and procurrent caudal-fin rays form during the postflexion stage. Larvae of both species initially are pigmented dorsally on the head and gut, posteriorly on the ventral margin of the tail, and on the mesial surface of the pectoral-fin base. Pigmentation gradually increases on the head and gut in both and on the pectoral fin in *E. kraussi*, and decreases on the ventral margin of the tail in both.

Enchelyurus ater, E. kraussi, and the Hawaiian endemic, *E. brunneolus*, are a monophyletic group with unknown sister-species relationships. Larval characters suggest the hypothesis that *E. ater* is the sister species to *E. brunneolus*, and *E. kraussi* is the sister species to the other two.

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The blenniid genus *Enchelyurus* (tribe Omobranchini) comprises five species of small, demersal, Indo-Pacific nearshore reef fishes. Based primarily on similarities in dentition and colour pattern, Springer (1972) considered three of these, *Enchelyurus ater* (Günther, 1877), *E. brunneolus* (Jenkins, 1903), and *E. kraussi* (Klunzinger, 1871), to be a monophyletic group, but he was unable to determine sister-species relationships among them

(Springer, 1982). *Enchelyurus kraussi*, apparently a species complex (V.G. Springer, pers. comm., August 1999), occurs in the Red Sea, the Gulf of Aqaba, the Indian Ocean, and the western Pacific Ocean as far north as Okinawa and east to the Mariana Islands, New Guinea, and Australia (Springer, 1982). *Enchelyurus ater* ranges throughout the oceanic islands south of the equator from Lord Howe Island and New Caledonia to the Tuamotu Archipelago (Springer, 1982). *Enchelyurus brunneolus* is endemic to the Hawaiian Islands (Springer, 1982), and thus is geographically remote from its nearest relatives.

Larval development of *E. brunneolus* was described by Watson (1987) and a transforming larva of *E. kraussi* was described by Kubo & Sasaki (2000). Nearly complete developmental series have been assembled for *E. ater* from the Tuamotu Archipelago, and for *E. kraussi* from eastern Australia, affording an opportunity to provide descriptions of the larval development of these species. In addition to the descriptions of larval development of *E. ater* and *E. kraussi*, the contribution of larval development to the interpretation of sister-species relationships in the *E. ater-brunneolus-kraussi* group is briefly considered.

Materials and methods

All specimens of *E. ater* were collected in February 1989 with an 83.5 cm mouth diameter, 0.5 mm mesh ring net towed in the upper 10 m of the water column (e.g., Leis *et al*., 1991) of Rangiroa (c. 15°02'S 147°45'W), Takapoto (c. 14°36'S 145°12'W) and Takaroa (c. 14°20'S 145°W) lagoons, in the Tuamotu Archipelago, French Polynesia. Specimens of *E. kraussi* were collected with a variety of plankton samplers at various times in the 1980s at various eastern Australian locations, primarily from the vicinities of Lizard Island (14°41'S 145°27'E) and One Tree Reef (c. 28°30'S 152°05'E) on the Great Barrier Reef (Leis & Goldman, 1983; Schmitt, 1984), and from Lake Macquarie (c. 33°S 151°30'E) (Miskiewicz, 1987) and the northern coast of New South Wales (c. 29°S 154°E). Larvae generally were fixed in the field in 5–10% seawater formalin and stored in 2.5–5% formalin or 70% ethanol.

Descriptions are based on 101 *E. ater* (2.3–11.4 mm; recently hatched preflexion through late postflexion stages) and 25 *E. kraussi* (1.6–14.5 mm; recently hatched preflexion through late postflexion stages). All specimens were measured to the nearest 0.04 or 0.08 mm at 25× or 12×, respectively, depending on specimen size, using a Wild M-5 binocular microscope with an ocular micrometer. Dimensions measured included body length (BL), preanal length (PAL), body depth (BD), head length (HL), head width (HW), snout length (SnL), eye diameter (ED), length of spine at angle of posterior preopercular margin (PrSL), and lengths of pectoral (P1L) and pelvic (P2L) fins. These dimensions, as well as developmental states and body parts referred to in the descriptions, are defined by Moser (1996) and Leis & Carson-Ewart (2000). In the following descriptions references to larval length always refer to BL of preserved larvae, and descriptions of pigmentation refer solely to melanistic pigment. Size series of 17 *E. ater* and 15 *E. kraussi* were lightly stained with alizarin red-S to aid in determining the sequence of fin development. Illustrations were made with the Wild M-5 microscope equipped with a camera lucida.

Identification. Larvae were identified by the series method. Late preflexion through late postflexion stage larvae were readily recognizable as belonging to the blenniid tribe Omobranchini on the basis of several meristic and morphological characters, especially head spination (e.g., Watson, 1983), and as *Enchelyurus* by their close resemblance to *E. brunneolus* (Watson, 1987). Briefly, larval *Enchelyurus* may be recognized by having a moderately broad head with short, rounded snout; a short, moderately broad gut (PAL usually c. 35–40% BL); a compressed tail; 33–36 myomeres; 13–16 (usually 14–15) pectoral-fin rays and VI–X (usually VII–IX) dorsal-fin spines; up to 6–7 preopercular spines, with the spine at the angle becoming longest by late preflexion stage (maximum length c. 25% HL, attained early in the postflexion stage); ornamentation (small prickles diminishing to low ripples and bumps) on the frontal, parietal, preopercular, articular and dentary bones; dorsal- and anal-fin pterygiophores lacking distal blades; and pigmentation primarily dorsally on the head and gut and on the ventral margin of the posterior half of the tail, with little or no pigment on the pectoral fins except commonly some on the pectoral-fin bases. *Enchelyurus ater* is the only *Enchelyurus* species (and the only representative of Omobranchini) known from the Tuamotu Archipelago, and myomere and fin-ray counts from the larger larvae from that location matched the vertebral and fin-ray counts of *E. ater* (e.g., Springer, 1972). Likewise, *E. kraussi* is the only *Enchelyurus* species reported from eastern Australia. At least seven other species of Omobranchini occur there as well, but all can be distinguished from *Enchelyurus* by meristic characters, for example by having more dorsal-fin spines and fewer pectoral-fin rays than *Enchelyurus* (e.g., Springer, 1972; Springer & Gomon, 1975). In addition, larval *Omobranchus* typically have a larger spine at the preopercular angle and more pigment on the pectoral fins and ventral margin of the tail, compared with *Enchelyurus*. Several *Omobranchus* species have prominent distal blades on the dorsal- and anal-fin pterygiophores (e.g., Watson & Miskiewicz, 1998; Kawaguchi *et al*., 1999), lacking in *Enchelyurus*. Fin-ray and myomere counts from the larger eastern Australian *Enchelyurus* larvae matched the fin-ray and vertebral counts of eastern Australian *E. kraussi* (e.g., Springer, 1972).

Material examined. All specimens of *E. ater* and *E. kraussi* are deposited in the Ichthyology Collection, Australian Museum, Sydney (AMS I). In the following list, the registration number is given first (first five digits—station number, last three digits—lot number), followed in parentheses by the number and size range of specimens.

Enchelyurus ater (Günther, 1877). AMS I.29054-001 (3: 3.2–3.4 mm); I.29055-001 (5: 2.6–2.9 mm); I.29056-002 (3: 2.8–3.6 mm); I.29074-001 (5: 2.9–8.3 mm); I.29084-001 (2: 2.3–2.4 mm); I.29085-001 (4: 2.9–3.1 mm); I.29096-001 (14: 3.3–8.1 mm); I.29097-001 (16: 3.1–8.6 mm); I.29098-001 (16: 2.8–8.6 mm); I.29099-001 (10: 3.0–

5.4 mm); I.29100-001 (16: 2.8–5.6 mm); I.29101-001 (3: 4.1–5.0 mm); I.29103-001 (2: 3.3–3.7 mm); I.29104-001 (1: 4.4 mm); I.29123-002 (1: 11.4 mm).

Enchelyurus kraussi (Klunzinger, 1871). AMS I.21754-009 (1: 11.5 mm); I.21758-003 (3: 8.6–11.2 mm); I.23050-023 (1: 3.2 mm); I.23053-084 (1: 3.2 mm); I.23077-009 (2: 3.1–4.3 mm); I.23135-021 (1: 12.0 mm); I.23151-005 (1: 3.6 mm); I.25131-001 (1: 5.5 mm); I.28394-005 (1: 14.5 mm); I.30852-006 (2: 1.6–2.0 mm); I.33797-001 (2: 12.1–12.3 mm); I.33798-001 (1: 12.1 mm); I.39117-001 (1: 11.5 mm); I.39210-001 (1: 4.8 mm); I.39210-002 (4: 3.3–4.2 mm); I.39541-001 (2: 3.2–3.7 mm).

Larval descriptions

Enchelyurus ater (Günther, 1877)

Figs. 1, 2

Morphology. Least developed specimens (2.3–2.4 mm) had recently hatched, as evident in presence of small yolk sac containing remnants of oil globule and possibly yolk. These small larvae are well developed with open mouth, pigmented eyes, and first 2 preopercular spines forming. Notochord flexion begins at 4.9–5.0 mm, is completed between 5.2–5.6 mm. Largest specimen, 11.4 mm, nearing settlement stage as evident in resorption of preopercular spines (process underway but incomplete), presence of adult-type teeth, and development of cephalic sensory pore system. Springer (1972) listed juvenile (presumably settled) *E. ater* as small as 11–12 mm.

Initially, head broad and rounded, snout short and blunt, eyes oval to somewhat rectangular (elongate horizontally), coiled gut short, tail elongate and compressed. Changes in most body proportions small during larval growth. Relative preanal length, head length, and snout length increase through early postflexion stage, then stabilize or decrease slightly. Relative body depth may increase slightly in postflexion stage (Table 1). Larvae become more compressed early in preflexion stage; relative head width stabilizes at about 70–80% HL by about 3 mm. Eyes become relatively smaller early in preflexion stage (Table 1), usually become round by beginning of notochord flexion. There are 34–36 myomeres (usually 34–35): commonly 6–7 preanal plus 27–28 postanal in preflexion stage larvae <4 mm, shifting to 9–10 preanal plus 24–26 postanal in flexion and postflexion stages (>5 mm).

First 2 preopercular spines located on anterior margin of lower limb and at angle of preopercle. A third spine added near upper end of upper limb before 3 mm. Maximum of 6–7 spines attained by about 4 mm. These persist through about 5.5 mm, then gradually decrease to 2–3 spines by late postflexion stage as smaller spines are resorbed or overgrown. Nearly 40% of larvae had more preopercular spines (usually 1) on one side (60% of these had more spines on right side). Early in preflexion stage spines are small and more or less evenly arrayed in single row along posterior preopercular margin. After 3 mm lowermost (= anteriormost) 1 or 2 spines, then spine at angle become longer than others. After 4 mm, spine at preopercular angle always longest, reaching maximum of about one-quarter HL early in postflexion stage (Table 1). As smallest spines begin to disappear, remaining spines usually form three groups, with 1 or 2 anteriorly on lower preopercular margin, largest spine at angle, and 1 or 2 near upper end of preopercle. Late in postflexion stage spines become shorter and blunter, and numbers of spines near ends of preopercle reduced to 0–1.

First small tooth present near mesial end of each

Table 1. Summary of measurements of *Enchelyurus ater*, expressed as percentage of body length (BL) or head length (HL). For each measurement the mean is given above and the range is given below. For eye diameter, eye length is given first and eye height is given second. N = number of specimens. Notochord flexion occurs within the 4.1–5.0 and 5.1–6.0 mm size categories.

BL (mm)	N	PAL/BL	BD/BL	HL/BL	P_1L/BL	P_2L/BL	HW/HL	SnL/HL	ED/HL	PSL/HL
2.1–3.0	21	36	20	23	8	0	96	14	52,44	8
		32–40	17–27	19–27	7–10	0–0	82–115	8–21	46–62, 37–54	3–12
3.1–4.0	29	34	17	23	8	0	75	17	42,37	9
		31–40	15–22	20–28	7–10	0–0	69–97	9–25	41–53, 32–47	6–15
4.1–5.0	24	37	20	25	10	0.1	79	20	42,41	16
		34–40	18–23	21–29	7–16	0–1	69–98	17–27	38–52, 37–45	10–24
5.1–6.0	12	38	21	25	12	1	76	21	42,42	21
		37–40	19–23	22–28	9–15	1–3	71–83	18–27	35–45, 35–45	16–26
6.1–7.0	2	40	23	26	16	3	81	19	45,44	27
		39–40	23–24	24–27	15–16	2–3	81–82	18–20	43–46, 42–46	26–28
7.1–8.0	5	40	23	25	17	8	76	16	45,45	24
		38–42	22–24	25–26	13–19	6–10	72–81	14–17	44–47, 44–47	22–26
8.1–9.0	7	39	22	25	17	9	75	16	44,44	21
		32–42	17–25	23–28	13–19	2–11	69–80	13–17	40–48, 40–48	19–23
11.1–12.0	1	41	21	25	16	16	68	17	35	15

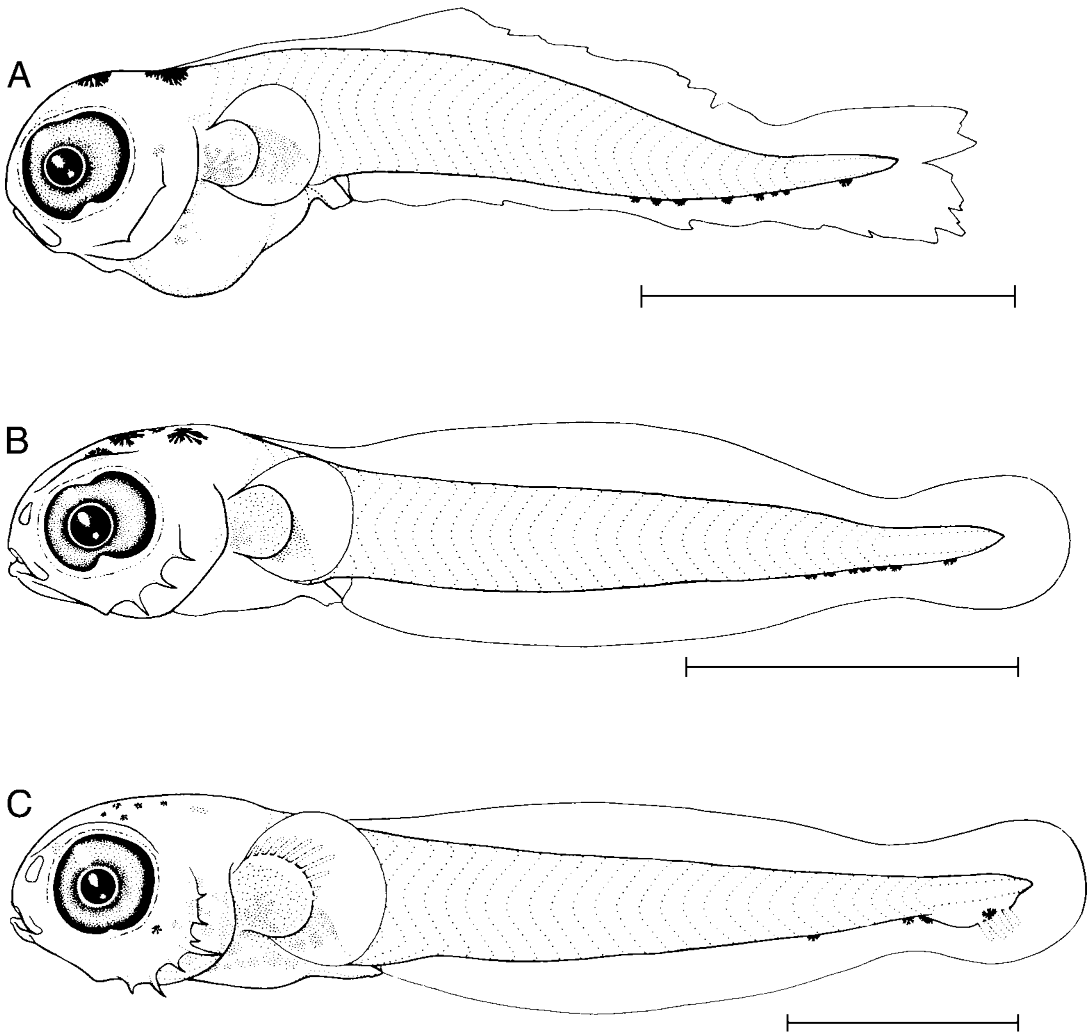

Figure 1 (part). *Enchelyurus ater*, lateral view. A, 2.4 mm (I.29084-001). B, 3.0 mm (I.29099-001). C, 4.4 mm (I.29098-001). D–F, see opposite. Scale bars = 1 mm.

premaxillary bone at 3.1 mm. Second premaxillary tooth added by 4.3 mm and third by 5.6 mm. First lateral premaxillary tooth develops near 8 mm, is larger than anterior teeth and separated from them by an edentulous gap. In largest larva 7 teeth present on each premaxillary bone: 5 anterior and 2 lateral. Anterior teeth have flattened adult form in this specimen.

Dentary teeth appear at about 3.7 mm: a small tooth present near symphysis and larger tooth located anterolaterally on short dorsal process of each dentary bone. Second small anterior tooth added by 4.3 mm and small anterolateral tooth added just posterior to dorsal process between 5–6 mm. In largest larva 6–7 teeth present on each dentary: 5 flattened, adult-type anterior teeth, large anterolateral tooth, and another, smaller lateral tooth on left side.

Frontal bones become ornamented with small spinules by about 4.1 mm and parietal and lower parts of preopercular, articular and dentary bones follow suit by 4.8 mm. Spinules persist through early postflexion stage, then become smaller and more rounded. By about 7 mm they are reduced to low ripples and small bumps.

Fin development. Smallest larvae have broad dorsal, anal and caudal finfolds and pectoral fan, but no preanal finfold or rays forming in any fin. Pectoral-fin rays begin forming first, by about 2.9 mm. Addition of rays is ventrad from uppermost two rays. Full complement of 14–16 rays (usually 15, rarely 16) completed late in flexion stage, by 5.3 mm (Table 2).

Principal caudal-fin rays second to begin forming, late in preflexion stage, and full complement of 7+6 rays present by late flexion stage. Procurrent caudal-fin rays form early in postflexion stage and full complement of 6–8+6–8 rays attained by about 8 mm. Procurrent rays added anteriorly from posteriormost ray.

Dorsal- and anal-fin anlagen form during preflexion stage, beginning at about 4.2 mm. Segmented rays form in both fins beginning at about mid-flexion; anal-fin rays apparently start forming slightly sooner than dorsal-fin rays. Anterior several segmented rays may form simultaneously within each fin and addition of rays is posteriorly in both fins. Full complements of 20–24 segmented dorsal-fin rays (usually 20–21) and 18–23 segmented anal-fin rays (usually 19–21) completed in postflexion stage by about 6.8 mm

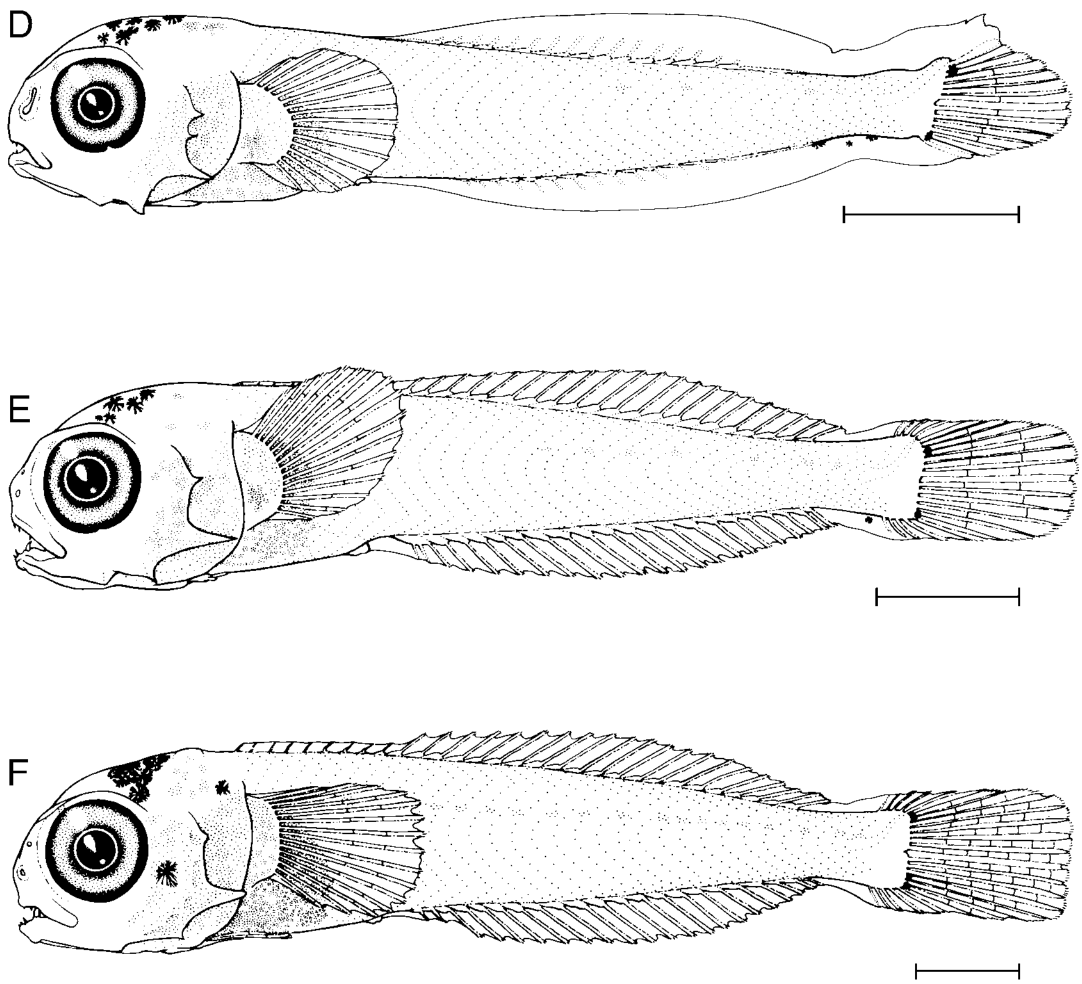

Figure 1 (continued). *Enchelyurus ater*, lateral view. D, 5.4 mm (I.29099-001). E, 6.3 mm (I.29098-001). F, 8.6 mm (I.29098-001). Scale bars = 1 mm.

(Table 2). Anal-fin spines may form simultaneously in postflexion stage; both present by 6.8 mm. Dorsal-fin spines begin to form early in postflexion stage, by about 5.9 mm. Posterior 3 spines may form simultaneously and addition is cephalad, with full complement of 8–10 (usually 9) attained by about 8 mm.

Pelvic-fin buds develop in preflexion stage by about 4.2 mm, and fin rays form early in postflexion stage, by 5.9 mm. Pelvic-fin spine forms by about 8 mm.

Pigmentation. Larvae lightly pigmented, except on head and gut. Head pigmentation initially consists of 1 or 2 pairs of large melanophores posteriorly over midbrain and none to few smaller melanophores more anteriorly over midbrain (Fig. 2), none or 1 anteriorly under forebrain (present in 44% of larvae 3 mm or smaller), and none or 1 just anterior to upper end of preopercle (present in 33% of larvae 3 mm or smaller). Pigmentation over midbrain area gradually increases and area usually covered by flexion stage. Forebrain melanophore usually present after 3 mm (present in about 85% of larvae >3 mm) and after 3.1 mm may spread upward onto anterior margin of forebrain. No other pigment forms on forebrain area through at least 8.6 mm, but by 11.4 mm a small dorsal melanophore is present above forebrain. Melanophore at upper end of preopercle nearly always present after 3 mm (present in 90% of larvae >3 mm). At about 4 mm melanophores form on inner surface of opercular area, beginning near middle of preopercle, and usually spread to cover much of area by about 6–7 mm. First melanophore on exterior surface of opercular area forms anterior to preopercular angle at about 4.2 mm, but no more than a few more form by 8.6 mm (none in 11.4 mm specimen). A melanophore may form in otic capsule as early as 2.7 mm, but usually capsule is unpigmented until about 4 mm. After 4 mm an epiotic melanophore commonly is present and a prootic melanophore occasionally occurs. Melanophores form on hindbrain during notochord flexion, just after 5 mm. This pigmentation initially consists of only a few dorsal and dorsolateral melanophores, usually only anteriorly, and gradually increases and spreads to cover much of hindbrain by about 8 mm. Melanophores form on ceratohyals after 6 mm, and nearly cover them after about 8 mm.

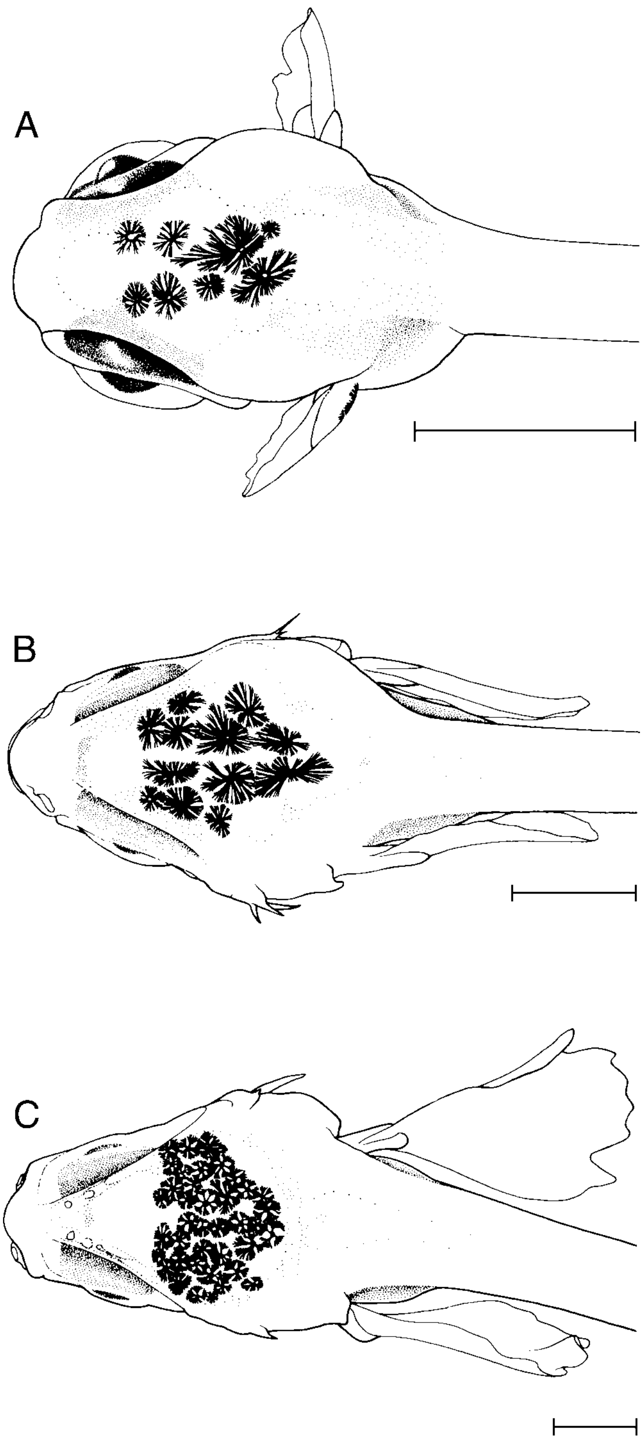

Figure 2. *Enchelyurus ater*, dorsal view of head. A, 3.0 mm (I.29099-001). B, 5.4 mm (I.29099-001). C, 8.6 mm (I.29098-001). Scale bars = 0.5 mm.

A melanophore, often large, is located proximally on lower mesial surface of pectoral base in all larvae except 11.4 mm specimen; there is no other pectoral pigment. A melanophore forms on cleithrum at level of pectoral-fin insertion by 2.6 mm, and others gradually added ventrally along cleithrum, eventually forming a series along most of its length below pectoral-fin origin. Pelvic fins unpigmented.

Table 2. Fin-ray counts of larval *Enchelyurus ater*. Abbreviations for larval stages are: Pr = preflexion; F = flexion; Po = postflexion. Cpri = principal caudal-fin rays; Cpro = procurrent caudal-fin rays; body length (BL) in mm.

BL	stage	D	A	P_1	P_2	Cpri	Cpro
2.3	Pr	0	0	0	0	0	0
2.9	Pr	0	0	2	0	0	0
3.0	Pr	0	0	0	0	0	0
3.6	Pr	0	0	4	0	0	0
4.4	Pr	0	0	10	0	2+2	0
4.4	Pr	0	0	11	0	2+2	0
4.8	F	0	8	14	0	5+5	0
5.3	F	17	16	15	2	7+6	0
5.4	F	15	14	14	0	6+6	0
5.4	F	16	14	15	0	7+6	0
5.7	Po	18	17	15	0	7+6	2+2
5.9	Po	III,20	19	15	2	7+6	1+1
6.8	Po	III,20	II,19	16	2	7+6	5+5
8.0	Po	IX,21	II,19	15	I,2	7+6	7+6
8.1	Po	IX21	II,18	15	I,2	7+6	7+7
8.6	Po	IX,22	II,20	15	I,2	7+6	7+7
11.4	Po	IX,22	II,19	15	I,2	7+6	8+8

Gut pigmentation initially largely limited to dorsum, except terminal section of hindgut is unpigmented. Melanophores spread ventrolaterally, covering upper 50–60% of gut before 3 mm and reaching ventrum by about 4.5 mm. One or two melanophores may be present anteroventrally on or near longitudinal midline in preflexion stage (present in 20%), but more commonly no ventral pigment on gut until flexion stage, when melanophores spread over ventrum from each side, meeting along longitudinal midline near end of stage (by 5.6 mm). Pigmentation on gut becomes dense during flexion and postflexion stages, except often sparser midlaterally, especially behind pectoral-fin bases, and in late flexion stage, along ventral midline. Melanophores in these sparsely pigmented areas often smaller than those in adjacent areas. During postflexion stage gut pigmentation may become noticeably denser in ventrolateral band along each side.

Postanal pigmentation initially consists of 2–9 (usually 3–6) melanophores more or less evenly spaced along ventral margin of last 3–11 (modally 6) myomeres plus 1–2 melanophores (usually 1) ventrally on notochord tip. Anterior melanophores disappear during flexion and early postflexion stages; thereafter none, or only posterior 1–3, remain. Remaining melanophore(s) may be on ventral margin, shallowly internal, or on caudal finfold near body margin.

Specimens ≤4 mm usually have single ventral melanophore near middle of notochord tip; after 4 mm there usually are 2 located proximally and distally on notochord tip. These become located at margins of lower and upper hypural plates, respectively, as caudal fin develops.

Internal dorsal melanophore series forms posteriorly over notochord during flexion stage and spreads cephalad to full length of vertebral column by about 7.6–8.6 mm, but becomes increasingly difficult to see as melanophores are obscured by overlying tissue in larger larvae. Melanophores over abdominal vertebrae typically are more widely spaced than those over caudal vertebrae.

Enchelyurus kraussi (Klunzinger, 1871)

Figs. 3, 4

Morphology. Smallest specimen (1.6 mm) has pigmented eyes, open mouth, a small preopercular spine, remnant of yolk sac, and probably had hatched not long before collection. Notochord flexion begins at about 4.3–4.8 mm, is completed by 5.5 mm. Most advanced larvae (11.5 and 14.5 mm) approaching settlement stage as shown by resorption of preopercular spines (incomplete), presence of adult-type teeth, and development of cephalic sensory pores. Springer (1972) listed an 11.4 mm juvenile (presumably settled) from the Seychelles Islands and Kubo & Sasaki (2000) described a pelagic, transforming specimen 12.9 mm from Japan. Size at transformation and settlement are unknown for eastern Australian *E. kraussi*, but probably are in the vicinity of 14–15 mm.

Head initially rounded and broad, gut short and coiled, tail elongate and compressed. During preflexion stage larvae become more slender as yolk consumed, then gradually become deeper-bodied and more compressed with slightly larger head and longer preanal length (Table 3). These dimensions change little thereafter, except relative preanal length increases slowly until late postflexion stage. Eyes initially large and oval to somewhat rectangular (elongate horizontally), becoming round between 3.4–3.9 mm. Snout moderately short, rounded, changes little. There are 33–35 myomeres (usually 34): 6–7 preanal plus 26–28 postanal through preflexion stage, shifting to 10 preanal plus 24 postanal by late postflexion stage (c. 11 mm).

Smallest specimen has 1 small spine on posterior preopercular margin (present only on right side). By 3.1 mm 3 spines present: one each near lower and upper ends of preopercle and another at angle. Maximum of 6–7 spines attained by 3.9 mm. When more than 3 spines present, arrangement is variable, with 1–3 spines along lower preopercular margin, single spine at the angle, and 1–3 along upper margin. Bilateral asymmetry in number of spines apparently uncommon: only 2 specimens had 1 more spine on one side than on other. As larvae grow, smaller preopercular spines are overgrown or resorbed: by midflexion (4.8 mm) only 3 remain and by mid-postflexion (c. 8 mm) only spine at angle remains. Early in preflexion stage spines are of similar length; the spine nearest each end of preopercle typically is slightly longer than other(s). These remain longest until about 4 mm when they are overtaken by spine at angle, which reaches a maximum of just over one-quarter HL by mid-postflexion stage (Table 3). Spine gradually resorbed near end of pelagic larval phase. In largest specimen (14.5 mm) resorption incomplete and spine remains short and blunt.

No teeth visible in 1.6 mm specimen and none visible on premaxillae in any preflexion stage specimen. A small conical tooth first visible near mesial end of each premaxilla in 4.8 mm midflexion specimen, and by end of stage another has been added on each side of this tooth. By mid-postflexion stage each premaxilla bears 5–6 teeth anteriorly, separated by an edentulous gap from 1 or 2 larger anterolateral teeth (when 2 present, anterior tooth usually largest). Anterior, conical larval teeth may

Table 3. Summary of measurements of *Enchelyurus kraussi*, expressed as percentage of body length (BL) or head length (HL). For each measurement the mean is given above and the range is given below. For eye diameter, eye length is given first and eye height is given second (by 5 mm BL the eyes are round and only eye length is given). N = number of specimens measured. The specimen in the 5.1–6.0 mm size class is undergoing notochord flexion.

BL (mm)	N	PAL/BL	BD/BL	HL/BL	P_1L/BL	P_2L/BL	HW/HL	SnL/HL	ED/HL	PSL/HL
1.6–2.0	2	38	22	24	11	0	105	14	49,43	7
		37–39	20–24	22–25	(N=1)	0–0	105–105	12–16	49–50, 41–45	5–9
3.1–4.0	9	35	18	23	8	0	85	19	40,37	10
		32–38	16–21	20–26	6–10	0–0	79–92	12–21	37–47, 31–41	5–13
4.1–5.0	3	37	19	24	10	<0.1	82	18	39,37	18
		36–37	19–20	23–25	10–11	0–0.2	77–90	16–21	37–40, 36–38	12–24
5.1–6.0	1	38	24	27	15	2	70	19	38	22
8.1–9.0	2	38	24	26	18	10	79	18	38	27
		38–39	23–26	25–28	17–19	8–11	79–80	17–20	37–38	27–28
11.1–12.0	4	44	24	26	19	17	73	16	36	13
		42–47	23–24	25–27	18–20	15–18	62–80	15–19	35–36	8–20
12.1–13.0	3	42	24	27	20	17	72	17	33	11
		41–43	24–24	26–28	19–21	16–18	71–72	16–18	33–34	7–13
14.1–15.0	1	41	22	24	19	16	79	19	34	9

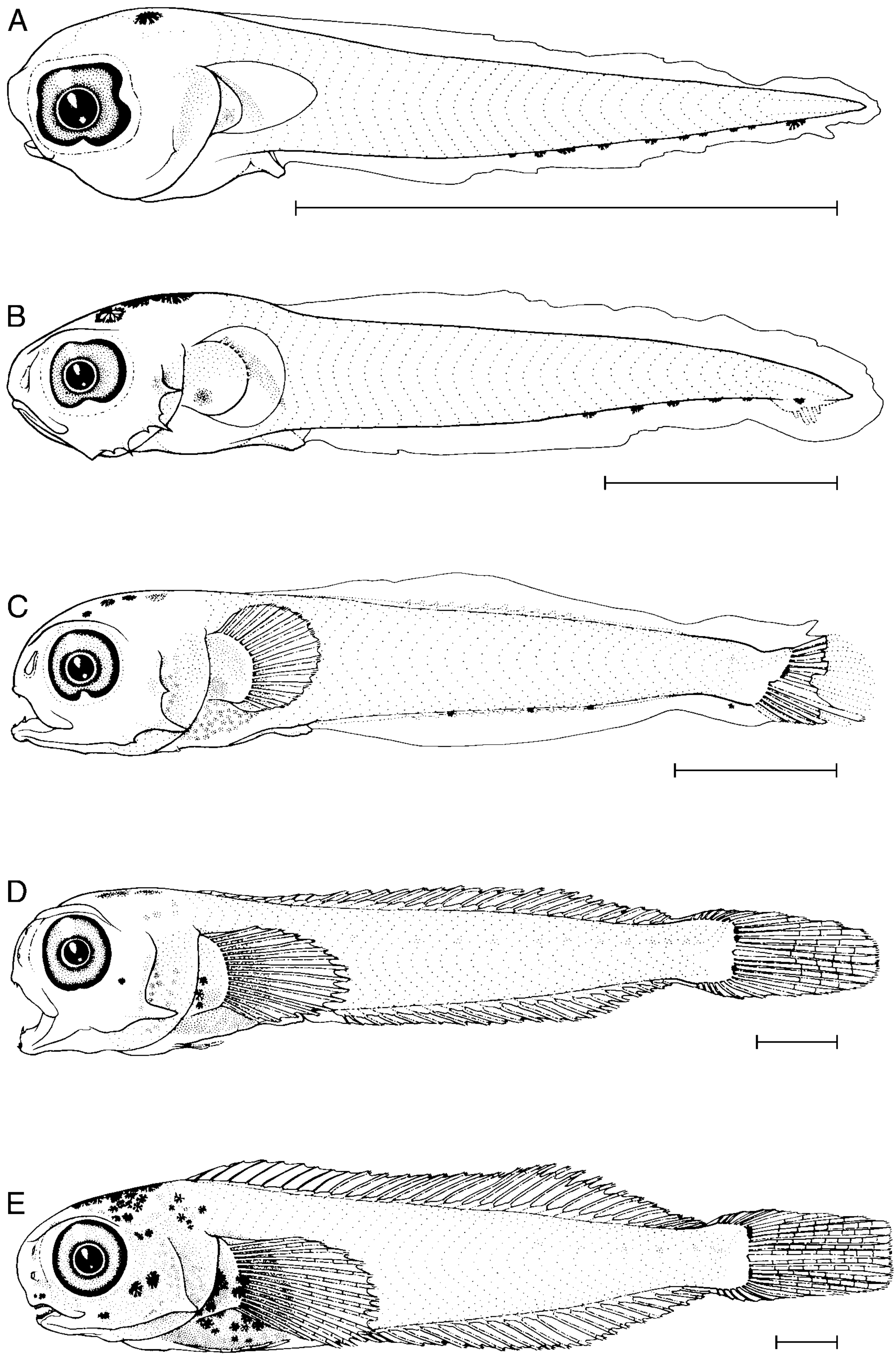

Figure 3. *Enchelyurus kraussi*, lateral view. A, 1.6 mm, preopercular spine present only on right side in this specimen, but shown as if it were present on the left (I.30852-006). B, 3.7 mm (I.39541-001). C, 4.8 mm (I.39210-001). D, 8.6 mm (I.21758-003); E, 11.5 mm (I.21754-009). Scale bars = 1 mm.

broaden into flattened adult form. By c. 11 mm all 5–9 anterior teeth are adult form and through 14.5 mm no premaxillary teeth added.

Dentary teeth first visible at 3.2 mm: each dentary bears a small, conical, anterior tooth near its mesial end and another, slightly larger, anterolaterally. Anterolateral tooth is attached to short dorsal process of dentary bone. No dentary teeth added through at least midflexion, but by end of stage another 2 small, conical teeth are present anteriorly. By mid-postflexion stage anterior teeth all acquiring adult form, anterolateral tooth is moderately large, and a small tooth is added just posterior to dorsal process. Occasionally, both lateral teeth are large on one or both dentaries. The 5–8 anterior teeth are separated by a short, edentulous gap from lateral teeth.

Frontal bones become slightly rugose at about 3.9 mm and by 4.2 mm both they and posteroventral parts of dentary bones are ornamented with small spinules. Spinules increase in density on frontals and dentaries and form on angular, articular, parietal and preopercular bones, including preopercular spines, during notochord flexion. Ornamentation persists through at least 14.5 mm, but smooths to low ripples and small bumps by 11.2 mm.

Fin development. Smallest specimen has dorsal, anal and caudal finfolds and pectoral fan, but lacks preanal finfold. Upper 2–3 pectoral-fin rays forming by 3.1 mm (Table 4); rays added ventrad. Full complement of 14–16 (usually 15) rays present by early postflexion stage (5.5 mm).

Principal caudal-fin rays next to begin forming, by about 3.6 mm. Addition of rays is anteriorly (= ventrally) and posteriorly (= dorsally) from central rays; full complement of 7+6 rays present by beginning of postflexion stage, when procurrent rays begin forming. Procurrent rays added anteriorly from posteriormost ray and full complement of 6–7+6–7 rays present by 8.7 mm.

Dorsal- and anal-fin anlagen form late in preflexion stage, by about 4.2 mm, and segmented fin-rays begin to form during flexion stage. Location and number of these first rays, direction(s) of initial addition of rays, and whether initial ray formation is simultaneous in both fins could not be determined. Last few segmented rays added caudad in each fin during early postflexion stage. Full complements of 21–24 segmented dorsal-fin rays (modally 22 rays), 18–20 segmented anal-fin rays (modally 19 rays) present by 8.7 mm. First dorsal-fin spines form early in postflexion stage (c. 5.5 mm). Posterior 3 spines may form simultaneously and addition is cephalad. Full complement of 7–9 spines (modally 8 spines in eastern Australian waters) present by 8.7 mm.

Pelvic-fin buds form late in preflexion stage, by 4.2 mm, and segmented rays first appear at beginning of postflexion stage. Full complement of 1 spine and 2 segmented rays present by 8.7 mm.

Pigmentation. Larvae lightly pigmented, except on head and gut. Head pigmentation initially consists of pair of large, dorsal melanophores posteriorly near midline of midbrain, few additional melanophores scattered more anteriorly over midbrain, usually a small melanophore internally at anterior margin of forebrain (none in 1.6 and 3.1 mm specimens), and usually 1–2 melanophores on inner surface near centre

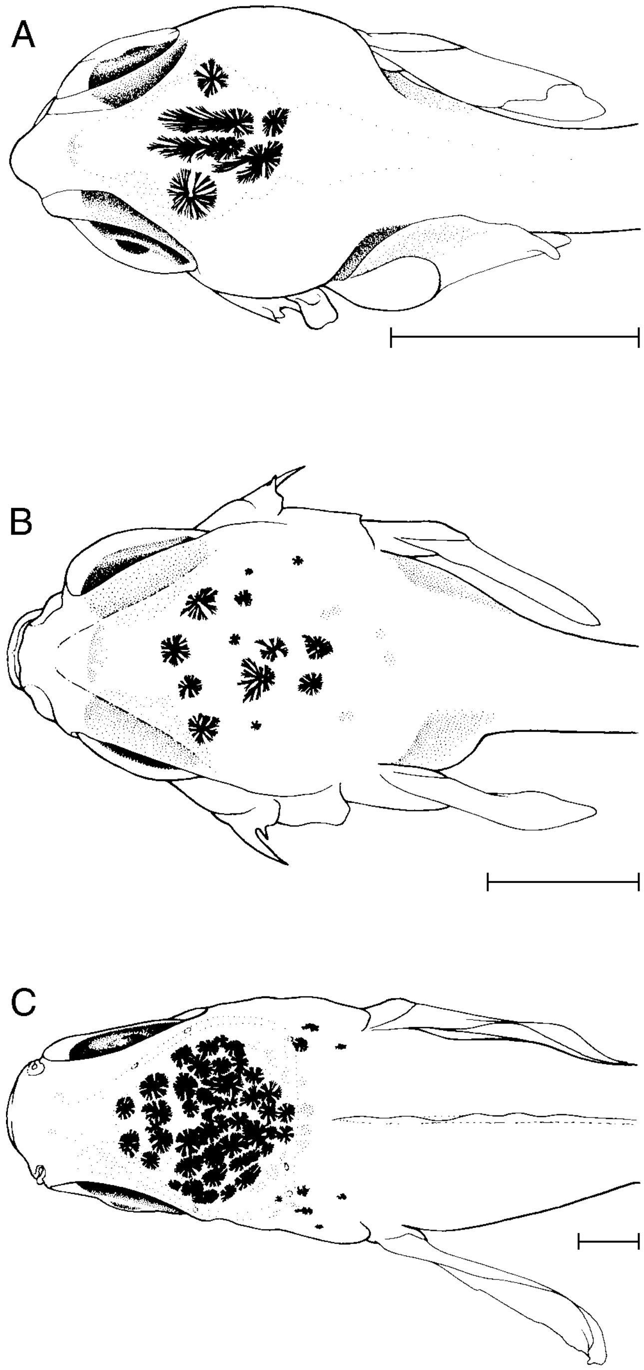

Figure 4. *Enchelyurus kraussi*, dorsal view of head. A, 3.3 mm (I.39210-002). B, 4.8 mm (I.39210-001). C, 11.5 mm (I.21754-009). Scale bars = 0.5 mm.

of opercular area (Figs. 3B, 4A). Dorsal pigmentation over midbrain area increases, completely covering it between late preflexion and early postflexion stage, and usually spreads forward over forebrain area early in postflexion stage (by 5.5 mm; occasionally absent in larvae as large as 11.5 mm). Melanophores usually form anteriorly on upper jaw and internally in ethmoid region at about 11.5 mm (absent in both areas in 12.3 mm specimen). Forebrain pigmentation unchanged until late postflexion stage (c. 11.5 mm) when few scattered melanophores are added. One to three melanophores form in otic capsule early in preflexion stage, by about 3.2 mm. Melanophores form on hindbrain early in postflexion stage and usually cover it (sparsely) by about 8.7 mm. External melanophores form on nape late in postflexion stage (c. 11.5–12 mm). Opercular pigmentation unchanged until early postflexion stage when melanophores form patch on central mesial surface, then spread to cover much of area and extend onto branchiostegal membranes by about 12 mm. Melanophores may form on mesial surface of ceratohyal, primarily near ceratohyal-interhyal articulation, between 11.5–14.5 mm (present in 3 of 7 specimens in this size range). External melanophore forms below eye, just anterior to preopercular angle, by 8.6 mm, and is joined at about 14.5 mm by one just below mid-eye and another just below anterior margin of eye.

Lower, proximal part of mesial surface of pectoral-fin base always is pigmented. Through mid-postflexion stage this pigment usually is 1 large melanophore (occasionally 2, 4 covering entire mesial surface in one specimen), but by 11.2 mm more melanophores are added, covering lower half of mesial surface. Melanophores form on outer surface by 8.6 mm. These initially are proximal, on lower half of base, and spread to cover much of lower half by 11.2 mm. Melanophores usually form on pectoral-fin rays at about 11.5 mm: 1 or 2 are located near bases of 1 or 2 of lower 8 rays. Melanophore forms on cleithrum at level of pectoral-fin insertion between 2.0–3.2 mm and more are added, first ventrad, then both ventrad and dorsad, forming a series along cleithrum from pectoral origin to near cleithral symphysis by end of preflexion stage.

Gut pigmentation initially is only dorsal (except terminal section of hindgut always is unpigmented). Ventral pigment occasionally is present in small preflexion stage larvae: 3.1 mm specimen has a small ventral melanophore at anterior centre of gut. Melanophores spread ventrad from dorsum during preflexion stage, beginning anteriorly and reaching ventrum by c. 4.2 mm, then completely encircle gut by mid-flexion. External melanophores form on abdominal area between 8.7–11.5 mm but remain sparse (absent in some) through at least 14.5 mm.

Postanal pigmentation initially limited to ventral margin of tail. Through most of preflexion stage 4–14 melanophores are arrayed irregularly along last 2–20 myomeres and notochord tip. Usually, spacing between first 2–3 melanophores in series is wider than that between more posterior melanophores. Last (or last 2) melanophore(s) in series nearly always located on notochord tip and becomes located on margin(s) of one (or both) hypural plates late in preflexion stage. Postflexion stage larvae nearly always have an elongate melanophore at distal margin of each hypural plate (sometimes 2 on upper plate). Ventral melanophores decrease in number after about 4 mm and by postflexion stage there are none. Internal melanophores form over notochord during postflexion stage, extending to full length by 8.6 mm, but are difficult to see anteriorly.

Table 4. Fin-ray counts of larval *Enchelyurus kraussi*. Abbreviations for larval stages are: Pr = preflexion; F = flexion; Po = postflexion. Cpri = principal caudal-fin rays; Cpro = procurrent caudal-fin rays; body length (BL) in mm.

BL	stage	D	A	P_1	P_2	Cpri	Cpro
1.6	Pr	0	0	0	0	0	0
3.1	Pr	0	0	2	0	0	0
3.2	Pr	0	0	4	0	0	0
3.3	Pr	0	0	4	0	0	0
3.4	Pr	0	0	3	0	0	0
3.6	Pr	0	0	7	0	2+2	0
3.7	Pr	0	0	8	0	2+2	0
3.9	Pr	0	0	7	0	0	0
4.2	Pr	0	0	12	0	3+3	0
4.8	F	12	12	14	0	7+6	0
5.5	Po	III,21	I,18	15	2	7+6	1+1
8.6	Po	VIII,21	II,19	15	I,2	7+6	6+6
11.2	Po	VIII,22	II,19	15	I,2	7+6	7+7
11.5	Po	VIII,23	II,20	15	I,2	7+6	6+6
14.5	Po	VIII,22	II,20	15	I,2	7+6	6+6

Comparisons

Larval *Enchelyurus ater* from the Tuamotu Archipelago, *E. brunneolus*, and eastern Australian *E. kraussi* closely resemble one another in most characters, but each is distinguishable by small differences in several characters. Among the 48 characters examined, *E. ater* and *E. brunneolus* are similar to one another, and both are different from *E. kraussi*, in eight or nine (Table 5: characters 3, 4, 13, 17, 19, 30, 32, probably 12; Tables 1, 3, 6: eye diameter), and *E. ater* is similar to *E. kraussi* (both different from *E. brunneolus*) in four (Table 5: characters 18, 25, 31; Tables 1, 3, 6: pectoral-fin length).

Enchelyurus ater and *E. brunneolus* both apparently acquire the first premaxillary teeth (character 4) earlier in development, and both probably settle from the plankton (3) at a smaller size than does *E. kraussi*. (Settlement size is unknown for *E. ater* and *E. kraussi*, but comparison of the developmental states of the largest larvae with similarly developed *E. brunneolus* suggests that *E. ater* and *E. brunneolus* settle at about the same size, and that *E. kraussi* settles at a larger size, at least in eastern Australian waters.) Both *E. ater* and *E. brunneolus* acquire ceratohyal pigmentation (30) beginning at about 6–7 mm, while *E. kraussi* develops it much later, at 11.5 mm or larger. This pigmentation typically is more extensive in *E. ater* than in the other two.

On the other hand, neither *E. ater* nor *E. brunneolus* develop dorsal pigmentation over the forebrain (19) as early as *E. kraussi*, and both usually retain the early oval to rectangular eye shape (13) somewhat longer. *Enchelyurus kraussi* has smaller eyes relative to head length than either of the other two, both of which have similar relative eye

Table 5. Comparison of characters in larval *Enchelyurus ater, E. brunneolus* and *E. kraussi*.

	character	*E. ater*	*E. brunneolus*	*E. kraussi*
	approximate size (mm) at:			
1	hatching	2.3	2.2	1.6
2	flexion	5.0–5.5	4.5–5.5	4.5–5.5
3	settlement	probably ~12	<12	probably ~15
4	first premaxillary teeth	3.1	2.9	4.8
5	first dentary teeth	3.7	3.6	3.2
6	first pectoral-fin rays	2.9	<3.2	≤3.1
7	first caudal-fin rays	4.4	4.0	4.2
8	first anal-fin rays	>4.4, <4.8	5.2	>4.2, <4.8
9	first dorsal-fin rays	>4.8, <5.3	5.2	4.8
10	first dorsal-fin spines	5.9	5.6	5.5
11	first pelvic-fin rays	5.9	5.5	5.5
12	single preopercular spine	>11.4	10	8
13	eyes round	4.4–5.0	4.5	3.4–3.9
	number of myomeres:			
14	preflexion	6–7+27–28	7+28	6–7+26–28
15	postflexion	9–10+24–26	8–9+25–27	10+24
16	max. no. preopercular spines	6–7	6–7	6–7
17	preopercular ornamentation	lower half	usually only lower half	full length
	melanophores on/in:			
18	forebrain, anterior margin	usually (+) by 3.3 mm	usually (-) before 9.3 mm	usually (+) by 3 mm
19	forebrain, dorsal	(-) through 8.6 mm	(-) before 9.3 mm	usually (+) by 5.5 mm
20	forebrain, ventral	(-) through 11.4 mm	(-)	(-)
21	midbrain, dorsal	(+)	(+)	(+)
22	midbrain, lateral	(-) through 8.6 mm	usually (-) before 7.2 mm	(-)
23	midbrain, ventral	(-) through 8.6 mm	(-)	(-)
24	hindbrain, dorsal	(+) by 5.4 mm	usually (+) by 5.8 mm	(+) by 4.8 mm
25	hindbrain, lateral	(-) before 6.0 mm	usually (+) by 4.2 mm	(-) before 8.6 mm
26	hindbrain, ventral	(-) through 8.6 mm	(-)	(-)
27	otic capsule	usually 1–2	1–2	1–3
28	roof of mouth/ethmoid area	(-) through 8.6 mm	usually (+) by 8.8 mm	usually (+) by 11.5 mm
29	pharyngobranchial	(+)	(+)	(+) by 3.3 mm
30	ceratohyal	(+) after 6 mm	(+) after ~7 mm	(+) by 11.5 mm in some
31	pectoral-fin base	(+), inner surface	(-)	(+), inner surface; (+), outer surface by 8.6 mm
32	pectoral-fin rays	(-) through 8.6 mm	(-)	(+) by 11.5 mm
33a	gut, preflexion stage	dorsal	dorsal	dorsal
33b	gut, postflexion stage	unevenly covered, often denser ventrolateral band	usually ~evenly covered, denser ventrolateral band in some	~evenly covered
	ventral margin of tail:			
34a	preflexion: range (mode)	3–11 (6)	2–10 (5)	4–14 (8,9,13)
34b	postflexion: range (mode)	0–3 (1,2)	0–2 (0)	0 (0)

size through about 7 mm (cf. Tables 1, 3, 6). *Enchelyurus kraussi* also may differ from the other two species in the larval length at which the number of preopercular spines is reduced to one (12), although the incomplete series of *E. ater* makes this character difficult to assess. In *E. kraussi* only the large spine at the angle remains by about 8 mm—well before settlement. In *E. brunneolus* this process is complete by about 10 mm—shortly before settlement. In the largest *E. ater* (11.4 mm) the process is underway but incomplete, suggesting that here too it is finished shortly before settlement. These characters

Table 6. Summary of measurements of *Enchelyurus brunneolus*, expressed as percentage of body length (BL) or head length (HL). For each measurement the mean is given above and the range is given below. N = number of specimens. Notochord flexion occurs within the 4.1–5.0 and 5.1–6.0 mm size classes.

BL (mm)	N	PAL/BL	BD/BL	HL/BL	P_1L/BL	SnL/HL	ED/HL	PrSL/HL
2.1–3.0	18	38	19	23	10	10	51	6
		33–41	18–28	19–27	5–13	6–14	44–60	0–11
3.1–4.0	11	38	19	23	11	18	46	9
		32–46	16–21	19–28	8–16	10–25	38–53	5–14
4.1–5.0	6	40	20	25	14	20	39	17
		36–47	17–23	23–27	10–17	17–23	33–41	11–21
5.1–6.0	4	44	23	28	20	18	41	22
		39–48	22–24	22–31	12–27	15–21	38–44	20–26
6.1–7.0	2	43	24	25	20	17	44	23
		42–44	22–26	23–26	20–20	16–18	43–45	20–25
7.1–8.0	2	40	22	27	25	14	40	24
		40–40	22–22	26–28	24–26	14–15	38–42	22–25
8.1–9.0	3	42	22	26	25	15	40	20
		39–46	20–24	24–29	23–28	13–18	38–43	16–24
9.1–10.0	1	40	21	25	24	17	41	17
10.1–11.0	2	44	22	27	27	15	36	2
		44–44	21–23	27–27	26–27	13–17	35–37	0–4
11.1–12.0	11	44	22	26	25	16	38	2
		43–48	20–24	24–28	22–26	11–19	36–41	0–7
12.1–13.0	1	41	19	25	27	15	39	0

suggest prolonged retention of an early developmental state in larval *E. ater* and *E. brunneolus*.

Larval *E. kraussi* develop preopercular ornamentation (17) in the form of small spinules and ripples extending the full length of the preopercle and out onto the spine at the angle during the flexion and postflexion stages (Fig. 5C). Larval *E. ater* and *E. brunneolus* acquire similar ornamentation, but it is restricted to the lower part of the preopercle in *E. ater* and usually occurs only on the lower part in *E. brunneolus* (Fig. 5A,B), although an occasional specimen also has small patches of spinules around the bases of some of the upper preopercular spines. This might be considered a gradient in the extent of preopercular ornamentation: *kraussi* > *brunneolus* > *ater*; however, because the upper preopercular ornamentation is uncommon in *E. brunneolus* it seems preferable to consider *E. ater* and *E. brunneolus* similar, and both different from *E. kraussi*, in this character. Ornamentation of this sort on any or all of the dentary, articular, angular, and preopercular bones may be a specialization of the Omobranchini, perhaps more extensively developed in *Enchelyurus* (at least in this species group) than in *Omobranchus*.

Characters in which larval *E. ater* resemble *E. kraussi* (and both differ from *E. brunneolus*) include the size at which melanophores form at the anterior margin of the forebrain (18) and laterally on the hindbrain (25), pigmentation of the pectoral-fin base (31), and relative pectoral-fin length (Tables 1, 3, 6). Both *E. ater* and *E. kraussi* acquire the anterior forebrain melanophore early in the preflexion stage: it is present in 44% of *E. ater* smaller than 3 mm and in 85% of larger specimens. Respective values for *E. kraussi* are 33% for larvae smaller than 3.2 mm and 100% for larger specimens. *Enchelyurus brunneolus* lacks this melanophore in the preflexion stage and rarely has it before about 9 mm, well into the postflexion stage. On the other hand, *E. brunneolus* develops lateral melanophores on the hindbrain early in the flexion stage (by about 4.2 mm), in contrast to during the postflexion stage in *E. ater* (by about 6 mm) and *E. kraussi* (by 8.6 mm).

Pectoral-fin pigmentation is light but nearly always present on the mesial surface of the base (31) in *E. ater* (lacking only in the 11.4 mm specimen) and apparently always is present in *E. kraussi*, in contrast to *E. brunneolus* which has none before late postflexion stage, when a single melanophore may form on the lateral surface of the base near the insertion in some specimens (most commonly the pectoral base is unpigmented before settlement). Larval *E. kraussi* also acquire melanophores on the lateral surface of the pectoral-fin base by 8.6 mm, and in contrast to *E. ater* and *E. brunneolus*, on one or two of the lower fin-rays (32) by 11.5 mm. The degree of pectoral-fin pigmentation thus might be viewed as a gradient: *kraussi* > *ater* > *brunneolus*. Relative pectoral-fin length is similar in *E. ater* and *E. kraussi*, and smaller in both compared with *E. brunneolus*, throughout larval development (Tables 1, 3, 6).

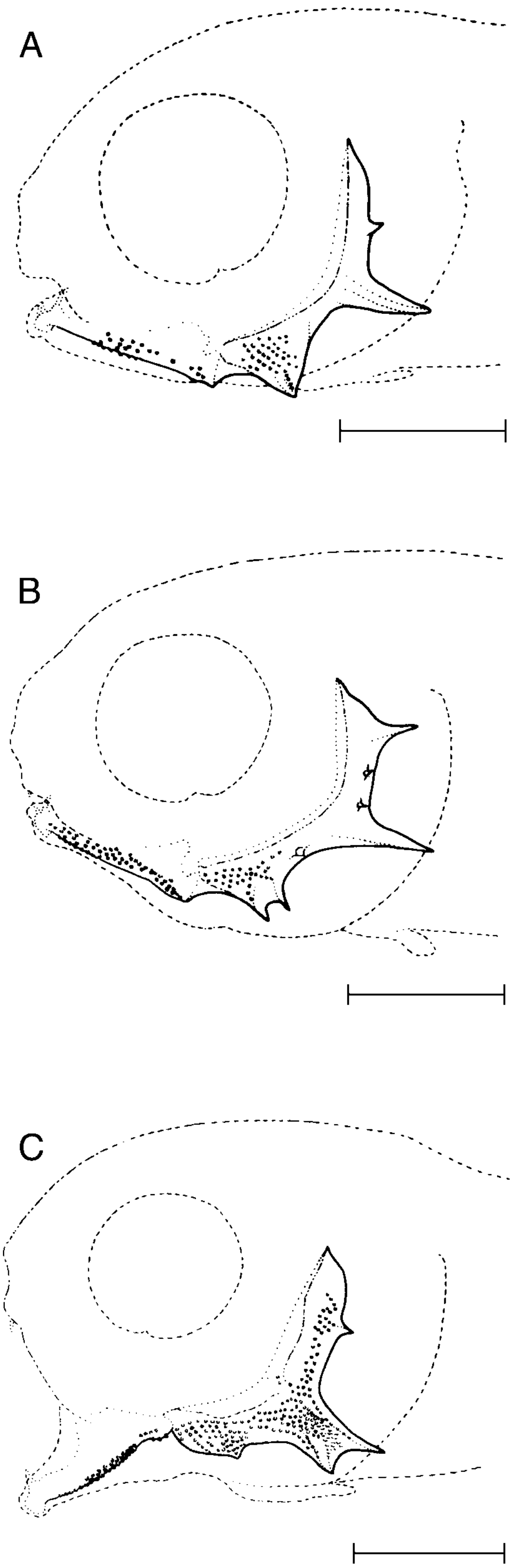

Figure 5. Ornamentation (slightly exaggerated for clarity) of the dentary, articular, angular, and preopercular bones of *Enchelyurus*. A, *E. ater*, 5.4 mm (I.29099-001). B, *E. brunneolus*, 5.9 mm (Kahe Transect Series, VM-3). C, *E. kaussi*, 5.5 mm (I.25131-001), the bifurcate major preopercular spine of this specimen is unusual. Scale bars = 0.5 mm.

Interrelationships

A formal phylogenetic analysis based on the larval characters of *Enchelyurus* was not done. Apart from the three *Enchelyurus* species, larval Omobranchini are known for only a few *Omobranchus* species (Mito, 1966; Visweswara Rao, 1970; Dotsu & Oota, 1973; Springer & Gomon, 1975; Houde *et al.*, 1986; Watson & Miskiewicz, 1998; Kawaguchi *et al.*, 1999). The interrelationships of these two genera are unknown (Springer, 1972) and thus an appropriate outgroup could not be selected. Blenniini has been hypothesised to be the sister group of Omobranchini plus Phenablenniini (whose larvae are unknown) and Nemophini (Springer, 1972; Smith-Vaniz, 1976; Bock & Zander, 1986; Williams, 1990). Among the three blenniin species only the larvae of *Blennius ocellaris* are known (Ford, 1922; Padoa, 1956; Russell, 1976). A cursory attempt was made to polarize the larval characters of *Enchelyurus*, using *B. ocellaris* as an outgroup. This required the assumptions that: 1) larval *Blennius ocellaris* are representative of the other two species of Blenniini; and 2) the characters presumed to be shared among the blenniins are plesiomorphic. Given these assumptions, and the limitations imposed by the level of detail available in the literature descriptions of larval *B. ocellaris*, only three morphological (3, 4, 13) and three pigmentation (18, 19, 31+32) characters (all but one of these, pectoral-fin pigmentation, may be interrelated) could be polarized. Among the morphological characters, *E. ater* and *E. brunneolus* display a presumed apomorphic state in acquiring teeth sooner and retaining an oval eye shape longer in development, and settling from the plankton at a smaller size (settlement size assumed for *E. ater*) than *B. ocellaris*. *Enchelyurus kraussi* is intermediate in that it acquires the round eye shape early like *B. ocellaris*, begins to develop teeth at an earlier stage than *B. ocellaris* but later than the other two *Enchelyurus* species, and probably settles from the plankton at a size smaller than *B. ocellaris* but larger than the others. Among the pigment characters, both *E. ater* and *E. brunneolus* share the presumed apomorphic state of delayed development of dorsal pigment over the forebrain area, in contrast to early development in *B. ocellaris* and *E. kraussi*. The presumed apomorphic state of delayed acquisition of internal forebrain pigment is displayed only by *E. brunneolus*; the other three acquire this pigmentation early in larval development. *Enchelyurus brunneolus* likewise is alone in displaying the presumed apomorphic state of unpigmented pectoral fins, in contrast to the extensively pigmented pectoral fins of *B. ocellaris*. *Enchelyurus ater* and *E. kraussi* display intermediate states, with pigment on the pectoral-fin base in both, and forming on some lower rays in *E. kraussi*.

These tenuous assessments of character polarity are an inadequate basis for demonstrating relationships, but they do suggest a hypothesis of relationships among the three *Enchelyurus* species: *E. ater* is the sister species to *E. brunneolus*, seemingly the most derived species in the group, and *E. kraussi*, perhaps the least derived, is the sister species to the other two.

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