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Larval Blennies from the Galapagos and Cocos Islands: Families Tripterygiidae, Dactyloscopidae, and Chaenopsidae (Perciformes, Blennioidei)

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Robert J. Lavenberg[2]

ABSTRACT. Postflexion larvae of ten eastern Pacific blennioid species from the Galapagos Islands and Cocos Island are described. Three families are treated: Tripterygiidae, Dactyloscopidae, and Chaenopsidae. The identifications were based on meristic data, and on comparisons of morphology between adults and large larvae. The larvae from the Galapagos Islands are *Lepidonectes corallicola* (Tripterygiidae); *Dactyloscopus lacteus, Myxodagnus sagitta, Platygillellus rubellulus,* and *Gillellus semicinctus* (Dactyloscopidae); and *Acanthemblemaria castroi* and *Chaenopsis schmitti* (Chaenopsidae). The larvae from Cocos Island are *Dactyloscopus pectoralis fallax* (Dactyloscopidae); and *Acanthemblemaria atrata* and *Stathmonotus* sp. (Chaenopsidae).

All larvae described herein possess the following characters: a relatively long and slender body; a melanophore anterior to the tip of the cleithral symphysis; ventral midline melanophores between pterygiophores of the anal fin; and a small head with a short and generally rounded snout (except in dactyloscopids and in the chaenopsid *Chaenopsis schmitti*). Larvae of *Lepidonectes corallicola* (Tripterygiidae) have a specific arrangement of melanophores on the pterygiophores of the third dorsal fin and at the base of spines of the second dorsal fin; pigment is found ventrally on the caudal peduncle and on the posterior margin of the hypural plates. Larvae of the dactyloscopids (*Dactyloscopus lacteus, Myxodagnus sagitta, Platygillellus rubellulus,* and *Gillellus semicinctus*) have large and pointed heads, short preanal length (30–35% standard length (SL)), and prominent dorsal and anal fins. The dactyloscopid larvae can be identified by specific combinations of characters: presence, number, and size of head melanophores; presence of pigmentation along dorsal margin of the body; presence of melanophores on the hypural borders; and fin structure and meristics. Most chaenopsid larvae possess a large and elongate melanophore in the midline along the basipterygium, a melanophore on the jaw angle, pigment dorsally to the anus, and a long preanal length (40–50% SL). Characters described herein suggest that some larval attributes may be informative for the elucidation of phylogenetic relationships within each family.

RESUMEN. Se describen las larvas en estado de postflexión de diez blenioídeos del pacífico este de las Islas Galápagos y de Isla del Coco. Las familias consideradas son Tripterygiidae, Dactyloscopidae y Chaenopsidae. Las identificaciones se basaron en información merística y en comparaciones de morfología de adultos con larvas avanzadas. Las larvas de las islas Galápagos son *Lepidonectes corallicola* (Tripterygiidae); *Dactyloscopus lacteus, Myxodagnus sagitta, Platygillellus rubellulus* y *Gillellus semicinctus* (Dactyloscopidae); y *Acanthemblemaria castroi* y *Chaenopsis schmitti* (Chaenopsidae). Las larvas de Isla del Coco son *Dactyloscopus pectoralis fallax* (Dactyloscopidae), y *Acanthemblemaria atrata* y *Stathmonotus* sp. (Chaenopsidae).

Características presentes en las larvas de todas las especies son: cuerpo relativamente largo y elongado, un melanóforo anterior de la sínfisis de los cleitros, una hilera ventral de melanóforos entre los pterigióforos de la aleta anal, y una cabeza pequeña con un hocico corto y redondeado (excepto en los dactiloscópidos y el chaenópsido *Chaenopsis schmitti*). Las larvas del blénido de tres aletas, *Lepidonectes corallicola,* tienen una configuración específica de melanóforos en los pterigióforos de la tercera aleta dorsal y en la base de algunas espinas de la segunda aleta dorsal; tienen además pigmento ventral en el pedúnculo caudal y en el margen posterior de las placas hipurales. Los dactiloscópidos (*Dactyloscopus lacteus, Myxodagnus sagitta, Platygillellus rubellulus* y *Gillellus semicinctus*) tienen larvas con una cabeza grande y puntiaguda, una distancia preanal corta (30–35% longitud estándar (LE)) y aletas dorsal y anal prominentes. Las especies pueden identificarse mediante combinaciones específicas de caracteres tales como presencia, número y tamaño de melanóforos cefálicos; presencia de pigmento dorsal sobre el cuerpo y en el borde posterior de las placas hipurales; y caracteres merísticos de las aletas. Las mayoría de las larvas de los chaenópsidos poseen un melanóforo grande y elongado ventral al basipterigio, un melanóforo en el ángulo mandibular, pigmento dorsal sobre el ano, y una mayor distancia preanal (40–50% LE). Los caracteres larvales descritos en este trabajo sugieren que algunos atributos pueden ser informativos para la elucidación de relaciones filogenéticas dentro de cada familia.

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INTRODUCTION

The blennioids are oviparous fishes (except for three viviparous genera) that lay their eggs attached to a nest substrate, and exhibit male parental care. The larvae are elongate and hatch with pigmented eyes and sparse pigmentation (Matarese et al., 1984; Stepien, 1986; Watson, 1996). Common features are the presence of large melanophores dorsally on the swimbladder and gut and small melanophores along the ventral margin of the trunk, between the pterygiophores of the long anal fin (Watson, 1996; Cavalluzzi, 1997).

The sizes of larvae at hatching and flexion vary depending on the species (Matarese et al., 1984), and the larvae do not show striking pigment patterns or morphological adaptations for pelagic life. Aside from some Blenniidae, the larvae of most blennioid families are largely limited to coastal waters (Watson, 1996). Indeed, some larvae have been observed to remain actively in coastal areas as they school in groups around kelp and other algae (Stepien et al., 1997).

Few characters are shared by all blennoid larvae, and most of them have been summarized by Matarese et al. (1984), Watson (1996), and Cavalluzzi (1997). These are: body moderately elongate; preanal distance between 30 and 50% of the standard length (SL); large swimbladder; melanophores on the ventral margin of the trunk (between pterygiophores of the anal fin); a melanophore on the tip of the cleithral symphysis (Herrera and Lavenberg, 1999); and six branchiostegal rays.

Matarese et al. (1984) summarized the larval characters of some Blennioidei, at a time when not many descriptions were available. The best known larvae are those of the families Blenniidae and Tripterygiidae, probably because of their wider distributions and greater species numbers. The knowledge of the larvae of the other four families, which are predominantly from the New World, has increased in recent years with the descriptions of larvae from the Gulf of California (Brogan, 1992), the California Current region (Watson, 1996), and the western Atlantic (Cavalluzzi, 1997). The larvae of species from the southeastern Pacific are less well known (Balbontín and Pérez, 1979; Perez, 1979).

Nineteen Blennioidei are known from the Galapagos Islands, twelve of which are endemic (Grove and Lavenberg, 1998). They belong to the families Tripterygiidae (one species), Dactyloscopidae (five species), Blenniidae (three species), Labrisomidae (seven species), and Chaenopsidae (three species). No species of the family Clinidae are known from the archipelago. In this paper, field-collected specimens mainly from the Galapagos Islands, obtained from plankton samples collected during the Allan Hancock expeditions, are described. Additionally, the larvae of three species from Cocos Island, Costa Rica, are included. The material considers postflexion larval stages and some juveniles. Larvae of the following species are described: Tripterygiidae, *Lepidonectes corallicola* (Kendall and Radcliffe, 1912); Dactyloscopidae, *Dactyloscopus lacteus* (Myers and Wade, 1946), *D. pectoralis fallax* (Dawson, 1975), *Myxodagnus sagitta* (Myers and Wade, 1946), *Platygillellus rubellulus* (Kendall and Radcliffe, 1912), and *Gillellus semicinctus* (Gilbert, 1890); and Chaenopsidae, *Acanthemblemaria castroi* (Stephens et al., 1966), *A. atrata* (Hastings and Robertson, 1999), *Chaenopsis schmitti* (Böhlke, 1957), and *Stathmonotus* sp. The larvae of *D. pectoralis fallax, A. atrata,* and *Stathmonotus* sp. were collected in Cocos Island. Larvae of six species of the family Labrisomidae (from the seven species cited for the archipelago) were described separately (Herrera and Lavenberg, 1999).

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MATERIALS AND METHODS

Most of the plankton samples were collected by the R/V *Velero III,* during the Allan Hancock Pacific expedition cruises to the eastern Pacific and Galapagos Islands. Sampling sites included Española, Santa María, Santa Cruz, Isabela, Baltra, and Genovesa Islands (Fraser, 1943). A single sample was collected in Chatham Bay, Cocos Island, Costa Rica. Samples were normally collected at night (at anchorage), using an electric light and dip nets. The larvae are housed in the larval fish collection at the Natural History Museum of Los Angeles County (LACM). The specimens were measured to the nearest 0.1 mm and illustrated with a camera lucida. The size range of the series illustrated was determined by the available material. Although the larval series are not complete because of the sporadic nature of the sampling, they still contain valuable ontogenetic information. Meristic data were obtained from collection specimens and from the literature. Measurements and definitions follow those of Leis and Rennis (1983).

The larvae of the three species of Blenniidae from Galapagos, *Hypsoblennius brevipinnis* (Günther, 1861), *Ophioblennius steindachneri* (Jordan and Evermann, 1898), and *Plagiotremmus azalea* (Jordan and Bollman, 1890), were also found together with the larvae described here and in a previous work (Herrera and Lavenberg, 1999). These three species have a wide distributional range in the eastern Pacific and their larvae have been described from the California region (Watson, 1996). Larvae of another blennioid, the dactyloscopid *Dactylagnus mundus* (Gill, 1862), were not found in the samples.

RESULTS

The following descriptions include general characterizations of morphology, dorsal- and anal-fin development, and pigmentation. The larval series are limited by the available material collected. For those species represented by a few individuals the descriptions are restricted to a usually narrow size range. Meristic data and information about preanal distance, a helpful diagnostic character of larval blennioid families, are summarized in Table 1.

Table 1. Selected meristic and morphologic data for species of Tripterygiidae, Dactyloscopidae, Blenniidae, and Chaenopsidae included in this study.

Species	Vertebrae	Dorsal*	Anal*	P1*	Pigmentation: Dorsal head	Pigmentation: Dorsal trunk	Pigmentation: Hyp. border	Pigmentation: Ventral gut	Preanal distance (%)	Reference
Tripterygiidae										
Lepidonectes corallicola	37–38[x]	III, XIII, 12–13	II, 21–22	17–18	+ (3 pairs)	+	+	+	41–43	1
Dactyloscopidae										
Dactylagnus mundus†	46–53	(VIII–XII), (28–34)	II, (35–41)	14–16	+	?	?	+		2, 3
Dactyloscopus lacteus	39–43	X–(XIII), (24)–28	II, 28–(31)		+ (1 large)	–	+	+	34–31	4
Dactyloscopus pectoralis fallax#	38–43	XI–XIII, (23–27)	II, 28–(32)		+	+	–	+	31	4
Myxodagnus sagitta	45–(50)	(VII)–X, 27–(31)	II, (33–37)	13–14	+ (1 large)	+	+	+ (1 large)	28–30	2
Platygillellus rubellulus	38–40	XVII–(XIX), 16–(18)	II, (26–29)	(13–15)	+ (2 pairs)	–	+	–	33–35	5
Gillellus semicinctus	(41)–47	(XI–XIV), (25–30)	II, (30–35)	(11–14)	–	–	–	+ (2 small)	30–32	6
Blennidae										
Hypsoblennius brevipinnis	29–31	XI–XIII, 11–13	II, 12–14	13–15	+	–	–	–	43–52	7
Ophioblennius steindachneri†	35–36	XI–XIII, 21–23	II, 22–24	15	–	–	+	–	37–42	3, 7
Plagiotremus azalea	46–51	VII–IX, 31–36	II, 26–30	(11–13)	+	+	+	–	43–50	3, 7
Chaenopsidae										
Acanthemblemaria castroi	43–46	XXIII–XXV, 12–14	II, 24–26	13–14	–	–	–	+	40–44	8
Acanthemblemaria atrata		XXIV–XXV, 12–13	II, 24–25	13	–	–	+	+	41–45	This study
Chaenopsis schmitti		XVII–XVIII, (33–36)	II, 34–35	13	–	–	–	–	40–44	8, 9, 10
Stathmonotus sp.	44–47	XXXVII–XLI	II, 20–(25)	9–11	–	–	–	+	52	11, this study

* Counts in parentheses are less frequent; ranges in parentheses indicate that both extreme values are less frequent; underscored are most frequent counts.

[x] Count from X-rayed specimens.

† Not found in samples but present in the Galapagos.

Collected from Cocos Island.

References: (1) Bussing (1991); (2) Dawson (1976); (3) Brogan (1992); (4) Dawson (1975); (5) Dawson (1974); (6) Dawson (1977); (7) Watson (1996); (8) Rosenblatt and McCosker (1988); (9) Stephens (1963); (10) Stephens et al. (1966); (11) Hastings and Springer (1994).

DESCRIPTION OF LARVAE

Family Tripterygiidae

A single triperygiid occurs in the Galapagos Islands, the endemic *Lepidonectes corallicola.* In general, the larvae of the Tripterygiidae are elongate and slightly compressed; have small short and rounded heads with no spination; have dorsal, anal, and pectoral fins that develop early (shortly after flexion); and have the spines of the first dorsal and on the anal fins that form last (Leis and Rennis, 1983).

Lepidonectes corallicola (Kendall and Radcliffe, 1912)

Figure 1

MATERIAL EXAMINED. From 2,281 specimens (6.2–18.3 mm SL), five are illustrated; LACM 45614-6 (8.3, 10.0, 13.0, and 15.1 mm SL) and LACM 45621-17 (17.2 mm SL).

MORPHOLOGY. The body is moderately elongate (preanal length 41–43% body length (BL)) with a small head and rather small and rounded snout. Flexion completed by 8.0 mm. Anal fin, third dorsal fin, and pelvic fins are apparent by 8.0 mm. First and second dorsal fin apparent by 13.0 mm SL. Pores of the preopercular and circumorbital sensory canal systems are evident by 17.2 mm SL.

PIGMENTATION. In small larvae (6.2 mm) a single dorsal melanophore is present on the nape; this melanophore becomes embedded with growth. Other cephalic pigmentation includes a pair of melanophores on the hindbrain (Figs. 1a–b), which increases to three pairs with the appearance of pairs on the midbrain and forebrain (Fig. 1e). Gut pigment consists of a single melanophore located ventroanteriorly (behind insertion of the pelvic fins).

By 8.3 mm SL three to five melanophores are present on the ventral midline of the caudal peduncle, and the posterior margins of the upper and lower hypural plates each possess a single melanophore. By 10.0 mm, dorsal midline melanophores are associated with the posterior portion of the third dorsal fin, and the posterior margin of the upper and lower hypural plates each possess two melanophores. By 15.1 mm SL, the second dorsal fin has a single melanophore at the base of spines 1, 3, and 7–11 (rarely associated with spines 2 and 6), the third dorsal fin has a single melanophore at the base of each soft ray, the posterior margins of the dorsal and ventral hypural plates have a wide band of pigment, two melanophores are present on the upper jaw, and small melanophores pepper the membrane between rays of the caudal fin, mainly in the lower half. By 17.2 mm SL, the juvenile stage is observed. Additional pigment includes a lateral band of small melanophores extending from the pectoral-fin base to the end of the caudal peduncle.

REMARKS. Below 10.0 mm SL, the larvae are similar in appearance to some labrisomids, especially those species lacking preopercular spines. However, pigmentation, meristics, and morphometrics can differentiate them. In *L. corallicola* dorsal midline melanophores develop from posterior to anterior (opposite for *Malacoctenus zonogaster,* Labrisomidae), length to the origin of the third dorsal fin is 60–63% SL in *L. corallicola* (68–71% SL in *M. zonogaster*), and preanal distance is 41–43% SL in *L. corallicola* (38–41% in *M. zonogaster*). After 10.0 mm SL, the presence of three distinct dorsal fins in *L. corallicola* separates this species from the labrisomids.

Family Dactyloscopidae

The family Dactyloscopidae is restricted to the New World, in the Pacific and Atlantic Oceans. A few descriptions of dactyloscopid larvae from the Gulf of California (Brogan, 1992), Baja California (Watson, 1996), and the Atlantic (Cavalluzzi 1997) are available. From these, the larvae of the sand stargazers can be characterized as having an elongate body, a short and compact gut, long and relatively high dorsal and anal fins, jugular pelvic fins, 5+5 principal caudal rays, and a large head with pointed snout and no cirri. The preanal length is short, compared to that of other families, and ranges from 28–35% SL (see Table 1). The species from the Galapagos show specific arrangements of cephalic, hypural, and trunk pigment. The posterodorsal region of the swimbladder is pigmented, but it is difficult to see the melanophores, especially in larger or more robust larvae (such as *Dactyloscopus*).

Dactyloscopus lacteus (Myers and Wade, 1946)

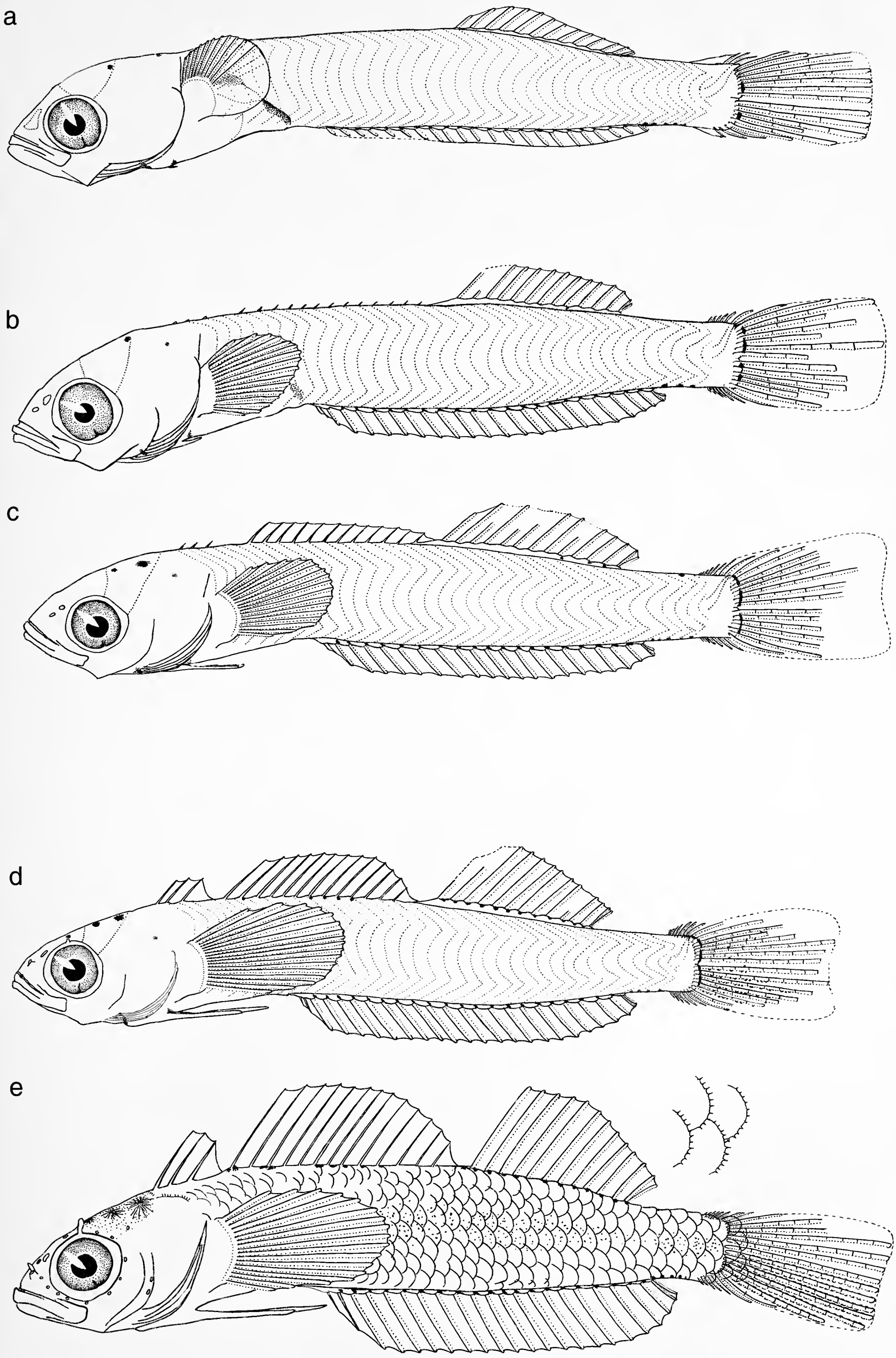
Figure 2

MATERIAL EXAMINED. Only two specimens collected; LACM 45628-5 (7.7 mm SL) and LACM 45617-2 (9.2 mm SL).

MORPHOLOGY. The head is large and deep with a pointed snout and a slight projection of the tip of the lower jaw. Preanal length reaches 31–34% SL. The larvae lack a notch on the ventral margin of the caudal peduncle, a character that is present in adults of many *Dactyloscopus* species (Dawson, 1975). At 7.7 mm, the anal-fin rays are longer and more prominent than the dorsal-fin rays, indicating that the anal fin develops earlier. At this size, only the rayed portion of the dorsal fin

→

Figure 1 Larvae of *Lepidonectes corallicola*: (a) 8.3 mm (b) 10.0 mm (c) 13.0 mm (d) 15.1 mm (LACM 45614-6) (e) 17.2 mm (LACM 45621-17)


a
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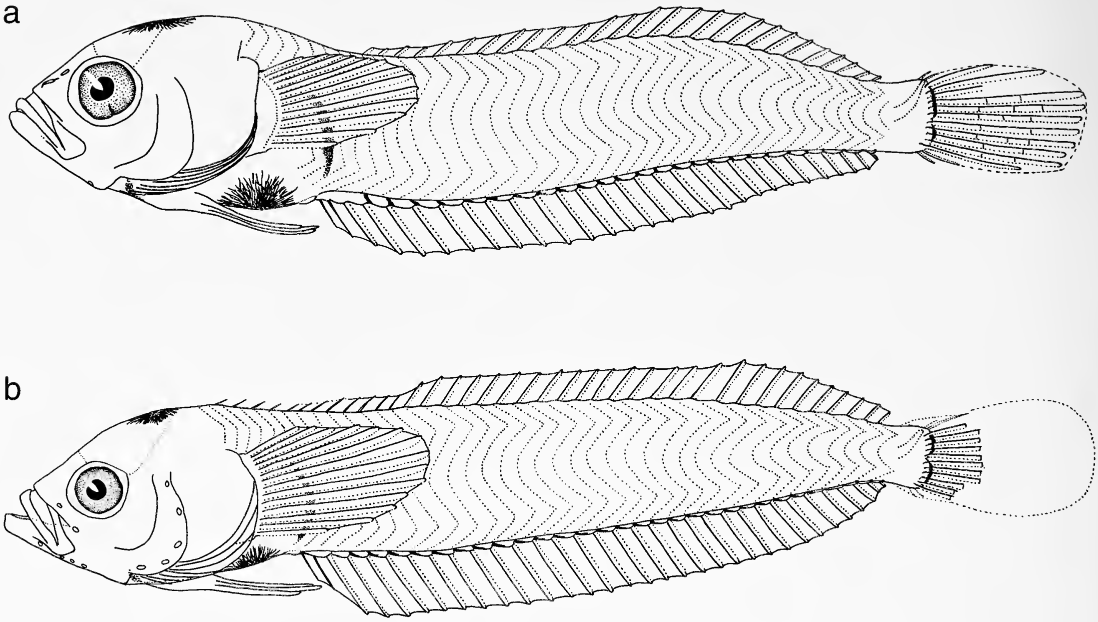

Figure 2 Larvae of *Dactyloscopus lacteus*: (a) 7.7 mm (LACM 45628-5); (b) 9.2 mm (LACM 45617-2)

has developed (Fig. 2a). By 9.2 mm all dorsal-fin spines have formed although they are not yet at their maximum length and sensory pores have formed on the preopercular border, the ventral margin of the lower jaw and below the eye (Fig. 2b).

PIGMENTATION. In addition to the pigmentation anterior to the tip of the basipterygium, *Dactyloscopus lacteus* has another small melanophore on the basipterygium, close to the tip. The two melanophores are very close and usually difficult to distinguish from each other when expanded. Two large dendritic melanophores are present; one dorsally on the head, and the other ventrally on the gut. No melanophores occur dorsally along the trunk or on the caudal peduncle. The posterior margins of the hypural plates are pigmented. This differs from *D. pectoralis* (Brogan, 1992), *D. byersi* (Watson, 1996), and *D. pectoralis fallax* (Dawson, 1975).

Dactyloscopus pectoralis fallax (Dawson, 1975)
Figure 3

MATERIAL EXAMINED. Description of a single specimen, LACM 45658 (10.0 mm SL), from three larvae (all near 10.0 mm SL) collected in Cocos Island, Costa Rica.

MORPHOLOGY. The body shape is similar to that of *Dactyloscopus lacteus.* The preanal length is 30–32% BL. At 10.0 mm SL head pores or dorsal spines have not yet formed, which may differ from *D. lacteus,* because the latter species had them by 9.2 mm (see Fig. 2b). The soft dorsal has formed although it has not reached its maximum size, and the dorsal spines are small projections.

PIGMENTATION. *Dactyloscopus pectoralis fallax* has a single dendritic melanophore dorsally on the head and another ventrally on the gut. The sole difference between *D. pectoralis* and *D. pectoralis*

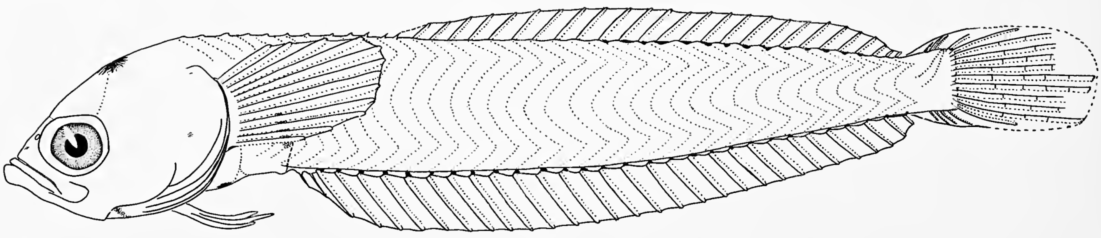

Figure 3 Larva of *Dactyloscopus pectoralis fallax*: 10.0 mm (LACM 45658-2)

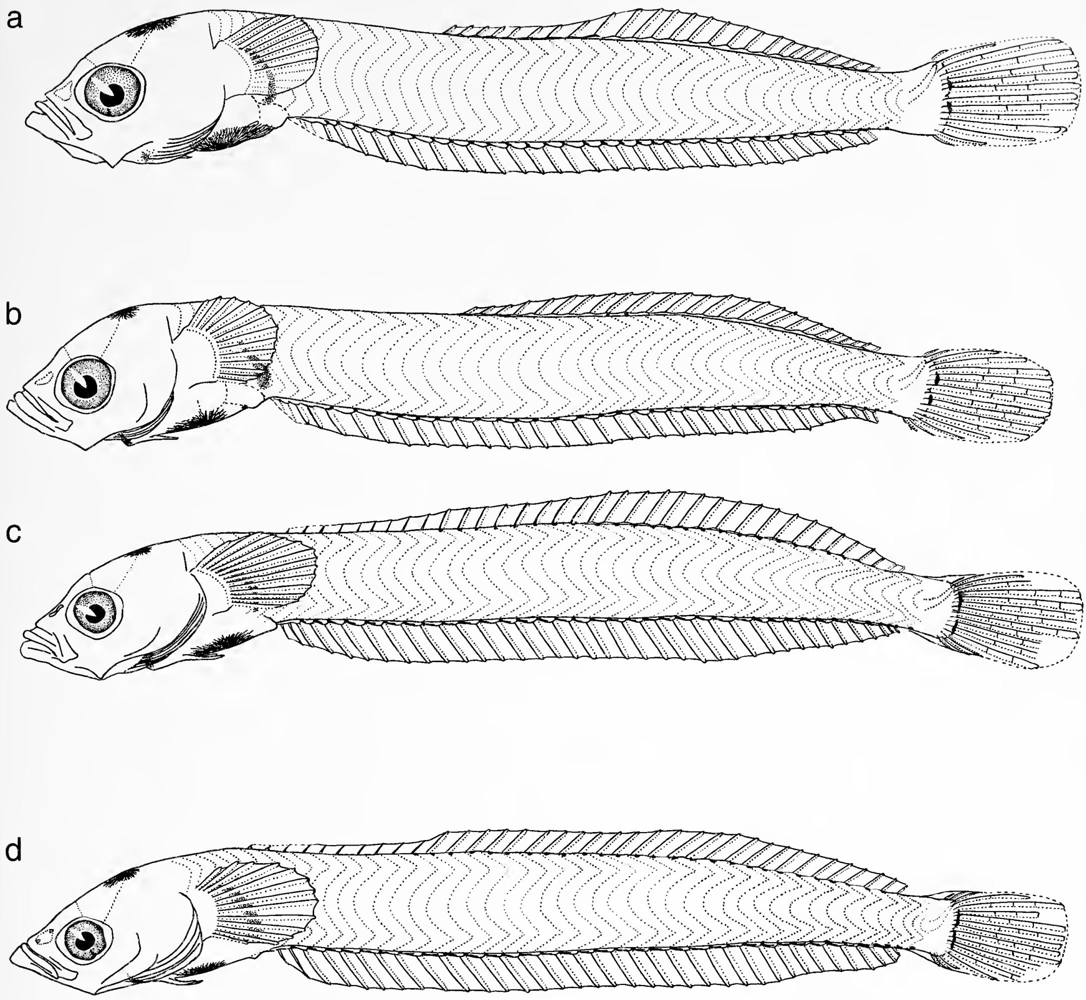

Figure 4 Larvae of *Myxodagnus sagitta*: (a) 7.3 mm (b) 8.8 mm (LACM 45625-7) (c) 11.6 mm (LACM 45623-10) (d) 13.4 mm (LACM 45625-7)

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fallax is the presence in the former of several melanophores ventrally on the gut (Brogan, 1992) that are not present in the latter. However, more specimens of *D. pectoralis fallax* should be examined to determine whether this pigment appears later in the ontogeny.

Myxodagnus sagitta
(Myers and Wade, 1946)
Figure 4

MATERIAL EXAMINED. From a total eighty-two specimens collected, in the size range of 7.0–14.0 mm, four are used for description; LACM 45625-7 (7.3 and 8.8 mm SL), LACM 45623-10 (11.6 mm SL), and LACM 45625-7 (13.4 mm SL).

MORPHOLOGY. Among the larval dactyloscopids studied, this species has the most slender and elongate body, the smallest head, and the shortest preanal distance (28–30% BL). The anal- and dorsal-fin rays have developed by 7.0 mm (Fig. 4a), whereas the dorsal spines develop later (Fig. 4c) The head is deep in small larvae, as in most dactyloscopids, but becomes depressed with development. The anterior projection of the lower jaw is slight in small larvae, and increases with size. Pelvic fins develop at an early stage (Fig. 4a), but they remain smaller than in all other species of the family.

PIGMENTATION. The cephalic pigmentation pattern of *Myxodagnus sagitta* resembles that of *Dactyloscopus lacteus,* with a large dendritic melanophore above the head and below the gut. Furthermore, a melanophore is present at the base of each dorsal ray, except in the last one to two rays. A small melanophore develops on the ventral margin of the caudal peduncle; these melanophores are lacking in *M. opercularis* (Brogan, 1992; Watson,

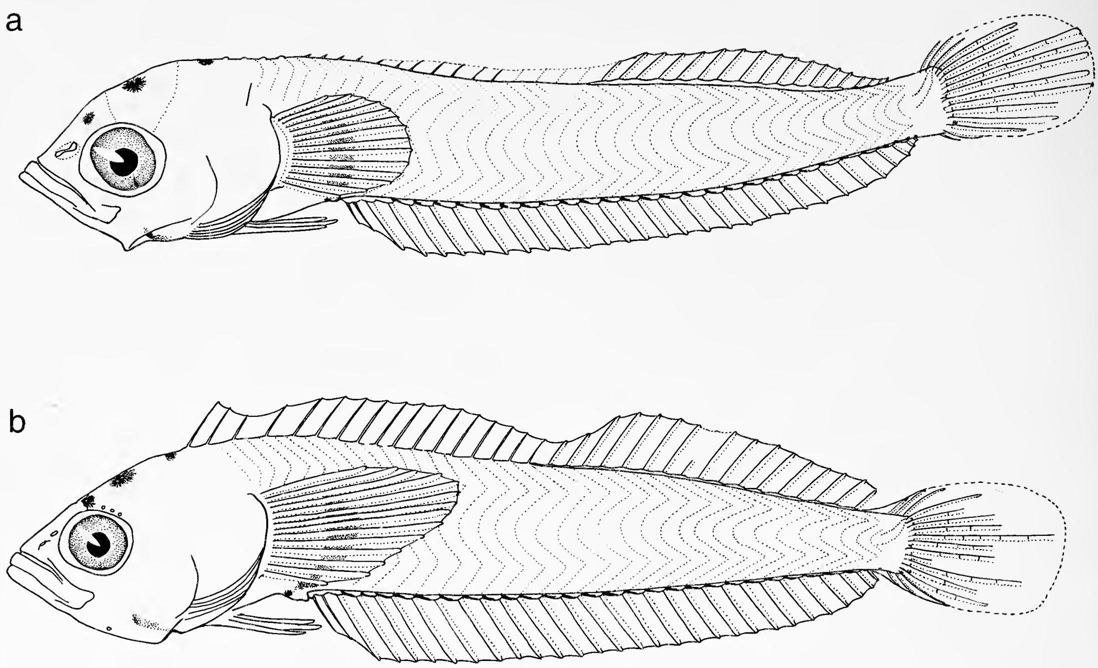

Figure 5 Larvae of *Platygillellus rubellulus*: (a) 8.9 mm (LACM 45614-11) (b) 11.1 mm (LACM 45621-10)

1996). In smaller larvae, the posterior edge of each hypural plate has one small melanophore on the border; these melanophores increase with development forming bands of pigment. In some specimens a small melanophore develops directly anterior to the anus (Fig. 4d).

Platygillellus rubellulus (Kendall and Radcliffe, 1912) Figure 5

MATERIAL EXAMINED. Two specimens, out of fifteen collected (size range 8.0–11.1 mm SL) are described; LACM 45614-11 (8.9 mm SL) and LACM 45621-10 (11.1 mm SL).

MORPHOLOGY. The body shapes of *Platygillellus rubellulus* and *Dactyloscopus lacteus* larvae are similar in having large heads and deep bodies anteriorly, but differing in cephalic pigmentation. The preanal length reaches 33–35% BL, which is the longest among the studied dactyloscopids. At 11.1 mm, three pores occur above the eye and one occurs on the margin of the lower jaw. The dorsal fin is notched anteriorly, with the third spine shorter than the adjacent ones, anterior and posterior. In addition, the third and fourth spines are more separated from one another than other dorsal spines. The last four dorsal spines decrease in size and first four dorsal-fin rays increase progressively in size. The relative sizes of spines and rays resembles a doubly notched dorsal fin (Fig. 5b).

PIGMENTATION. Pigment pattern is the same in both illustrated larvae. Two pairs of melanophores occur dorsally on the head; a large pair above the midbrain, and a small pair over the forebrain. A single melanophore is present on the nape. Except for a small single melanophore before the anus, no ventral melanophores are found on the gut. A single and small melanophore occurs on the ventral margin of the caudal peduncle just behind the last anal-fin ray. Another ventral midline melanophore is found immediately anterior to the ventral hypural plate. This melanophore varies in position from the space between fourth and fifth caudal rays (lower hypural), on the fifth ray, in the space between the last two procurrent caudal rays, and slightly in front of the first procurrent caudal ray.

Gillellus semicinctus (Gilbert, 1890) Figure 6

MATERIAL EXAMINED. Of the forty specimens collected, three are used for description: LACM 45614-19 (6.5, 10.0, and 12.4 mm SL).

MORPHOLOGY. The larvae are more elongate than those of *Dactyloscopus lacteus* and the head is proportionally smaller. The preanal length reaches 30–32% SL. Figure 6 shows the approximate formational sequence of the dorsal- and anal-fin spines and rays, and the subtle projection of the lower jaw with development. At 6.5 mm flexion is complete, the anal fin is beginning to develop, and the dorsal fin has not formed (Fig. 6a). In the largest larva, 12.4 mm, the first three dorsal spines, which are separated from the following spines in the form of a finlet, are present. Their lengths de-

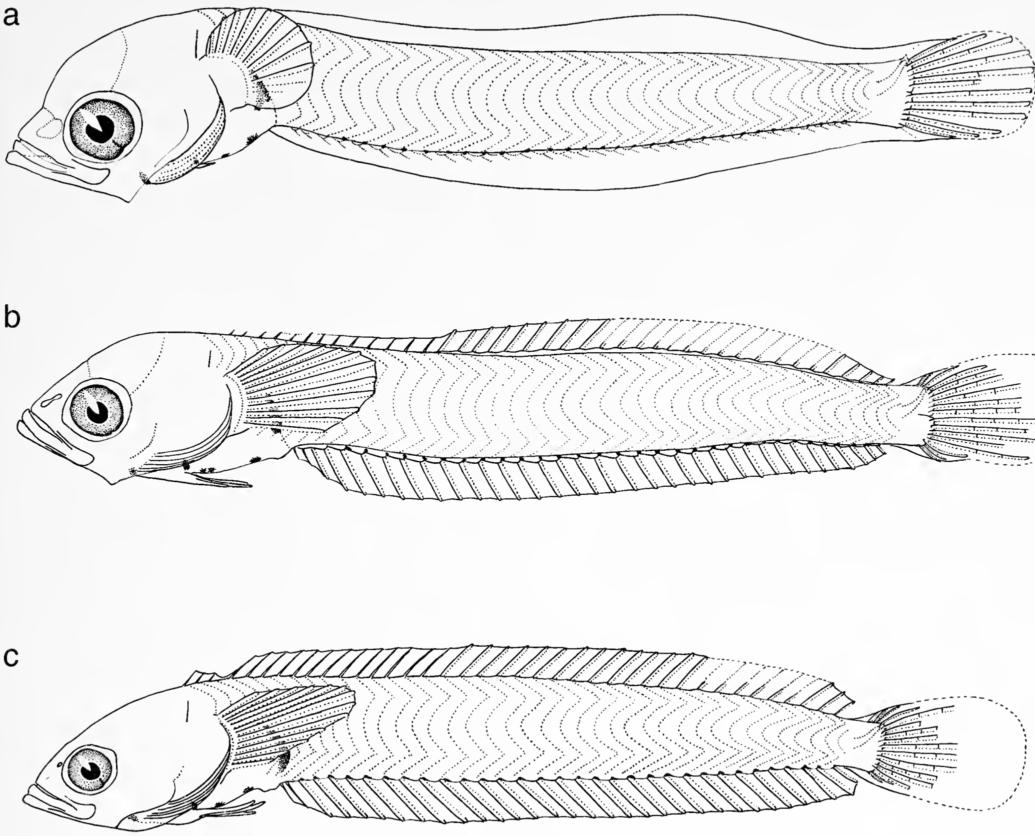

Figure 6 Larvae of *Gillellus semicinctus*: (a) 6.5 mm, (b) 10.0 mm, and (c) 12.4 mm (LACM 45614-19)

crease progressively from the first to the third (Fig. 6c). Posteriorly, the dorsal spines and rays are approximately the same size, and the border of the dorsal fin is straight.

PIGMENTATION. Pigment pattern does not change in the size range studied. The larvae of *Gillellus semicinctus* have two or three small melanophores ventral to the gut. One (or two in some larvae) is always just posterior to the insertion of the pelvic-fin rays, and the second is located more posteriorly next to the anus. A ventral and internal melanophore is also present behind the cleithra. Pigment is absent dorsally on the head, which is an uncommon feature in the family that has been also reported in larvae of two other species of *Gillellus* from the western Atlantic, *G. jacksoni* and *G. uranidea* (Cavalluzzi, 1997). This lack of pigment may be a reductive specialization characterizing the genus.

Watson (1996) described larvae of a *Gillellus* species, tentatively ascribed to *semicinctus*. However, in his series the pretransformation specimens (<13.3 mm) develop preopercular spines and a ventral series of melanophores at the anal-fin base that is not continuous. The larvae described here do not have preopercular spines and a continuous melanophore series occurs between pterygiophores. The differences may be due to intraspecific variation or the larvae may belong to different species.

REMARKS ON DACTYLOSCOPID LARVAE

The relationships between the eight dactyloscopid genera have been studied by Doyle (1998) using morphological data. *Heteristius* is the basalmost taxon, and *Platygillellus* is the next basalmost taxon. The remaining six genera are divided into two clades; one of them includes *Gillellus* (together with *Leurochilus* and *Sindoscopus*) and the other comprises *Dactyloscopus, Dactylagnus,* and *Myxodagnus*. Some of the larval characters presented here are congruent with the relationships hypothesized by Doyle (1998). A large, single, medial dendritic melanophore occurs dorsally on the head and ventral to the gut in the derived clade comprising *Dactylagnus, Myxodagnus,* and *Dactyloscopus*. These genera also share the same general body shape, with a straight anterior profile of the dorsal fin and a shorter preanal distance. In the other derived clade, the larvae of *Gillellus* lack cephalic melanophores, which represents a derived condition. Unfortunately, larvae of the other two genera of the clade, *Leurochilus* and *Sindoscopus,* are not known.

The larvae of the phylogenetically more primitive *Platygillellus* show features that can be considered plesiomorphic and include small melanophores in pairs above the brain (vs. large and single), a longer preanal distance (vs. shorter), a dorsal fin divided into regions (vs. straight margin), and several small ventral melanophores on the gut (vs. single and large).

Family Chaenopsidae

The tube blennies are found in tropical and temperate coastal waters of the New World, in both the eastern Pacific and western Atlantic. Compared to other blennies, chaenopsid larvae have a relatively longer and straighter gut with a prominent dorsally pigmented swimbladder. Most species have a large and elongate melanophore midventral at the basipterygium area. Other larval characters include the presence of pigment dorsally to the anus, pelvic fins that are inserted close to the base of the pectoral fin, rugae in the gut, ventral pigment on gut and breast, no dorsal pigmentation, and a broad and serrated premaxilla with a long ascending process (Brogan, 1992).

Acanthemblemaria castroi (Stephens et al., 1966)

Figure 7

MATERIAL EXAMINED. From the 712 larvae examined, in the size range of 5.3 mm notochord length (NL) to 16 mm SL, five were used for descriptions: LACM 45621-1 (5.3 mm NL), LACM 45644-1 (8.4 mm NL), LACM 45614-1 (12.4 mm SL), LACM 45623-1 (14.0 mm SL), and LACM 45614-1 (16.0 mm SL).

MORPHOLOGY. Larvae are characterized by elongate body, preanal length of 40–44% BL, small and rounded head with a short snout, developing bifid nasal cirri, and bifid orbital cirri. Flexion occurs after 5.3 mm and is complete by 10.0 mm, at which time the dorsal and anal-fin rays develop. The dorsal spines begin to develop by 12.0 mm.

PIGMENTATION. In addition to the general blennioid pattern, the larvae of *Acanthemblemaria castroi* have melanophores that become embedded during development located above the swimbladder and anus; a melanophore on the mandibular angle by 12.4 mm SL (Fig. 7c); a single melanophore on the nape that becomes partially embedded with growth (Figs. 7b-e); and three to four small melanophores that are present during all stages on the ventral midline of the caudal peduncle (Fig. 7a). No pigment occurs ventrally on the gut, or on the posterior border of the hypurals.

Acanthemblemaria atrata (Hastings and Robertson, 1999)

Figure 8

MATERIAL EXAMINED. Five larvae from a total of 214 collected in Chatham Bay, Cocos Island, Costa Rica, in the size range of 4.1–18.4 mm, are illustrated: LACM 46011-1 (4.1 mm NL, 5.3 mm NL, 6.9 mm SL, 11.8 mm SL), and LACM 45658-1 (18.4 mm SL)

MORPHOLOGY. The larvae are similar in morphology and meristics to those of *Acanthemblemaria castroi,* but differ slightly in pigmentation. The largest specimen (18.4 mm SL) has both single nasal cirri and single orbital cirri; while larval pigmentation is still present, heavy cranial spination appears along with sensory pores of the mandibular, nasal, occipital, preopercular, and orbital series. The dorsal- and anal-fin formation is similar to that of *A. castroi.*

PIGMENTATION. The larvae of *Acanthemblemaria atrata* show the same pigment pattern as *A. castroi,* but in addition exhibit a band of melanophores on the posterior margin of the hypural plates. Further, one or two melanophores develop ventrally on the anus (Figs. 8a–c); these melanophores disappear during development (Figs. 8d–e). A more complete larval series is described for this species, which allows following of the formation pattern of the ventral melanophore on the basipterygium. Two elongate melanophores develop laterally in early stages, converging anteriorly in an inverted V-shaped pattern, with the wings of the V fusing along the midventral margin (Brogan, 1992).

Chaenopsis schmitti (Boelke, 1957)

Figure 9

MATERIAL EXAMINED. Only two specimens collected; LACM 45614-3 (8.0 and 14.6 mm SL).

MORPHOLOGY. Among all the blennioids considered here, this species has the most slender and elongate body. The preanal length ranges from 40–44% BL. The snout is pointed and increases in length with size. At 8.3 mm SL only the posterior rays of the dorsal fin are developed, whereas anal-fin rays are just forming. By 14.6 mm, the rayed portion of both the dorsal and anal fin are formed, and the dorsal-fin spines are appearing.

PIGMENTATION. The larvae of *Chaenopsis schmitti* possess single melanophores at the mandibular angle, midlaterally on the preoperculum, and on the hindbrain. No melanophores are present on the caudal peduncle.

Stathmonotus sp.

Figure 10

MATERIAL EXAMINED. A single specimen was collected in Chatham Bay, Cocos Island, Costa Rica; LACM 45634-15 (8.3 mm SL). Although the genus has not been reported there, the specimen can be tentatively ascribed to the species *Stathmonotus culebrai* based on meristic data. Also, *S. culebrai* is the only species of the genus from Pacific Central America (Hastings and Springer, 1994).

MORPHOLOGY. The general shape of the larva is similar to that of *Stathmonotus stahli* and *S. hemphilli* (Brogan, 1992; Cavalluzzi, 1997), with a

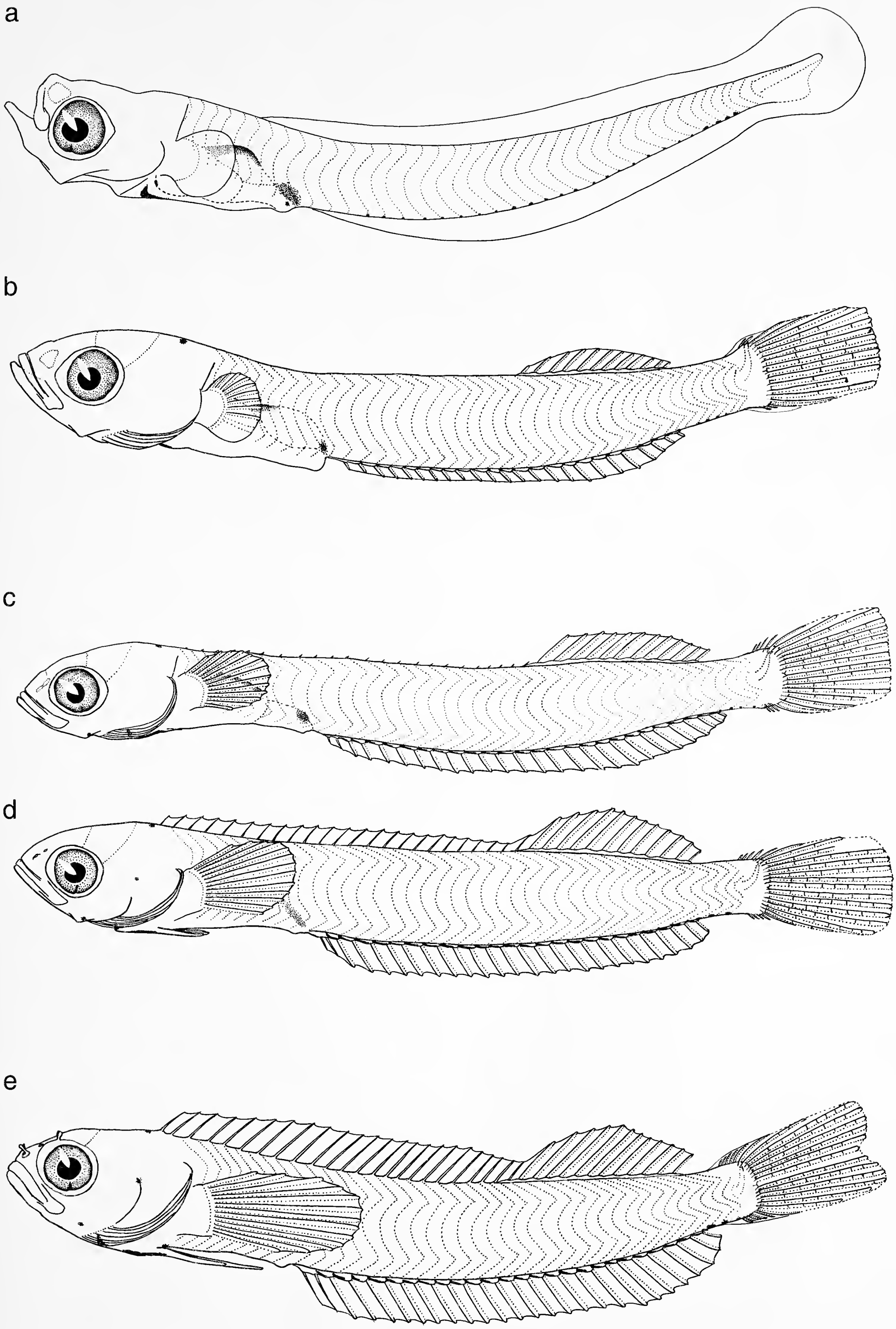

Figure 7 Larvae of *Acanthemblemaria castroi*: (a) 5.3 mm (LACM 45621-1) (b) 8.4 mm (LACM 45644-1) (c) 12.4 mm (LACM 45614-1) (d) 14.0 mm (LACM 45623-1) (e) 16.0 mm (LACM 45614-1)

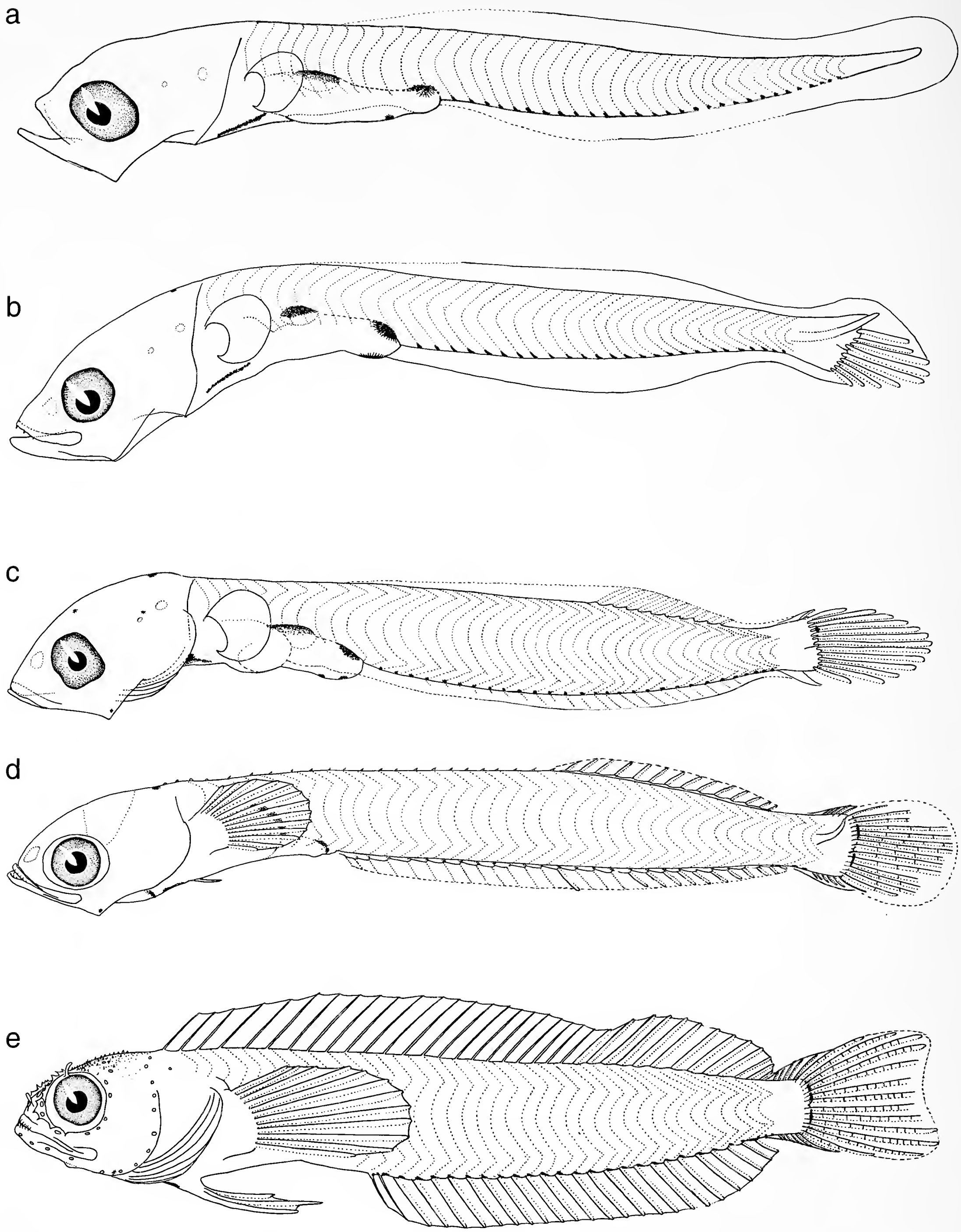

Figure 8 Larvae of *Acanthemblemaria atrata*: (a) 4.1 mm (b) 5.3 mm (c) 6.9 mm (LACM 46011-1) (d) 11.8 mm (e) 18.4 mm (LACM 45658-1)

small and round head, and a prominent swimbladder. The preanal length reaches approximately 50% BL (the longest among chaenopsids); the dorsal fin originates behind the level of the pectoral-fin base (vs. anterior to the pectorals in the other three chaenopsids); and the number of pectoral-fin rays is low (9–11 vs. 13–14 in other Chaenopsidae). In adult *Stathmonotus* all dorsal-fin elements are

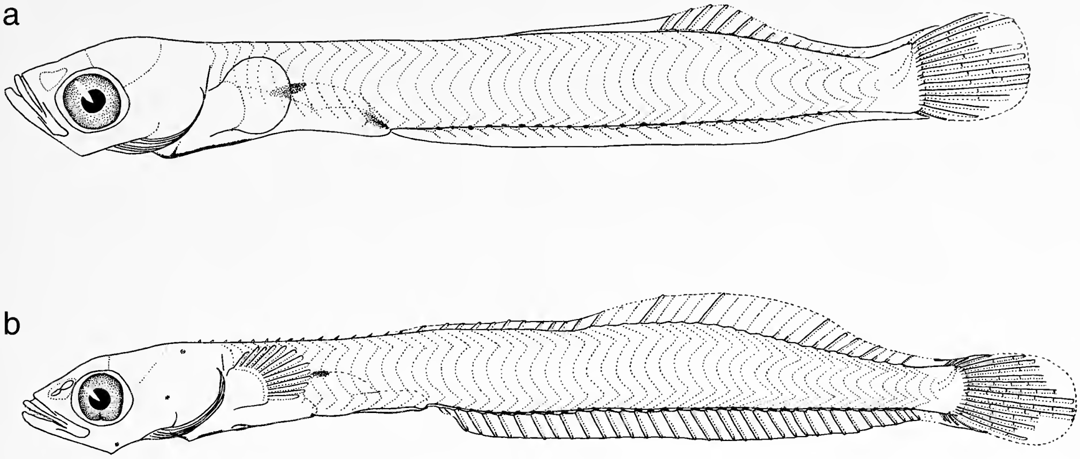

Figure 9 Larvae of *Chaenopsis schmitti*: (a) 8.0 mm (b) 14.6 mm (LACM 45614-3)

spines (37–41). In the larva, the dorsal fin is composed by two portions, with twenty-one spines and seventeen soft rays, which indicates that the most posterior spines of the adult dorsal fin are the result of secondary ossification.

PIGMENTATION. The specimen appears to be somewhat bleached and some pigment may be missing. The larva has a pair of small ventral melanophores immediately behind the insertion of the pelvic-fin rays, a single ventral melanophore on the gut, and a melanophore over the anus. No melanophores appear on the trunk, caudal peduncle, or the hypural margins. The midventral melanophore at the basipterygium is not visible, but it may be embedded, as in *Stathmonotus sinuscalifornici* at a similar size (Brogan, 1992). The pigmentation of this specimen lacks the expanded and stellate melanophores along the ventral margin of the trunk and gut of *S. sinuscalifornici* (Brogan, 1992) or the lines of melanophores near the dorsal (of *S. hemphilli*) and ventral margin of the trunk of *S. stahli* (Cavalluzzi, 1997).

REMARKS ON CHAENOPSID SPECIES

An interesting character of postflexion larvae of all species is the presence of an elongate pigment patch midventral to the basipterygium, observed and illustrated by Brogan (1992) from larvae of the Chaenopsinae (Hastings and Springer, 1994), such as *Emblemaria, Chaenopsis,* and *Coralliozetus.* The pigment patch results from the convergence at the ventral midline of two more lateral and usually elongate melanophores. Although the ventral melanophore is not visible in large larvae of *Neoclinus* and *Stathmonotus,* it does form in preflexion larvae and becomes embedded during the development (Brogan, 1992).

DISCUSSION

The Blennioidei exhibit reproductive features that are generally associated with low dispersal capabilities such as low fecundity, demersal spawning, some form of parental care, robust larvae, and short larval period. The larvae of most families, excluding Blenniidae, have few specializations (Watson, 1996), and the number of larval characters available to study relationships is low. Cavalluzzi (1997) described the larvae of two species of Dactyloscopidae and two of Chaenopsidae and discussed the use of life history characters for elucidating relationships within the suborder Blennioidei. He found no synapomorphies based on larval morphology that support the monophyly of the suborder. The chaenopsid and dactyloscopid larvae described herein, plus the description of the larvae of six labrisomid species (Herrera and Lavenberg,

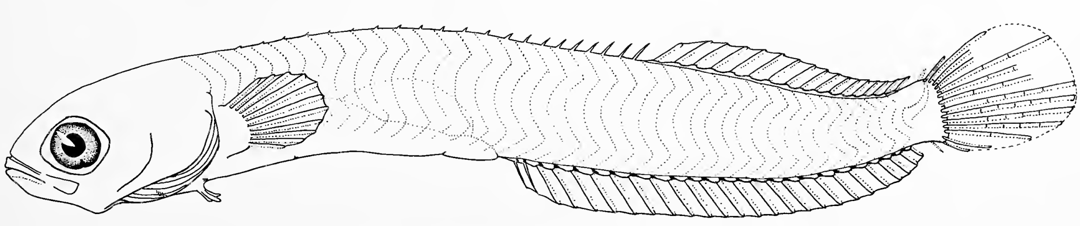

Figure 10 Larva of *Stathmonotus* sp.: 8.3 mm (LACM 45634-15)

1999), did not help to resolve further synapomorphies. However, variation among larvae may help to elucidate relationships within and among families.

Among dactyloscopids, the larvae of the phylogenetically primitive genus *Platygillellus* possess plesiomorphic characters such as paired cephalic melanophores and a discontinuous anterior profile of the dorsal fin. Larvae of the more derived genera *Myxodagnus, Dactyloscopus,* and *Dactylagnus,* which constitute a clade (Doyle, 1998), possess a single large melanophore on the head and ventrally on the gut, and a continuous and straight anterior dorsal-fin profile. The larvae of *Gillellus,* another derived dactyloscopid unrelated to the previous clade, lack cephalic melanophores and the anterior margin of the dorsal fin is discontinuous. Unfortunately, the larvae of the other two genera of the clade (*Sindoscopus* and *Leurochilus*) have not been described. Although the absence of cephalic melanophores may be considered a derived feature within Dactyloscopidae (e.g., also observed in the primitive tripterygiids), it is not possible to establish whether the loss is derived from a plesiomorphic condition (small paired melanophores) or a relatively more derived condition (large and single melanophores). Nevertheless, these characters are consistent with the dactyloscopid relationships of Doyle (1998).

Chaenopsid have larval features that are consistent with phylogenetic relationships obtained by Hastings and Springer (1994) from adult morphology. The phylogenetically more primitive genus *Neoclinus* (previously considered a labrisomid), has larvae that develop several melanophores dorsally on the head and has a comparatively short preanal distance (<39% SL). More derived chaenopsids lack dorsal head pigmentation and have longer preanal distances (40–57%). Also, the phylogenetically primitive *Neoclinus* has a well-defined pigment pattern dorsally on the trunk, with melanophores at the base of the dorsal-fin spines and in between the pterygiophores of the soft rays (Watson, 1996); this feature is absent in all remaining and more derived chaenopsid larvae (Brogan, 1992; Watson, 1996; Cavalluzzi, 1997), although it is common in labrisomids and in the basal tripterygiids.

The larvae of all Chaenopsid genera examined so far possess an elongate melanophore midventrally on the basipterygium that results from the fusion of two melanophores that develop laterally and converge on the ventral midline (Brogan, 1992). An elongate melanophore on the basipterygium is also observed in the labrisomid Starksiini *Starksia galapagensis* (Herrera and Lavenberg, 1999). Based on molecular evidence, Stepien et al. (1997) considered the labrisomids a paraphyletic group and hypothesized that the tribe Starksiini was more closely related to Chaenopsidae than were other Labrisomidae. Although the larval evidence is suggestive, further work is needed to confirm the affinities between Chaenopsidae and Starksiini.

Among blennioid larvae, other melanophore characters do not seem to be informative about relationships above genus level, although it remains to be determined whether they are useful at lower taxonomic level (i.e., between species). For example, a band of melanophores is present in the posterior margin of the hypural plates in the species *Hypsoblennius jenkinsi, H. sordidus, Dactyloscopus pectoralis fallax, Acanthemblemaria atrata,* and *Malacoctenus zonogaster,* but it is absent in their respective congenerics *H. brevipinnis, D. lacteus, A. castroi,* and *M. tetranemus* (Balbontín and Pérez, 1979; Stevens and Moser, 1982; Herrera and Lavenberg, 1999).

In conclusion, the phylogenetic significance of larval pigment characters still remains to be determined. However, as suggested by Cavalluzzi (1997), it seems, that pigment characters may be more important for low taxonomic level (i.e., inter- or intrageneric) than for higher taxonomic level comparisons.

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