Larvae of checked swallowtail (*Odontanthias borbonius*) (Teleostei: Serranidae: Anthiadinae), with comparisons of spiny ornamentation in related anthiadine species

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Abstract—The larval morphology of the checked swallowtail, the anthiadine *Odontanthias borbonius*, is described based on 4 postflexion specimens collected from the southern East China Sea and its vicinity. This represents the first morphological information about the larvae of the genus *Odontanthias*. The larvae have distinguishing characteristics such as a deep and hunchbacked body, pointed snout, minimal pigmentation, and highly developed spiny ornamentation. The ornamentation is found on most of the exposed head bones, fin spines, and larval scales. In particular, the spination on the maxilla is new information in anthiadine larvae. These characteristics including scale and/or fin element features are shared by larvae of 2 other anthiadine genera, *Baldwinella* and *Sacura*. However, since there are some differences in the spiny ornamentation patterns, comparisons of the patterns were made between *Odontanthias* and *Baldwinella*, and between *Odontanthias* and *Sacura*. Spiny ornamentation in larvae may be useful in resolving current taxonomic issues such as clarification of the generic classification of *Odontanthias* and *Sacura*.

Introduction

Serranid fishes of the subfamily Anthiadinae are small to medium-sized sea basses found worldwide in habitats of hard substrates such as rocks or coral reefs from shallow to deep seas in tropical, subtropical, and temperate zones (Anderson and Heemstra, 1980; Randall, 1980; Anderson and Heemstra, 2012). At least 248 valid species in 31 genera have been described (Anderson, 2018; Parenti and Randall, 2020; Fricke et al., 2022); however, due to the limited availability of fishing and collection gear, deep-reef anthiadines have not been well documented (Randall, 1980, 1996; Rocha et al., 2018). The Indian Ocean to the central Pacific region has the richest anthiadine fauna, with 190 species in 22 genera, compared to that of the eastern Pacific/Atlantic region, with 36 species in 14 genera. This subfamily is most diverse in the western Pacific with 114 species in 19 genera (Anderson, 2018).

The anthiadine genus *Odontanthias*, for which the larvae of one species is described in this article, includes very colorful species found over hard substrates at about 100–400 m depth (Randall and Heemstra, 2006). Seventeen valid species of *Odontanthias* have been described globally, and, with the exception of a single species reported from the Atlantic, all are from the Indo-Central Pacific region (Randall and Heemstra, 2006; White, 2011; Carvalho-Filho et al., 2016; Gill and Russell, 2019; Zajonz et al., 2020; Fricke et al., 2022).

There is a lack of morphological information about the anthiadine larvae of the Indo-Central Pacific region and the eastern Pacific/Atlantic region. From the latter, the larvae of 12 species in 5 genera have been described (Kendall, 1979, 1984; Baldwin, 1990). Baldwin (1990) and Richards et al. (2006) divided them into 4 groups by morphological characters such as spiny ornamentation on the head, fin spines, larval scales, and pigmentation. Their Group 1, consisting of 3 species in 2 genera, share well-developed spinous ornamentation and specific pigmentation dorsally on the body. Based on these larval characters, along with some adult ones, these 3 species were placed in a new genus, *Baldwinella* (Anderson and Heemstra, 2012). In contrast, despite the higher species richness, larval information is mostly lacking from the Indo-Central Pacific region, and larvae and/or juveniles of only 9 species in 8 genera have been described (Fourmanoir, 1976; Baldwin and Neira, 1998; Okiyama, 2014).

In this paper, the morphological development of checked swallowtail, the anthiadine *Odontanthias borbonius*, is described based on 4 postflexion larvae, representing the first information about larvae of the genus *Odontanthias*. Their spinous ornamentation patterns are compared with those of similar larval anthiadine species, and comments are provided about the potential utility of spiny ornamentation patterns in resolving taxonomic issues, such as the generic distinctions between *Odontanthias* and *Sacura*.

This paper is a contribution to this special collection of papers to commemorate the remarkable career of H G. Moser, who was a world expert on the morphology and taxonomy of fish larvae. The larvae of the Serranidae were not one of his primary research interests, but the time-series collections he worked with in the California Current region documented the different development stages of serranid larvae and all the other species found there (Moser, 1996). Thus, the present contribution is in the spirit of documenting the remarkable taxonomic and morphological diversity of fish larvae that was part of the legacy of H G. Moser.

Materials and methods

Larvae examined in this study were collected in the southernmost area of the East China Sea and at a point about 350 km east of Taiwan during a Japanese eel cruise on the R/V *Hakuho Maru*, which was conducted by the Ocean Research Institute (presently, Atmosphere and Ocean Research Institute), University of Tokyo from 26 August to 2 October 1986. To collect fish larvae in oblique tows, an Isaacs-Kidd mid-water trawl (IKMT, 8.7-m^2 mouth opening, 0.5-mm mesh size) and a hexagon net (Hex, 10.4-m^2 mouth opening, 1.0- to 8.0-mm mesh sizes) were used. Plankton samples collected were fixed in a 10% buffered sea water–formalin solution, then fish larvae and juveniles were sorted out and preserved in 70% ethanol on-board.

The collection data of the 4 postflexion larvae examined are as follows (lengths of larvae are standard length [SL] in millimeters unless stated otherwise): SNFR 24108, 1, 5.7 mm, 24°47.0´N, 123°13.1´E, IKMT (no data on net depth), 13 September 1986; SNFR 24109, 1, 8.4 mm, 24°47.1´N, 123°11.3´E, Hex from 90-m depth, 13 September 1986; SNFR 24110, 1, 8.8 mm, 24°46.6´N, 123°18.5´E, Hex (no data on net depth), 12 September 1986; SNFR 24111, 1, 11.2 mm, 23°00.0´N, 124°45.2´E, IKMT from 480-m depth, 8 September 1986. These specimens are deposited in the SNFR collections of the Fisheries Technology Institute (formerly, Seikai National Fisheries Research Institute).

To facilitate accurately counting meristic characters and observing spinous ornamentation, 3 specimens (5.7–8.8 mm) were cleared and stained for bone and cartilage (Potthoff, 1984), and the largest specimen (11.2 mm) was stained by alizarin red S (Springer and Johnson, 2000).

Measurements to the nearest 0.1 mm were taken with a USB digital camera (J-Scope DS-3500, Sato Shouji Inc., Kawasaki, Japan) attached to a binocular microscope (Nikon SMZ1000, Nikon Corp., Tokyo, Japan). Body measurement methods follow Leis and Carson-Ewart (2000) except for head width (HW). It is here defined as the distance between the posterior ends of the supraorbital ridges on both sides. Preopercular spine length is defined as the distance from the lateral preopercular ridge to the posterior tip of the elongate spine at angle. Lengths of 1st–5th dorsal-fin spines, 1st–3rd anal-fin spines, and pelvic-fin spine were also measured. Terminology for body parts follows Leis and Carson-Ewart (2000). All proportions are based on percent SL, unless otherwise noted.

Counts were made for dorsal fin (D), anal fin (A), pectoral fin (P_1) and pelvic fin (P_2), vertebrae (V), and branchiostegal rays (Br). The last ray of the dorsal and anal fins was counted as one when branched to the base. If present, pored lateral line scales (LLp), scales above the lateral line (TRa), and scales below the lateral line (TRb) were counted: LLp–the number of pored scales on the lateral line; TRa–the number of scales in the transverse row from the origin of the dorsal fin downward to the scale just before the lateral-line scale; TRb–the number of scales in the transverse row from the origin of the anal fin upward to the scale just before the lateral-line scale. Development of scale shape and squamation was observed.

Terminologies of spiny ornamentation and body-shape categories follow Baldwin (1990) and Leis and Carson-Ewart (2000), respectively. Unless stated otherwise, morphological descriptions and illustrations were made on the left side of the body. Head bones examined for spiny ornamentation are the following: articular, frontal, infraorbitals, interopercle, lacrimal, maxilla, opercle, parietal, posttemporal, premaxilla, preopercle, pterotic, subopercle, supracleithrum, supraoccipital, supraorbital, and tabulars. The categories of the ornamentation modes of selected head bones and their definitions are shown in Table 1.

Identification was done by a combination of the meristic counts. For larvae without a complete set of counts of dorsal-, anal-, and pectoral-fins, and LLp, Tra, and TRb, the correspondence of the pigment and spinous ornamentation patterns was also examined.

Results

Morphology

Figure 1 shows illustrations of the entire body and the dorsal view of the head in the 8.4-mm larva. Table 2

Table 1

Category of ornamentation modes of selected head bones in larvae of checked swallowtail (*Odontanthias borbonius*) collected in the East China Sea in 1986. *SP*=spine; *SR*=serrate ridge; SL=standard length.

Head bone	Category of ornamentation mode I	II	III
Frontal	< 10 *SR*s, *SP*s	≧10 *SR*s, *SP*s	≧20 *SR*s, *SP*s
Infraorbitals	< 15 *SP*s (inner edges on 4 bones), < 5 *SP*s (outer edges on 4 bones)	< 20 *SP*s (inner edges on 4 bones), < 10 *SP*s (outer edges on 4 bones)	≧30 *SP*s (inner edges on 4 bones), ≧15 *SP*s (outer edges on 4 bones)
Interopercle	1 elongate serrate *SP*, 3 smooth, small *SP*s	1 elongate serrate *SP*, 8 small *SP*s (mostly smooth)	1 elongate serrate *SP*, 8 small *SP*s (mostly with *SR*)
Opercle	5 > *SR*s	10 < *SR*s	no mode
Parietal	1 vertically oriented smooth ridge	1–2 vertically oriented *SR*s, *SP*s	4 vertically oriented *SR*s, *SP*s
Posttemporal	2 *SP*s laterally with serrate ridge (upper), 2 small *SP*s (lower)	6 *SP*s laterally with serrate ridge (upper), 2 small *SP*s (lower)	no mode
Preopercle[1]	*SP* at angle < 25% SL, 3 *SP*s dorsal to angle, 1 *SP* ventral to angle	*SP* at angle > 30% SL, 5 *SP*s dorsal to angle, 2 *SP*s ventral to angle	*SP* at angle > 30% SL, 7 *SP*s dorsal to angle, 4 *SP*s ventral to angle
Subopercle	1 *SP* laterally with smooth ridge	2–3 *SP*s laterally with *SR*	3 *SP*s laterally with *SR*, 2 short *SR*s
Supracleithrum	1 smooth, retrorse *SP*	1 smooth retrorse *SP* laterally with *SR*	upper and lower margins of retrorse *SP* with serrations
Supraoccipital	serrate cockscomb-like crest laterally without *SR* and *SP*	serrate cockscomb-like crest laterally with *SP*s	serrate cockscomb-like crest laterally with *SR*
Supraorbital	< 10 *SR*s, *SP*s	≧10 *SR*s, *SP*s	≧20 *SR*s, *SP*s
Tabulars	1–2 *SP*s on anterior and posterior edges of 2 bones	4–6 *SP*s on anterior and posterior edges of 2 bones	no mode

[1]Secondary spination of serrate ridge or serrations is present on some spines dorsal and ventral to spine at angle (see the Head spination section in Results).

lists morphometric and meristic data of 4 larval specimens examined, and Table 3 shows their ornamentation patterns on the head bones, fin spines, scales, and teeth.

The laterally compressed and hunchbacked body is moderately deep (body depth=33% SL) and wide (HW=32% SL) in the smallest (5.7 mm, not illustrated) and becomes deeper (body depth=44–47% SL) and narrower (HW=29–26% SL), respectively, in the larger specimens (8.4–11.2 mm) (Fig. 1, Table 2). The triangular-shaped head is very large and occupies about half the size of the body (49–55% SL). The snout is pointed and large (15–18% SL). The round eye is small (10–13% SL). The eye orbit surrounds the eye with a relatively wide space. The oblique mouth is large, and its posterior tip reaches near to the posterior margin of the eye. The coiled gut is large and becomes larger with body growth, resulting in an increase in the preanal length (53–64% SL). The small, conical larval teeth project outward from the lower margin of the premaxilla (Fig. 1, Table 2).

The long-based dorsal fin is single: 10 spines and 14 (5.7 mm) or 16–17 (8.4–11.2 mm) soft rays (Table 2). The 4th dorsal spine is the longest, and the 3rd and 4th spines are stout. The short-based anal fin has 2 spines and 8 soft rays, and 3 spines and 7 rays in 5.7 mm and 8.4–11.2 mm, respectively. The 2nd spine is the longest, and the 1st and 2nd spines are stout. The pectoral fin is located under the horizontal midline of the body and has 17 soft rays. The pelvic fin is early-forming, and the 1st soft ray is longer than the spine, reaching beyond the origin of the anal fin in the smallest specimen. The soft ray is remarkably elongate and reaches at least the midpoint of the anal-fin base in the large larvae, extending to the base of the caudal fin in the 8.8-mm specimen (Fig. 1, Table 2).

The 11.2-mm larva possesses spinous ornamentation only on the 2nd to 5th dorsal-fin spines and pelvic-fin spine (Table 3). The anterior and posterior margins on the dorsal-fin spines are entirely serrate, and the 3rd and 4th spines have another serrate ridge on both lateral sides of the spine. The pelvic-fin spine has a serrate ridge laterally on the inner and outer sides, and 2 parallel serrate ridges occur along the long axis on the ventral

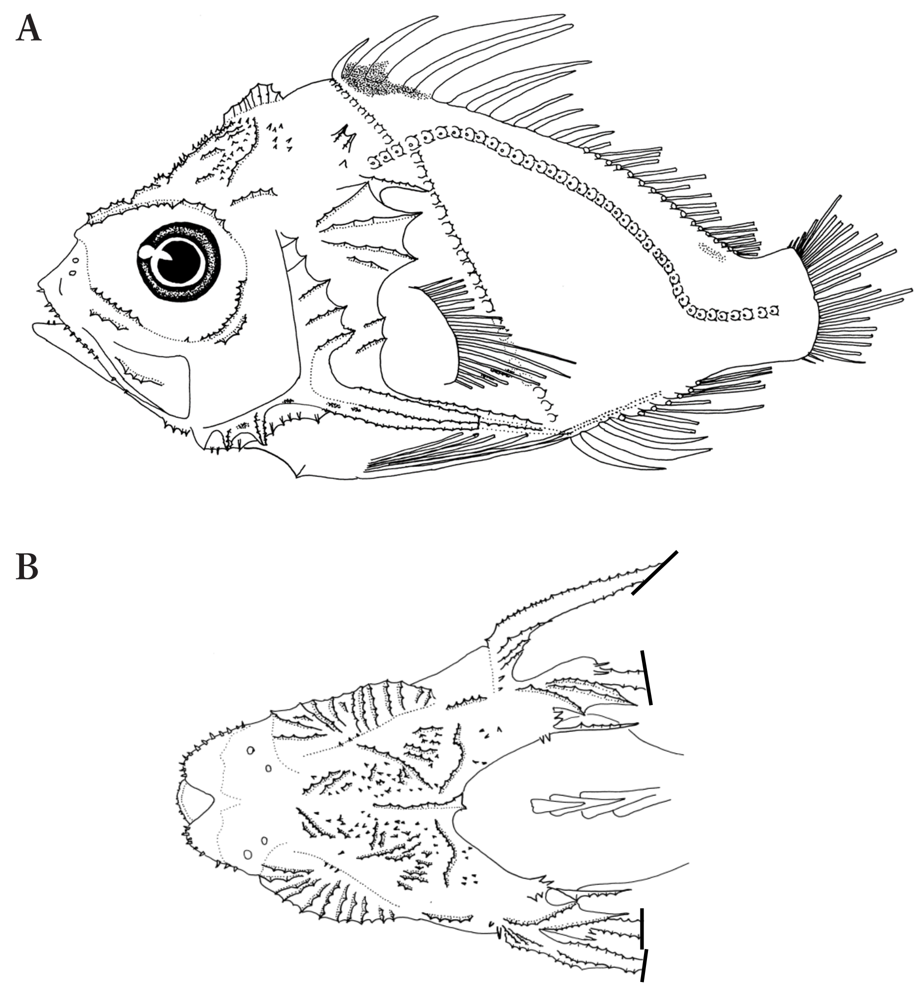

Figure 1

Illustrations of a checked swallowtail (*Odontanthias borobonius*) larva in 8.4 mm standard length collected in the East China Sea in 1986: (**A**) whole body and (**B**) dorsal view of the head (head length: 4.1 mm). Myomeres are not shown, and scales are only depicted for pored lateral line scales, scales above the lateral line, and scales below the lateral line in panel A. The elongate preopercular angle and interopercular spines are not drawn completely in panel B.

side of the spine. Larval teeth increase in number with growth of the body: about 5 teeth in the 5.7-mm specimen, about 12 in the 8.4-mm, about 13 in the 8.8-mm, and about 20 in the 11.2-mm (Table 3).

The larval scales are present on the cheek and middle part of the tail in the 5.7-mm specimen: cycloid scales on the cheek, and cycloid or spinous scales with 1 or 2 spinules on the tail (Table 3). In the large larvae (8.4–11.2 mm), spinous scales with 1–5 spinules are spread widely on the trunk, tail, abdomen, pectoral-fin and caudal-fin bases, and head except the back, snout, and jaws. Spinules originating from the posterior margin of the scale plate increase in number with growth of the body; however, the pored lateral line scales only have 2 spinules. The relative size of the spinules decreases with increasing body length, and they are small in the 11.2-mm specimen. Spinules of scales at the middle part of the tail are at about a 45° angle to the scale plate in the 8.8-mm larva. Pored lateral line scales originate from the posttemporal bone, arch significantly upward, then curve downward to the lateral midline under the 9th dorsal-fin soft ray before extending in a straight line to terminate at the caudal-fin base (Fig. 1, Table 3).

The 3 large specimens (8.4–11.2 mm) have full complements of meristic characters (Table 2): D X, 16 or 17; A III, 7; P_1 17; P_2 I, 5; V 26; LLp 40–43; TRa 8; TRb

Table 2

Morphometric and meristic data of larval checked swallowtail (*Odontanthias borbonius*) collected in the East China Sea in 1986. SL=standard length; approx.=approximately.

	SNFR 24108	SNFR 24109	SNFR 24110	SNFR 24111
Body size (SL: mm)	5.7	8.4	8.8	11.2
Proportion (% of SL)				
Head length	50.9	48.8	50.0	55.4
Eye diameter	10.5	10.7	10.2	13.4
Snout length	17.5	15.5	15.9	15.2
Predorsal-fin length	33.3	34.5	38.6	34.8
Preanal length	52.6	58.3	63.6	63.4
Body depth	33.3	44.0	44.3	47.3
Head width	31.6	28.6	27.3	25.9
Preopercular-spine length	21.1	32.1	31.8	31.3
1st dorsal-fin spine length	1.8	6.0	5.7	2.7
2nd dorsal-fin spine length	7.0	16.7	15.9	13.4
3rd dorsal-fin spine length	10.5	23.8	26.1	30.4
4th dorsal-fin spine length	15.8	40.5	38.6	damaged
5th dorsal-fin spine length	8.8	16.7	damaged	21.4
1st anal-fin spine length	12.3	13.1	15.9	11.6
2nd anal-fin spine length	17.5	16.7	19.3	17.9
3rd anal-fin spine length	17.5[1]	13.1	17.0	14.3
Pelvic-fin spine length	29.8	28.6	33.0	35.7
Counts				
Dorsal fin	X, 14[2]	X, 17	X, 17	X, 16
Anal fin	II, 8	III, 7	III, 7	III, 7
Pectoral fin	17	17	17	17
Pelvic fin	I, 5	I, 5	I, 5	I, 5
Vertebrae	26	26	26	no count
Pored scales on lateral line	unformed	approx. 40	approx. 43	41
Scales above lateral line	unformed	8	8	8
Scales below lateral line	unformed	20	approx. 21	approx. 19
Branchiostegal rays[3]	3+4	3+4	3+4	3+4

[1]Soft ray.
[2]Fin incomplete.
[3]Branchiostegal rays: ceratohyal+epihyal.

19–21; Br 3 (ceratohyal)+4 (epihyal). The smallest specimen (5.7 mm) has full complements of the pectoral and pelvic fin rays, vertebrae, and branchiostegal rays. However, the dorsal fin (X, 14), anal fin (II, 8), and scales are not completely formed, and the LLp, TRa, and TRb scales are not fully developed (Table 2).

Head spination

Figures 1 and 2 show illustrations of the whole body and the dorsal view of the head, and the head spination in the 8.4-mm larva, respectively. Figure 3 shows photos of the whole body (Fig. 3A), opercle (Fig. 3B), maxilla (Fig. 3C), and supraoccipital crest (Fig. 3D) of the 11.2-mm specimen. Table 3 indicates the developmental patterns of the head spination in the 4 specimens examined based on definitions of ornamentation modes in Table 1.

The frontal, interopercle, parietal, preopercle, subopercle, supracleithrum, supraoccipital, supraorbital, and opercle are ornamented at least by 5.7 mm (Table 3). The frontal of the 5.7-mm specimen has a short serrate ridge over the forebrain, 3 serrate ridges over the midbrain, and a few spines. The ridges increase in number and size with growth of the body, being arranged conspicuously in a concentric rhombic pattern with the ridges on the right side: 12–18 ridges and some spines in the 8.4-mm and 8.8-mm larvae; about 20 ridges and some spines in the 11.2-mm specimen. The interopercle has a large spine and several short spines ventral to the large one. The uppermost large spine underlying the equally long preopercular spine at angle is serrated on the dorsal and ventral margins and has a serrate ridge on the outer and inner lateral sides. The short spines ventral to the large one are smooth or serrate and increase in number with growth of the body: 3 and 8 smooth, thin spines in the 5.7-mm and 8.4-mm larvae, respectively; one of 8 spines has a lateral,

Table 3

Ornamentation on head bones, fin spines, scales, and teeth in larvae of checked swallowtail (*Odontanthias borobonius*) collected in the East China Sea in 1986. Roman numerals indicate the categories of ornamentation described in Table 1. Arabic numerals indicate the number of serrate ridges (*SR*s) and spines (*SP*s). Numerals in parenthesis indicate the number of erect spinules at the posterior margin of the scale plate. In the 11.2-mm specimen, spinules on the scale plate are 2–5 in number and are relatively small. Cs=cycloid scale; Ss=spinous scale; SL=standard length; approx.=approximately.

Body size (SL)	5.7 mm	8.4 mm	8.8 mm	11.2 mm
Ornamentation on head bones and fin spines				
Frontal	I	II	II	III
Interopercle	I	II	II	III
Parietal	I	II	II	III
Preopercle	I	II	II	III
Subopercle	I	II	II	III
Supracleithrum	I	II	II	III
Supraoccipital	I	II	II	III
Supraorbital	I	II	II	III
Opercle	I	I	I	II
Infraorbitals	–	I	II	III
Posttemporal	–	I	I	II
Tabulars	–	I	I	II
Articular	–	4 *SP*s	6 *SP*s	approx. 17 *SP*s
Lacrimal	–	10 *SP*s	12 *SP*s	approx. 16 *SP*s
Maxilla	–	1 *SR*	2 *SR*s	3 *SR*s
Pterotic	–	5 *SP*s	5 *SP*s	6 *SP*s
Dorsal-fin spines	–	–	–	present[1]
Pelvic-fin spine	–	–	–	present
Larval teeth				
Number	approx. 5	approx. 12	approx. 13	approx. 20
Ornamentation on scales				
Mid lateral tail	Cs, Ss (1-2)	Ss (3)	Ss (3)	Ss
Cheek	Cs	Ss (2-3)	Ss (3-4)	Ss
Dorso- and ventro-lateral tail	–	Ss (1-3)	Ss (2-3)	Ss
Lower opercle	–	Ss (2-3)	Ss (3)	Ss
Otic portion[2]	–	Ss (2-3)	Ss (3)	Ss
Abdomen	–	Ss (1-3)	Ss (3)	Ss
Pectoral-fin base	–	Ss (1-3)	Ss (3)	Ss
Caudal-fin ray base	–	Ss (2-3)	Ss (2-3)	Ss
Upper trunk	–	Ss (2-3)	Ss (2-3)	Ss
Isthmus	–	Ss (1)	Ss (2-3)	Ss

[1]2nd to 5th dorsal-fin spines with serrations.
[2]Unornamented portion surrounded by pterotic, posttemporal, and opercle bones.

serrate ridge in the 8.8-mm larva; and 7 or 8 spines laterally with a short serrate ridge in the 11.2-mm specimen. A smooth, vertically oriented ridge is present on the parietal of the 5.7-mm larva. The ridge of the 8.4-mm larva is serrate, and 2 widely based spines are present on the bone. The 8.8-mm and 11.2-mm larvae have 2 and 4 vertically oriented serrate ridges, and 2 and 3 spines, respectively. The smallest larva (5.7 mm) has the medial preopercular ridge with 3 widely based spines dorsal to the long spine at angle, one large spine (21% SL, Table 2) at angle, and one widely based spine ventral to the spine at angle: upper and lower spines adjacent to the elongate spine at angle have a serrate and a smooth lateral ridge, respectively. The large spine at angle has serration on the upper and lower margins and a serrate ridge on the lateral portions on the outer and inner sides. It becomes remarkably long (>30% SL, Table 2) in the 8.4–11.2-mm larvae. Spines dorsal and ventral to the large spine at angle increase in number with growth: there are 5 and 2 of them, respectively, in the 8.0-mm larvae, and 7 and 4, respectively, in the 11.2-mm larva. Some of these spines have a serrate ridge laterally and serrations on the tip: the serrate ridge is present on the spine dorsal and adjacent to the large spine at angle in the 5.4-mm specimen, 3 and 2 spines dorsal and ventral to the spine at angle, respectively, in 8-mm specimens, and 5 and 4

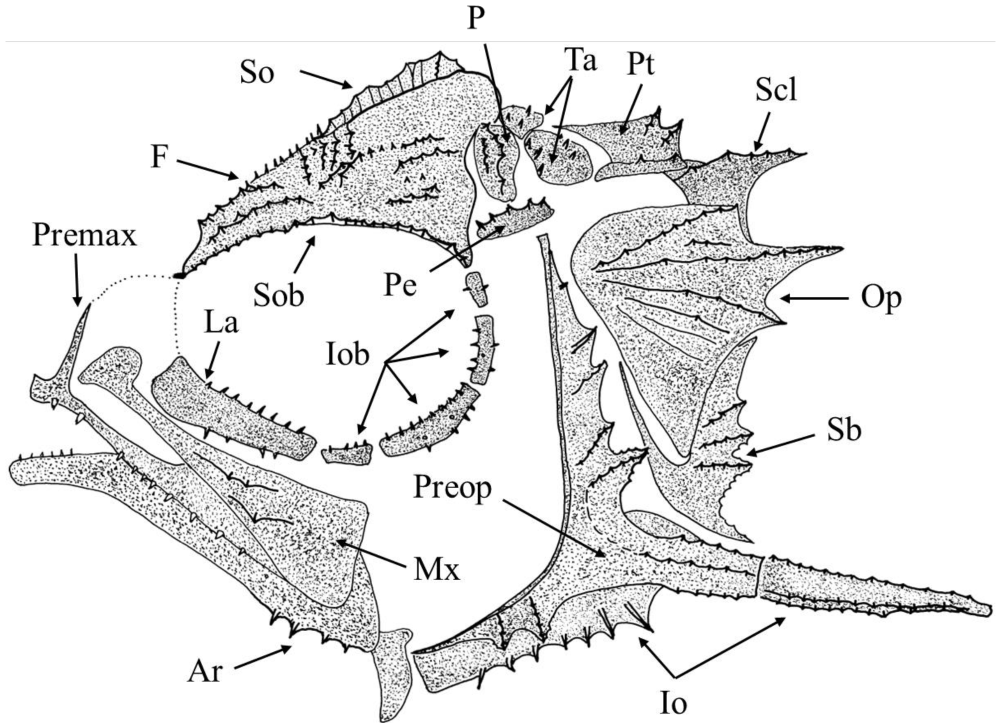

Figure 2

Illustration of the head spination of a checked swallowtail (*Odontanthias borbonius*) larva in 8.8 mm standard length collected in the East China Sea in 1986. The drawing was made of the right side and reversed. Head bones examined for spiny ornamentation and their abbreviations are as follows: articular (Ar), frontal (F), interopercle (Io), infraorbitals (Iob), lacrimal (La), maxilla (Mx), opercle (Op), parietal (P), pterotic (Pe), premaxilla (Premax), preopercle (Preop), posttemporal (Pt), subopercle (Sb), supracleithrum (Scl), supraoccipital crest (So), supraorbital ridge (Sob), and tabulars (Ta). Note that the preopercle spine at an angle is damaged.

spines dorsal and ventral to the spine at angle, respectively, in 11.2-mm specimen; serrations of the tip of spine are present on the spine dorsal and adjacent to spine at angle in 8.4–11.2-mm larvae, and 2 spines ventral to the spine at angle in 11.2-mm specimen. Small spines are visible on the anterior margin of the preopercle only in the 11.2-mm larva. There are 1–3 smooth or serrate spines on the subopercle: only a single smooth spine laterally with a low smooth ridge in the 5.7-mm larva; 2–3 spines with a serrate ridge in the 8-mm larvae; 3 spines with the ridge and 2 additional, short serrate ridges in the 11.2-mm specimen. The supracleithrum in the 5.7-mm larva has a smooth, retrorse spine and has a serrated ridge laterally in other specimens. The spine of the 11.2-mm larva has additional serrations on the dorsal and ventral margins. In the 5.7-mm specimen, a low cockscomb-like supraoccipital crest is posteriorly raised and angulate at the posterior end, and is serrate along its full margin. There are vertically oriented smooth ridges laterally on the supraoccipital crest and a bubble pattern at its base. In the 8.4-mm and 8.8-mm larvae, the bubble-like pattern disappears on the crest, and a spine protrudes outward on the lateral surface of 2–4 vertical ridges. The protrusions form a serrate ridge in the 11.2-mm specimen (Fig. 3D). The supraorbital ridge expands widely outward and is ornamented with low, serrate ridges and spines. The ridges increase in number with growth: 6 ridges at 5.7 mm, about 12–13 ridges at 8.0 mm, and about 20 ridges at 11.2 mm. The opercle in the 5.7-mm larva has 3 spines on the posterodorsal margin, each accompanied by a ridge originating from the anterior margin of the bone: the uppermost ridge is smooth, the remaining 2 are slightly serrate, and the middle ridge is the longest. In the 8.4- and 8.8-mm specimens, several additional serrate ridges appear ventral to the 3 previously mentioned ridges. The bone in the 11.2-mm larva is covered entirely by about 15 serrated ridges, each with a small spine on the posterior tip.

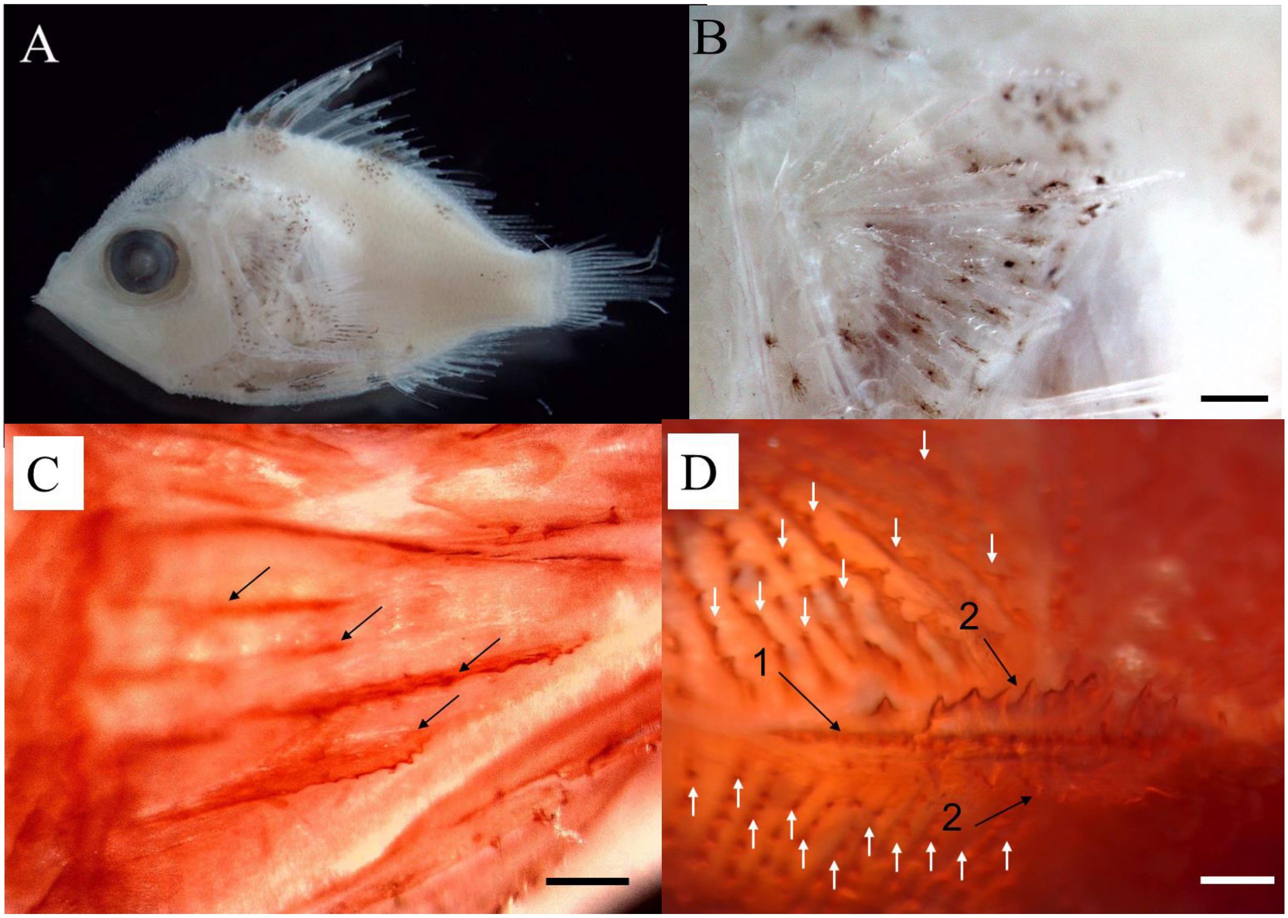

Figure 3

Images of the spiny ornamentation of a checked swallowtail (*Odontanthias borbonius*) larva in 11.2 mm standard length collected in the East China Sea in 1986: (**A**) whole body; (**B**) serrate ridges on the opercle; (**C**) 4 serrate ridges (arrows) on the maxilla (right side) in an alizarin-stained preparation; (**D**) the dorsal view of frontal and supraoccipital crest showing serrate ridges on frontal (white arrows), serration on dorsal margin of crest (1), and outward projecting serrate ridge laterally on crest (2) in an alizarin-stained preparation. Scale bar=0.2 mm.

The infraorbitals, posttemporal, and tabulars are ornamented by 8.4 mm (Table 3). The 8.4-mm specimen has small spines on all 4 infraorbital bones: 1, 8, 4, and 1 spines on the inner margins of the 1st to 4th bones, respectively, and 4 spines on the outer margin on the 2nd bone. The spines increase in number with growth: 4, 9, 4, and 2 spines on the inner margins of the 1st to 4th bones, respectively, and 4 and 2 spines on the outer margin on the 2nd and 3rd bones, respectively, in the 8.8-mm larva; about 30 and 15 spines on the inner and outer ridges of the 4 bones in the 11.2-mm specimen. The 8.4- and 8.8-mm larvae have 2 spines laterally with a serrate ridge on the dorsal posttemporal and 2 small spines on the ventral bone. The 11.2-mm specimen has a plate-like ridge on both bones: the upper has 6 spines laterally with a serrate ridge, and the lower has 2 spines. Each of 2 tabulars has 1–2 small spines on the anterior and posterior ridges in the 8.4- and 8.8-mm larvae, and 4–6 small spines in the 11.2-mm larva.

Spines and serrate ridges are developed on the articular, lacrimal, maxilla, and pterotic at least by 8.4 mm (Table 3). The articular has 4 spines in the 8.4-mm specimen, 6 spines in the 8.8-mm specimen, and about 17 spines in the 11.2-mm specimen. There are 7 small spines and 3 small spines on the upper and lower ridges of the lacrimal, respectively, in the 8.4-mm specimen, 8 and 4 spines in the 8.8-mm specimen, and about 9 and 7 spines in the 11.2-mm specimen. The maxilla has one serrate ridge laterally on the posterior portion in the 8.4-mm larva: 2 serrate ridges in the 8.8-mm larva, and 3 (4 in the right side of the body) serrate ridges in the 11.2-mm larva. The pterotic has spines dorsally on the plate-like ridge: 5 spines in the 8.4- and 8.8-mm larvae and 6 spines in the 11.2-mm specimen.

Pigmentation

Pigment patterns of the 8.4-mm and 11.2-mm larvae are shown in Figure 1 and Figure 3 (A and B), respectively. The pigment of the 4 larvae in this study was slightly faded because they were examined about 36 years after collection.

The 5.7-mm to 8.8-mm larvae are sparsely pigmented. They share the same pigment patterns on the dorsolateral portion of the trunk and tail, and on the lateral portion of the posterior lower jaw and the angled preopercular spine. A blotch is present beneath the 3rd to 4th dorsal-fin spines in the 5.7-mm specimen. The pigment under the spinous dorsal fin extends to the base of fin spines and membrane between the 2nd and 4th in the 8.4-mm specimen, and 1st and 4th spines in the 8.8-mm specimen, respectively. A cluster of melanophores appears on the trunk under the posterior dorsal-fin rays. The elongate preopercular spine at angle has pigment on its base. Melanophores are present on the posterior lower jaw in all larvae. The smallest larva (5.7 mm) has pigment on the dorsolateral portion of the head posteriorly and over the posterior anal-fin base on the right side of the body. The specimen has a large melanophore on the base of the lower lobe of the caudal fin, where no scales are formed yet. Three melanophores are present on the lower portion of the pectoral fin in the 8.4-mm larva. The pelvic fin is pigmented in the 8.4- and 8.8-mm specimens.

The 11.2-mm larva is moderately pigmented. Melanophores are more numerous in the areas that pigment was noted in the smaller larvae. Pigment is also newly present dorsally on the body, laterally on the trunk and caudal peduncle, on the opercle and otic regions, and dorsal to the anal-fin spines. A cluster of large melanophores at the base of dorsal fin spines 8 and 9 extends both onto the spines and membrane, and ventrally onto the dorsal portion of the body.

Discussion

Identification

Anthiadine larvae have a large, extremely spiny head including an interopercular spine, early-forming pelvic fin, and anterior dorsal-fin elements, anus located beyond midbody, 25–26 myomeres, and a hunchbacked body (Leis and Rennis, 2000a). These distinguishing characteristics are shared by the larval specimens that were examined in this study.

At present, 15 genera and 59 species of anthiadines are known to occur in Japanese waters (Suppl. Table 1). However, some apparently undescribed species have been reported based on underwater photos (Senou, 2013).

A set of full complements of meristic counts in the largest 3 specimens (8.4–11.2 mm, Table 2) is the following: D X, 16–17; A III, 7; P_1 17; P_2 I, 5; V 26; LLp 40–43; TRa 8; TRb 19–21; Br 3+4. A combination of these counts matches that of the genus *Odontanthias* adults, in particular only that of *O. borbonius* (Suppl. Table 1). Therefore, the larvae examined can be identified as this species, assuming the larvae are of a species already reported in southern Japanese waters.

Anthiadine larvae morphologically related to *Odontanthias borbonius* larvae

This study describes the detailed morphological characteristics of *O. borbonius* larvae of 5.7 to 11.2 mm. The general characteristics of larvae of this species are a deep hunchbacked body, large head, pointed snout, small round eyes, large oblique mouth with its posterior tip near the posterior margin of the eye, and small, conical, outward-projecting teeth on the upper jaw. The pelvic fin is early-forming. Anterior dorsal- and anal-fin spines are stout. The first soft ray of the pelvic fin is longer than the spine, and its posterior tip almost reaches at least the posterior anal-fin base or the caudal-fin base in larvae more than 8 mm. Spiny ornamentation is well developed on most exposed head bones, fin spines, and scales, and pigment is sparse to moderate.

The morphological characteristics of *O. borbonius* are mostly shared by *Baldwinella* spp. (Baldwin, 1990; Richards et al., 2006) and *Sacura margaritacea* (Fourmanoir, 1976; Kojima, 2014). Baldwin (1990) and Richards et al. (2006) defined larvae of *Baldwinella* (including red barbier [*Hemanthias vivanus*], streamer bass [*Pronotogrammus aureorubens*], and bigeye bass [*P. eos*]) as having a cockscomb-like supraoccipital crest, well-developed spinous ornamentation on other head bones and serrated dorsal-, anal-, and pelvic-fin spines, spinous larval scales, and pigment on the spinous dorsal-fin membrane. Kojima (2014) illustrated and briefly described 5.3-mm and 9.7-mm larvae of *S. margaritacea* from southern Japan. The larvae have a deep body, oblique large mouth, pointed snout, large gut, cockscomb-like supraoccipital crest, spination on other head bones and scales, no serration of fin spines, and pigment on the anterior tip of the lower jaw. Fourmanoir (1976) illustrated an 11-mm larva identified as *S. margaritacea* and described its morphology including a 15-mm specimen: the 1st pelvic-fin soft ray of the 11-mm larva reached the caudal fin base, and the 3rd dorsal-fin spine of the 15-mm specimen was filamentous. The trailing edges of the first 2 anal-fin spines in his drawing were seen to be serrate, but this was not mentioned in the text.

Table 4

Differences of selected spiny ornamentation patterns among larvae of checked swallowtail (*Odontanthias borbonius*) collected in the East China Sea in 1986, *Baldwinella* (3 species) and *Sacura margaritacea*. Type 1 larval scale has 1 to 5 erect spinules at the posterior edge of the scale plate, while type A has a single erect spinule at the center of the scale plate.

Species	Maxilla	Opercle	Articular	Dorsal-fin spines	Pelvic-fin spine	Anal-fin spines	Larval scales	Source
Odontanthias borbonius	present	present	present	present	present	absent	type 1	This study
Baldwinella species	absent	absent	present	present	present	present	type A	Baldwin (1990)
Sacura margaritacea	absent	present	absent	absent	absent	absent	type 1	Fourmanoir (1976), Kojima (2014)

Larvae of *Baldwinella* spp. and *S. margaritacea* are similar to *O. borbonius* larvae in body shape, spinous ornamentation, and pigmentation. Therefore, larval spinous ornamentation informative for anthiadine generic classification is compared among *O. borbonius*, *Baldwinella*, and *S. margaritacea* next.

Comparisons of spinous ornamentation among larvae of 3 genera

Spiny ornamentation in fish larvae is presumed to be related to reduction of predation or to enhancement of flotation during the pelagic larval phase and provides useful information for identification and taxonomy in the beryciform, scorpaeniform, and perciform larvae that have some of the most well-developed spination of any fish larvae (Moser, 1981, 1996).

All of the spination found in *O. borbonius* larvae (Table 3, Fig. 2) except serrate ridges on the maxilla and opercle and some fin spines are shared with *Baldwinella* spp. and *S. margaritacea*. However, there are some differences in the detailed patterns of the ornamentation among these larvae (Table 4).

Among anthiadine larvae, serrated ridges on the maxilla are found only in *O. borbonius*. A serrate ridge is formed on the posterior lateral portion of the maxilla by 8.4 mm, and the ridges increase 3 or 4 in the 11.2-mm larva (Figs. 1, 2, and 3C). Randall and Heemstra (2006, fig. 8) illustrated several obliquely straight striations on the maxilla of a 26-mm juvenile of *O. tapui* from the southern central Pacific Ocean but did not describe the striations in the text. These striations may be remnants of serrated ridges in the larval stage. However, the striations were not found on the maxilla of about 2-cm *O. borbonius* juveniles (Okamoto[1]).

Spination on the maxilla is known in some beryciform (Mundy, 1990; Baldwin and Johnson, 1995; Konishi, 1999), perciform lethrinid (Johnson, 1984; Leis and Rennis, 2000b; Kojima and Mori, 2014), and acanthuriform caproid (Gill and Leis, 2019) larvae. The maxilla ornamentation in the beryciform *Beryx* larvae consists of one or 2 tiny spines at the anterior tip but no serrate ridges (Mundy, 1990; Baldwin and Johnson, 1995; Konishi, 1999). Normally, serrate ridges occur on the supramaxilla in beryciform fish larvae (Baldwin and Johnson, 1995; Konishi and Okiyama, 1997; Jordan and Bruce, 1998; Miskiewicz et al., 1998; Konishi, 1999). Among the perciform percoid fish larvae, only lethrinid larvae have maxilla spination (Johnson, 1984). Lethrinid larvae develop a relatively deep, ventrally projecting serrate ridge laterally on the maxilla posteriorly (Leis and Rennis, 2000b; Kojima and Mori, 2014; Y. Konishi, personal observ.). In contrast, the spination of *O. borbonius* larvae has at least 4 serrate low ridges that project outward. Gill and Leis (2019, figs. 8 and 9) illustrated a serrated ridge on the maxilla of the acanthuriform boarfish (*Capros aper*) larvae of 4.2-mm notochord length and 5.2-mm SL but not in a *C. aper* larva of 15 mm (their fig. 10). Clearly, serrate ridges on the maxilla are very limited among larvae of marine fish taxa.

Serrate ridges on the opercle are present in *O. borbonius* and *S. margaritacea* but not in *Baldwinella* spp. larvae. On the upper portion of the opercle in the 5.7-mm larval *O. borbonius*, there are 3 ridges with or without serrations, the posterior tips of which are small spines. The serrate ridges increase in number with growth and, at least by 11 mm, cover all the opercle except the scaled upper- and lowermost portions. A 9.7-mm larva of *S. margaritacea* has 3 serrate ridges that terminate in small spines on the upper region of the opercle, and the remaining areas without ridges are scaled (Kojima, 2014). In *Baldwinella* spp. larvae, only 3 small spines without a serrate ridge are

[1]Okamoto, M. 2022. Personal commun. Mar. Fish. Res. Dev. Cent., 1-1-25 Shinurashimacho, Yokohama 221-0031, Japan.

depicted at the posterior margin on the upper portion of the opercle (Kendall, 1979; Baldwin, 1990). These spines are presumably a precursor to the 3 spines on the opercle of adults, one of the 4 diagnostic characters of serranid fishes (Johnson, 1983). The serrated articular is shared by *O. borbonius* and *Baldwinella* spp. larvae (this study; Baldwin, 1990), but it is not present in *S. margaritacea* (Kojima, 2014).

The largest (8.4-mm, 8.8-mm, and 11.2-mm) specimens of *O. borbonius* develop secondary spiny ornamentation on the supraoccipital crest, preopercular spines dorsal and ventral to the angle, interopercular spines ventral to the dorsal margin, subopercular spines, and posttemporal spines. This secondary spination was not described in *Baldwinella* spp. (Baldwin, 1990) or *S. margaritacea* (Kojima, 2014), but Kojima (2014) illustrated a 9.7-mm larval *S. margaritacea* with a short, serrated ridge laterally on 2 preopercular spines dorsal to the elongate spine at angle.

Only the largest (11.2 mm) *O. borbonius* larva examined has serrated fin spines: 2nd to 5th dorsal-fin spines are serrated on the anterior and posterior margins; laterally, there is a serrate ridge; and the pelvic-fin spine has 4 serrate ridges laterally (Table 3). *Baldwinella* spp. larvae develop serrations on the 2nd to 4th dorsal-fin spines, pelvic-fin spine, and 2nd anal-fin spine (Baldwin, 1990). No fin-spine serrations are described or illustrated in *S. margaritacea* by Kojima (2014), but Fourmanoir (1976) illustrated serrations on the posterior edge of the first 2 anal-fin spines.

The larvae of these 3 genera develop spiny larval scales. Scales of *O. borbonius* have 1–5 erect spinules at the posterior margin of the scale plate (Table 3). The number of spinules depends on the position on the body and larval size, but each pored lateral line scale has 2 spinules. In *S. margaritacea*, 2 or 3 spinules are present on the posterior edge of scales (Kojima[2]). Larval scales of *Baldwinella* spp. have a single spinule originating near the center of the scale plate (Baldwin, 1990). In the Percoidei, spinous larval scales are present in the Bramidae, Ephippidae, Haemulidae, Kyphosidae, Lethrinidae, Branchiostegidae, Malacanthidae, Pentacerotidae, Priacanthidae, Scatophagidae, and Sparidae (Johnson, 1984). Branchiostegid, malacanthid, priacanthid, and bramid larvae develop *Baldwinella*-type spiny scales with a single spinule at the center of the scale plate (Y. Konishi, unpubl. data). Beryciform larvae of the families Anomalopidae, Anoplogastridae, Diretmidae, Monocentridae, and Trachichthyidae also possess spinous scales, but their scales have 1 to 4 erect spinules at the center of the plate (Baldwin and Johnson, 1995; Konishi, 1999).

[2]Kojima, J. 2022. Personal commun. Mar. Ecol. Res. Inst., 300 Iwawada, Onjuku, Chiba 299-5105, Japan.

From the above comparisons, *O. borbonius* larvae possess the most well-developed ornamentation among known anthiadine larvae.

Comments on the distinction of *Odontanthias* and *Sacura*

Gill and Russell (2019) indicated that the generic distinction of *Odontanthias* and *Sacura* is unresolved. In their phenetic, neighbor-joining tree derived from mitochondrial cytochrome *c* oxidase subunit I sequences of *Meganthias*, *Odontanthias*, and *Sacura* species, Zajonz et al. (2020) concluded that *Odontanthias* and *Sacura* species form a single genetic lineage, suggesting that *Sacura* may be a junior synonym of *Odontanthias*. However, a more robust molecular phylogenetic analysis is needed. As described above, there are some differences in the spiny ornamentation patterns between the larvae of *O. borbonius* and *S. margaritacea,* but the distribution of those patterns among all species of *Odontanthias* and *Sacura* is unknown. The morphology of larval anthiadines has proved useful in the past in resolving generic issues. For example, Baldwin (1990) noted that the larvae of *Hemanthias vivanus, Pronotogrammus aureorubens,* and *P. eos* are strikingly similar, and Anderson and Heemstra (2012) used that information and comparative data from adults to establish a new genus, *Baldwinella,* for those 3 species. The differences in spination between larvae of *O. borbonius* and *S. margaritacea* raise questions about the synonymy of *Odontanthias* and *Sacura* suggested by molecular genetic analysis, but the larval morphology of additional species of these genera should be examined to better understand the interrelationships of anthiadine fishes.

Conclusions

The small- to medium-sized serranid anthiadine fishes from shallow to deep coral reef habitats are most diverse in the Indo-Central Pacific region, but the larvae of relatively few species have been described. This study describes the larvae of the anthiadine *O. borbonius* in the size range of 5.7–11.2 mm SL for the first time and compares their morphological features to other related anthiadine species. *Odontanthias borbonius* larvae have the most developed spiny ornamentation. There are differences in a few characters of the ornamentations among these species. The differences between larvae of *O. borbonius* and *S. margaritacea* raise questions about the synonymy of *Odontanthias* and *Sacura* suggested by molecular genetic analysis, but the larval morphology of additional species of these genera should be examined to better understand the interrelationships of anthiadine fishes.

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