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PHYLOGENETIC RELATIONSHIPS OF *TANYEMBLEMARIA ALLENI*, A NEW GENUS AND SPECIES OF CHAENOPSID (PISCES: BLENNIOIDEI) FROM THE GULF OF PANAMA

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ABSTRACT

Tanyemblemaria alleni, described from a single specimen from Islas Perlas, Panama, is unique among chaenopsids in having the dorsal portion of the second infraorbital expanded, the posterior margin of the preopercle with serrations and short spines, five anal-fin pterygiophores inserted anterior to the first caudal vertebra, and XXVII dorsal-fin spines. It is also distinctive in lacking a nasal cirrus and in having an elongate body, an elongate first dorsal-fin spine, spines on the ventral margin of the first infraorbital, exposed ridges on the nasals, and a raised ridge on the frontals with pits anterior to the ridge. *Tanyemblemaria* shares two apparent apomorphies, widely separate nasals and reduced vomerine dentition, with *Emblemaria, Hemiemblemaria, Lucayablennius* and *Chaenopsis*. Autapomorphies are proposed for each of these genera and their interrelationships are hypothesized based on morphological characters. *Chaenopsis* and *Lucayablennius* are sister groups, *Hemiemblemaria* is their sister group, but the relationships of *Tanyemblemaria* are unresolved; it is either the sister group of these three genera or, more likely, the sister group of *Emblemaria*.

The Chaenopsidae comprises a distinctive group of about 60 species of New World marine blennioid fishes. Despite the relatively recent and thorough coverage of its alpha taxonomy (Stephens, 1963; 1970; Smith-Vaniz and Palacio, 1974), new taxa of chaenopsids continue to be found. Among them is a new species, recently collected from the tropical eastern Pacific. This species, described herein, is distinctive in a number of morphological features. Given its apparent phylogenetic relationships within the Chaenopsidae, a new genus is erected for it.

Stephens (1963; 1970) hypothesized two lineages within the Chaenopsidae, one with fused nasals and one with separate nasals. Within the latter lineage, he noted that *Hemiemblemaria, Lucayablennius* and *Chaenopsis* have "widely diverging nasals." This character, if stated another way, "nasals lateral to the ascending premaxillary processes," supports the monophyly of a clade comprising these three genera, plus *Emblemaria* and the new genus. All other chaenopsids and closely related blennioids have nasal bones overlying the ascending premaxillary processes. Additional characters supporting the monophyly of this clade and hypotheses of its intrarelationships are presented in this study.

MATERIALS AND METHODS

Counts and measurements were made according to Stephens (1963). Sensory pore terminology follows Smith-Vaniz and Palacio (1974) except that pores on the frontal bones were subdivided into 1) "F1," a secondary canal or pore on the medial side of the supraorbital canal, dorsal to the temporal canal (Fukao, 1980; 1987); 2) "F2," a similar canal or pore medial to the supraorbital canal, but anterior to "F1" (Fukao, 1980; 1987); 3) "median frontals," opening on the medial side of the supraorbital canal anterior to F1 and F2 (Rosenblatt and McCosker, 1988); and 4) "anterofrontals," pores along the interorbit, anterior to the supraorbitals and the median commissural pore (Johnson and Greenfield, 1976). Osteological specimens were prepared according to Dingerkus and Uhler (1977).

Representatives of all chaenopsid genera were examined (see Material Examined); all known species were examined for those genera containing three or fewer species (*Lucayablennius, Hemiemblemaria,*

Table 1. Character scores for chaenopsid genera. Character numbers refer to those in Appendix Table 1. Characters varying within a genus are scored as "?"

	Character number			
	1–10	11–20	21–30	31–40
Ingroup Genera				
Tanyemblemaria	11111?0000	0000000000	0001111112	1111111110
Emblemaria	1111110000	0000000000	00?1110001	0000?00?00
Chaenopsis	11?1111111	1111111111	111?001112	111110000?
Lucayablennius	1111111111	1111111111	1110001112	1100100001
Hemiemblemaria	1111111111	1111100000	0000001100	0000000000
Outgroup Genera				
Acanthemblemaria	0000000000	0000000000	0000001000	0100?10000
Ekemblemaria	00?0?00000	00?0000000	0000?01000	0000111000
Coralliozetus	0000000000	0?00000002	001?000000	0?00100111
Emblemariopsis	0000010000	0?01?00002	000?010001	0000?00000
Protemblemaria	0001?00000	0200000000	?0?0000000	0000100111
P. lucasana	0000000000	0200000002	1100010001	0000100001
Mccoskerichthys	0000000000	0200100000	1000?01100	1101000000
Stathmonotus	0?01100000	0000100000	1010?0?00?	010?100001
Neoclinus	0010000000	0200100000	1000?0?100	?000000000

Protemblemaria and *Ekemblemaria*), while representative species were examined for more speciose genera. For those speciose genera whose intrarelationships have been recently hypothesized (*Acanthemblemaria*, see Hastings, 1990; *Coralliozetus*, Hastings, in prep.), representatives from the first two ingroup branches were selected. For genera lacking recent hypotheses of intrarelationships (*Emblemaria, Chaenopsis* and *Emblemariopsis*), species were selected based on availability of specimens and so as to encompass the range of morphological variation known within each genus. Outgroups of the Chaenopsidae sensu stricto (Stephens, 1963) were also examined, including the monotypic *Mccoskerichthys*, two species of *Stathmonotus*, and two species of *Neoclinus*.

Hypotheses of phylogenetic relationships are based on 40 discretely coded morphological characters (Appendix Table 1). Informative characters for the clade of primary interest, as well as characters with states shared by members of this clade and other chaenopsid genera, were scored for each genus (Table 1), as well as *Protemblemaria lucasana* which differs from its congeners in several characters. Three multistate characters (12, 20 and 28) were considered unordered, while a fourth (30) was linearly ordered (Appendix Table 1). Characters with more than one state within a genus were scored as unknown for that genus.

Parsimony analyses were conducted using the exhaustive and branch and bound options of PAUP (Swofford). Because the relationships of the clade of primary interest with other chaenopsid genera are not fully resolved, the outgroup substitution method (Donoghue and Cantino, 1984) was employed, using each of the remaining genera listed above, both alone and in combination. Alternative topologies and character evolution were explored using MacClade (Maddison and Maddison).

Material Examined.—The following is a partial list of material examined with the total number and number of cleared-and-stained (CS) specimens indicated parenthetically. Institutional abbreviations follow Leviton et al. (1985).

Clade of Primary Interest. *Chaenopsis alepidota*: UAZ 82-1 (1 CS), UAZ uncat. (1 CS), SIO 62-212 (50), SIO 65-351 (90); *C. coheni*: SIO 61-247 (34), SIO 61-249 (19), SIO 65-295 (15, 2 CS); *C. limbaughi*: UAZ uncat. (1 CS); *C. roseola*: USNM 221168 (1 CS); *Emblemaria atlantica*: ANSP 133225 (10), UWF 2937 (1 CS), UWF 3666 (1); *E. caldwelli*: FMNH 87922 (21, 2 CS), FMNH 87923 (16), FMNH 90504 (22); *E. hypacanthus*: SIO 74-124 (139), UAZ 66-57-1 (20), UAZ 68-42 (2 CS), UAZ 69-3-9 (19), UAZ uncat., PAH 8315 (4 CS); *E. piratica*: UAZ 68-73-15 (2), UAZ 71-61-6 (3, 1 CS); *Hemiemblemaria simulus*: UF 19112 (1 CS), UMML 4710 (4), UMML 15055 (1 CS), UMML 31197 (2); *Lucayablennius zingaro*: FMNH 96749 (8, 2 CS), FMNH 96759 (8).

Other Chaenopsids and Outgroups. *Acanthemblemaria chaplini*: ANSP 100878 (7, 1 CS), ANSP 100882 (22), ANSP 144938 (9, 2 CS); *A. aspera*: ANSP 121873 (22), FMNH 93967 (37), FMNH 93972 (39, 2 CS), FMNH 93974 (37); *Coralliozetus springeri*: SIO 67-34 (53, 2 CS), SIO 67-37 (20), UAZ 85-17 (8, 2 CS); *C. angelicus*: UAZ 77-42 (16, 2 CS), UAZ 77-20 (144, 40 CS); *Ekemblemaria myersi*: SIO 61-250 (45), UAZ 69-46 (1 CS), UAZ 69-48 (26), UAZ 70-23 (1 CS), UAZ 82-21 (28, 2 CS); *E. nigra*: UMML 22455 (64, 2 CS), SIO 76-45 (10); *E. lira*: USNM 219829 (1 CS), USNM 316854 (1), USNM 316855 (1); *Emblemariopsis diaphana*: UF 11882 (5, 1 CS), UF 47329 (1), UMML

9230 (7); *E. signifera*: FMNH 87930 (5), FMNH 96852 (4), UF 18902 (1 CS); *E. tayrona*: UMML 34185 (4, 1 CS); *Protemblemaria bicirris*: SIO 62-726 (90), UAZ 73-94 (7, 1 CS), UAZ uncat. PAH-8319 (36), PAH 8417 (2 CS), PAH 8423 (40); *P. punctata*: ANSP 103562 (18), ANSP 103564 (13), ANSP 103565 (18, 2 CS), ANSP 103567 (9); *P. lucasana*: SIO 65-32 (9), SIO 65-317 (24), SIO 65-329 (19), SIO 65-343 (44), SIO 65-347 (8, 2 CS), UAZ 73-94 (14, 2 CS); *Mccoskerichthys sandae*: LACM 32547-51 (6), LACM 32566-38 (10 CS), SIO 70-359 (13), SIO 75-404 (255); *Stathmonotus sinuscalifornici*: SIO 62-124 (2 CS), UAZ 71-36 (23, 2 CS), UAZ 75-33-11 (15), UAZ 75-37-23 (19, 2 CS); *S. stahli*: UF 18902 (10, 2 CS); *Neoclinus stephensae*: LACM 38626-1 (10, 1 CS); *N. blanchardi*: SIO 60-67 (2); SIO UNCAT. (ICS).

Tanyemblemaria new genus

Diagnosis.—A chaenopsid, unique in having the upper portion of the second infraorbital expanded, the posterior margin of the preopercle with serrations and short spines, five anal-fin pterygiophores inserted anterior to the first caudal vertebra, and XXVII dorsal-fin spines. Notable, but not unique, in lacking a cirrus on the anterior nostril and in having an elongate body, an elongate first dorsal-fin spine, spines on the ventral margin of the first infraorbital, widely separate nasals, exposed ridges on the nasals, and a raised ridge on the frontals.

Type Species.—Tanyemblemaria alleni new species.

Etymology.—tany (Greek for long) + *emblemaria* (a genus of chaenopsid blennies), in reference to its elongate body. Gender, feminine.

Tanyemblemaria alleni new species

Figures 1–3

Holotype.—USNM 309963, male, 54.3 mm SL, Isla del Rey, Islas Perlas, Panama (ca. 8°17′30″N, 78°52′30″W), 17 m, 4 May 1990, G. R. Allen, D. R. Robertson, and R. Steene.

Description.—Body slender and elongate (Fig. 1). Head slightly pointed (Fig. 2), mouth terminal; lower jaw not projecting beyond upper. Maxillary extending posteriorly about one half of eye diameter past level of posterior margin of orbit. Maxillary not visible externally; sheathed anteriorly by first infraorbital and posteriorly by a fold of skin. Upper lip continuous across snout, without a median notch. Supraorbital cirrus flattened, unbranched, length less than one half orbital diameter. Anterior nostril with a prominent tube, without a cirrus. Posterior nostril with a raised rim. Testis in a single lobe; accessory organ in a single, hollow lobe.

Adductor mandibularis section A_2 (Winterbottom, 1974) extending dorsally to midline over posterior portion of neurocranium; anteriorly, A_2 muscles insert along posterior margin of a prominent, raised ridge on frontals (Fig. 3a). No spines along frontal ridge. Frontals, anterior to ridges and muscles, with pits, resembling a honeycomb. Supraorbital margin with a series of low, rounded serrations (Fig. 3a). Orbital margin of lateral ethmoid slightly thickened, without spines or serrations.

Dorsal fin XXVII, 24 (51 total elements); dorsal fin continuous, without a notch between spinous and segmented-ray portions; anteriormost spine elongate (Figs. 1, 2, 3e), approximately 1.5 times as long as remaining spines, which are more-or-less uniform in length. Anal fin II, 38. Caudal fin with 13 segmented and 4 upper and 3 lower procurrent rays; weakly lanceolate. Dorsal and anal fins connected to caudal fin by a membrane. Pectoral fins 13-13; distinctly pointed, central rays longest; most rays broadly flattened. Pelvic fins I,3-I,3; relatively short, second (longest) ray shorter than pectoral fin; third ray splintlike, shorter than pelvic spine; membrane between rays weakly incised. Vertebrae 16 + 39. Cephalic

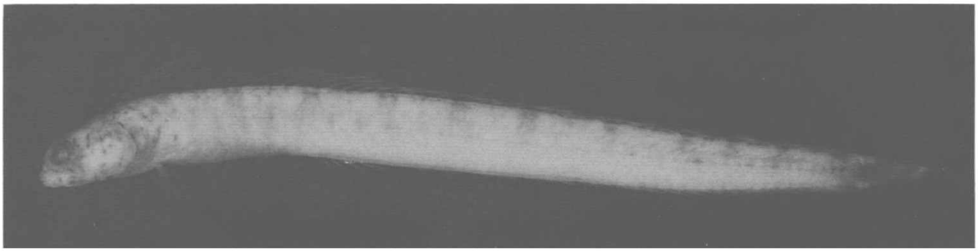

Figure 1. Holotype of *Tanyemblemaria alleni* (USNM 309963, 54.3 mm SL male).

sensory pores (left-right sides): mandibular, 4-4; common, 1-1; preopercular, 4-4; posttemporal, 4-4; lateral supratemporal, 1-1; median supratemporal, 1; anterior infraorbital, 3-3; posterior infraorbital, 3-3; supraorbital, 2-2; F1, 0-0; F2, 0-0; median frontal, 0-0; commissural, 1; anterofrontal, 1-1; nasal, 1-1.

Measurements (in mm) of the holotype are as follows: SL, 54.3; total length, 59.0; predorsal length, 12.5; preanal length, 18.4; head length (to posterior margin of gill membrane), 9.6; head length (to upper insertion of gill membrane), 8.6; head width (maximum), 3.5; head width (at upper insertion of gill membrane), 3.1; bony orbital diameter, 2.2; pigmented eye diameter, 1.9; bony interorbital width, 0.4; body depth (at anal-fin origin), 4.4; maximum body depth, 4.4; orbital cirrus length, 0.8; dorsal-fin spine I length, 6.4; dorsal-fin spine II length, 4.3; dorsal-fin spine III length, 3.9; last dorsal-fin spine length, 3.5; first dorsal-fin ray length, 3.5; pectoral fin length (longest ray), 4.9; pelvic-fin ray 1 length, 2.9; pelvic-fin ray 2 length, 3.7; pelvic-fin ray 3 length, 0.6; caudal fin length (longest ray), 4.7.

Osteology.—Nasals widely separate, lying lateral to ascending premaxillary processes; ascending processes not extending posteriorly beyond nasals. Nasals with prominent raised ridges and a single row of projecting ossified knobs.

Two infraorbitals (Fig. 3c); lateral surface of both with numerous pits. First infraorbital (lacrimal) excludes second entirely from suborbital margin above

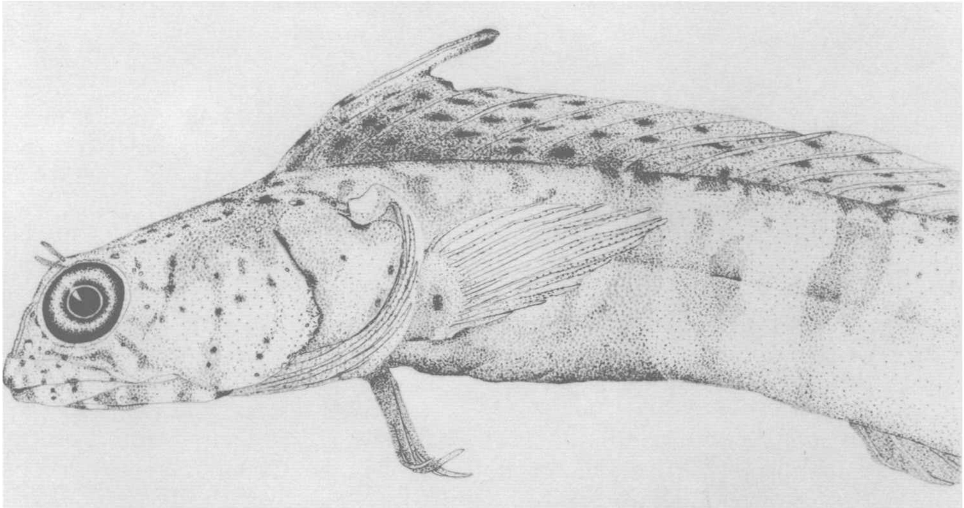

Figure 2. Drawing of the anterior region of holotype of *Tanyemblemaria alleni*.

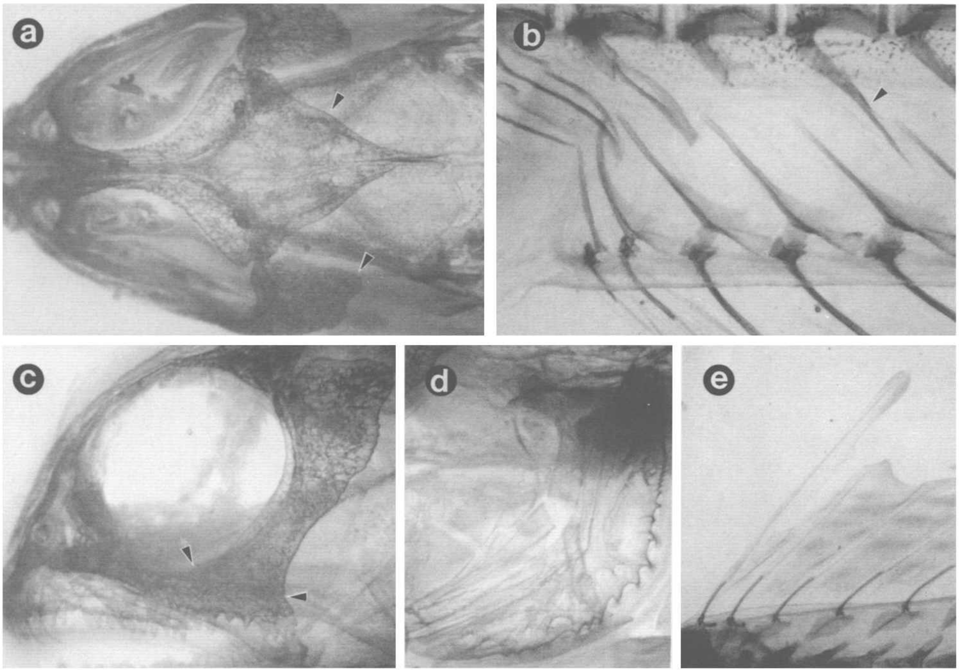

Figure 3. Osteology of *Tanyemblemaria alleni* (cleared-and-stained holotype). a) Dorsal view of head; upper and lower arrows indicate, respectively, the raised frontal ridge (character 36, Appendix Table 1) and the expanded dorsal margin of the second infraorbital. Note also the serrate supraorbital margin. b) Anterior anal-fin pterygiophores (31); arrow indicates the first hemal spine. c) Lateral view of head; arrows indicate the suture between the first and second infraorbitals (39). Note also the spines on the ventral margin of the first infraorbital and the expanded dorsal portion of the second infraorbital. d) Lateral view of preopercle; note serrations and spines along posterior margin. e) Anterior dorsal fin; note prolonged first spine (24) and incomplete ossification of all spines.

upper jaw. Lateral surface of first infraorbital with a shallow depression posteriorly; orbital margin smooth, ventral margin with strong spines. Second infraorbital with upper portion broad and greatly expanded posteriorly (Fig. 3a, c); orbital and posterior margins smooth. Posterior margin of preopercle with serrations and spines (Fig. 3d): upper, vertical portion with a series of evenly-spaced serrations, followed ventrally by more widely-spaced, pointed spines; horizontal portion with short spines. Lateral face of hyomandibula with a broad, anteriorly-directed spur. Mesopterygoid autogenous; restricted posteriorly to region dorsal to quadrate, not paralleling ectopterygoid.

Three dorsal-fin pterygiophores inserted anterior to first neural spine. Five anal-fin pterygiophores inserted anterior to first hemal arch (Fig. 3b). Abdominal cavity extending posteriorly to level of fourth anal-fin pterygiophore. Pleural ribs on precaudal vertebrae 3–15; fragmentary pleural ribs on vertebra 16. Epipleural ribs on precaudal vertebrae 1–16, those on last few threadlike. Caudal fin with a single epural; epural free, not inserted in a sheath of bone on urocentral vertebra. Hypural 5 absent.

Two branchiostegals inserted on lateral surface of epihyal, 2 on lateral surface of posterior, expanded portion of ceratohyal, and 2 below anterior portion of ceratohyal; all branchiostegals slender, not expanded distally. Urohyal wedge-shaped. First and second basibranchials ossified, third and fourth unossified.

Upper 2 pectoral-fin radials articulating with scapula, third with both scapula and coracoid, and fourth with coracoid. Upper arm of scapula thin, without a horizontal stay to cleithrum. Two postcleithra; ventral portion of lower postcleithrum thin, not expanded.

Anterior margin of each side of dentary with an outer row of 5, anteriorly-directed, blunt teeth, followed posteriorly by 3 large, vertical canines, and a row of 14 shorter canines; a patch of small pointed teeth, about 3 teeth wide, medial to anterior portion of outer row. Each premaxilla with an outer row of 6 large canines, followed posteriorly by a row of 10 shorter canines; a patch of small pointed teeth, 2–3 teeth wide medial to anterior portion of outer row. Anterior margin of vomer triangular; vomer with 3 small, pointed teeth, not arranged in a row and not contiguous with palatine tooth row. Palatine abutting vomer, without a space separating them. Palatine teeth uniserial, 11 on left palatine and 14 on right palatine; middle teeth largest, posteriormost smallest.

Coloration of Holotype in 75% Ethanol (Figs. 1, 2).—Head and body peppered with fine melanophores, some of which are expanded, giving a mottled effect. Nape peppered with melanophores, some expanded into irregular blotches. Cheek peppered with melanophores, several expanded into small, irregular spots. Posterior margin of preopercle with five dark spots: dorsalmost elongate, at upper end of preopercle; ventralmost just posterior to end of lower jaw, and conspicuous in ventral view. Chin with three pale bands and intervening dense melanophores; anteriormost pale band continuous across isthmus and extending upward across lips; second and third pale bands only on rami of lower jaw, interrupted by dense melanophores across branchiostegal membrane. Lips with scattered melanophores. Two dense clusters of melanophores on first infraorbital: first beneath anterior orbital margin, second posterior to first pale band on chin. Branchiostegal membrane and isthmus densely peppered with melanophores except for first chin band. Supraorbital cirrus peppered with melanophores.

Body densely covered with melanophores except for an immaculate region just posterior to pectoral fin. Body pattern generated primarily by expansion of certain groups of melanophores. Eleven dorsal saddles: anteriormost weak, at level of pectoral-fin insertion; second at level of mid-abdomen, third at level of anus, 4–10 along dorsal-fin base, and last at caudal peduncle. Second and third saddles extending ventrally across abdomen; first and fourth through tenth extending ventrally to midline where they gradually fade into background coloration; last extending ventrally across caudal peduncle. Areas between saddles variously mottled with melanophores. Midline with about 17 faint dots. Abdomen densely covered with melanophores, most of which are expanded. Genital papilla and area anterior to anus immaculate.

Dorsal-fin flap covered with fine melanophores. No ocellus or blotch on anterior dorsal fin. Anterior dorsal fin covered with fine melanophores, concentrated into two or more irregular rows of spots, continuing posteriorly across segmented-ray portion of dorsal fin, where they become indistinct. Anterior anal-fin covered with dense melanophores, becoming less dense posteriorly. Anal fin without a basal or distal band, and no row of spots along anal-fin base. Caudal fin with a diffuse blotch centrally and three ill-defined bands of melanophores, posteriormost at tip of fin. Pectoral-fin base densely peppered with fine melanophores, concentrated in a small blotch on lower half of fin base; a smaller blotch along fleshy ridge above pectoral-fin base. Lower pectoral-fin peppered with melanophores along entire length; central and upper pectoral-fin immaculate. Pelvic fin and base densely peppered with melanophores.

Fresh Coloration (based on a kodachrome slide).—No bright colors evident except for a small orange blotch on cheek at posterior margin of upper jaw, a slight yellowish cast to lower portion of cheek and opercle, and several white spots or blotches on head, body and dorsal fin. Posterior margin of second infraorbital with a crescentic row of white spots; nape with a few scattered white spots; opercle, pectoral-fin base, and proximal portion of pectoral-fin rays each with a single large white blotch; entire length of body with alternating white and dark saddles. Midline, from mid-abdomen to caudal-fin base, with a series of white blotches, becoming horizontally elongate posteriorly. Anterior dorsal fin white, accentuating rows of black spots; tips of most dorsal-fin elements, including entire length of elongate first spine, white. Caudal fin with irregular bands of white alternating with black.

Distribution.—*Tanyemblemaria alleni* is known only from the holotype, collected at Isla del Rey, Islas Perlas, Panama.

Etymology.—*alleni,* in honor of Gerald R. Allen, collector of the holotype, in recognition of his contributions to the study of fishes.

RELATIONSHIPS

Tanyemblemaria alleni is clearly a member of the Chaenopsidae (sensu stricto, Stephens, 1963), with which it shares the derived character states of two rather than four infraorbitals (Fig. 3c), an incomplete ossification of the dorsal-fin and anal-fin spines (Fig. 3b, e), a fleshy flap anterior to the first dorsal-fin spine (secondarily lost in some chaenopsids), the mesopterygoid restricted posteriorly rather than paralleling the ectopterygoid, a concave interorbit (flat in *Hemiemblemaria*), palatine teeth in a row (or rows) rather than a patch, a single testicular lobe, and a single testicular accessory organ (Hastings and Patzner, in prep.). It lacks one apparent apomorphy of the Chaenopsidae, the presence of a broad or bladelike posteriormost branchiostegal.

Tanyemblemaria shares some apparently derived character states with a variety of chaenopsids. It shares with *Acanthemblemaria* and *Ekemblemaria* raised ridges (Fig. 3a) on the frontals (character 36, Appendix Table 1) which mark the anterior extent of adductor mandibularis A_2 muscles on the neurocranium. Some chaenopsids lacking ridges, such as *Mccoskerichthys, Lucayablennius* and female *Coralliozetus* species (Hastings, 1991), lack these muscles on the dorsal neurocranium; other chaenopsids lacking ridges have muscle fibers extending farther forward on the neurocranium. Both *Tanyemblemaria* and *Ekemblemaria* have numerous pits on the region anterior to the frontal ridges (37). These pits, which appear to result from uneven deposition of bone (Hastings, 1991), are large with irregular margins in *Tanyemblemaria* (Fig. 3a), and smaller and more regular in outline in *Ekemblemaria. Tanyemblemaria* shares with *Coralliozetus* and *Protemblemaria* absence of a horizontal scapular stay (38) and the second infraorbital excluded from the suborbital margin (39). A scapular stay is also absent in some species of *Emblemaria,* and a reduced stay is characteristic of *Lucayablennius* (Fig. 5c). The second infraorbital is excluded from the suborbital margin in some species of *Acanthemblemaria* (Hastings, 1990). *Tanyemblemaria* shares with *Chaenopsis* (see below), *Mccoskerichthys* and some species of *Stathmonotus* an elongate body (34). However, *Mccoskerichthys* and *Stathmonotus* are outgroups of the Chaenopsidae sensu stricto (Hastings and Springer, in prep.) and apparently not closely related to *Tanyemblemaria.*

A parsimony analysis indicates that *Tanyemblemaria* is a part of a monophyletic clade comprising *Hemiemblemaria, Lucayablennius, Chaenopsis* and *Emble-*

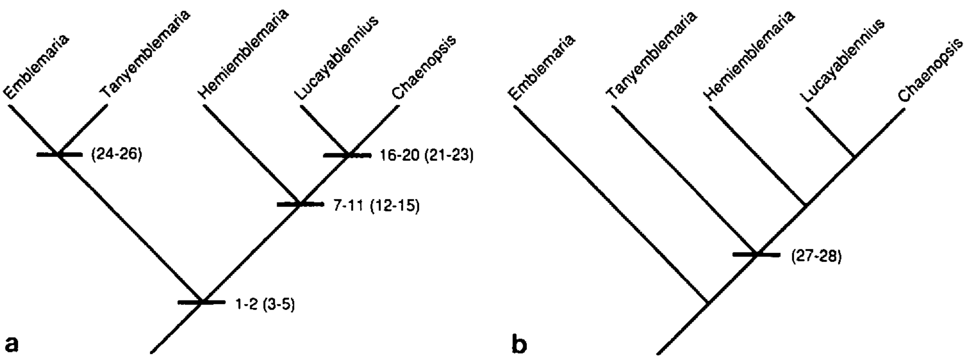

Figure 4. Alternative phylogenetic hypotheses for *Tanyemblemaria* and related chaenopsids. a) Most parsimonious topology, and b) an equally parsimonious topology depending upon outgroups used (see text). Character numbers at internal nodes refer to those in Appendix Table 1; unequivocal synapomorphies are followed, parenthetically, by homoplastic synapomorphies.

maria. This relationship is supported primarily by 2 apomorphies (1–2; Fig. 4a). First, in these genera, the nasal bones are displaced lateral to the ascending premaxillary processes (Fig. 5a, b). In other chaenopsids and the outgroups *Neoclinus, Stathmonotus* and *Mccoskerichthys,* the nasals overlie the ascending premaxillary processes and in many of these, the nasals are fused along their medial margins (Stephens, 1963; Rosenblatt and Stephens, 1978). Second, *Tanyemblemaria* shares with *Hemiemblemaria, Lucayablennius, Chaenopsis* and *Emblemaria* a unique condition of the palatovomerine dentition; the vomerine teeth are small or absent and are not contiguous with the palatine tooth row. In other chaenopsids and close relatives (except *Stathmonotus* which lacks teeth on the palatine), the vomerine teeth are relatively large and contiguous with a row of still larger teeth on the palatine.

Tanyemblemaria also shares with *Emblemaria, Hemiemblemaria, Lucayablennius,* and *Chaenopsis* at least three homoplastic characters (3–5), including the loss of the neural spur (Hastings, 1990), which is present, however, in *Chaenopsis roseola,* absence of the F2 sensory pore (also absent in *Protemblemaria*), and absence of the median frontal pores (also absent in *Protemblemaria* and one species of *Ekemblemaria*). Another character, the presence of incised or threadlike pelvic-fin rays in females (6), is shared by these genera (as well as *Emblemariopsis*), but the condition of the pelvic fin of female *Tanyemblemaria* is unknown.

Three of the genera constituting this clade, *Tanyemblemaria, Hemiemblemaria,* and *Lucayablennius,* are monotypic and distinctive. *Tanyemblemaria* has at least 4 autapomorphies. First, the upper margin of the second infraorbital is expanded posteriorly (Fig. 3a, c), while it is slender in all other chaenopsids (Stephens, 1963, fig. 2; Smith-Vaniz and Palacio, 1974, fig. 7; Rosenblatt and Stephens, 1978, figs. 3, 6–9). Second, the posterior margin of the preopercle has serrations above and short spines at its angle and along its lower margin (Fig. 3d). The posterior margin of the preopercle is smooth in adults, juveniles, and, as far as known, larvae of all other chaenopsids. Third, *Tanyemblemaria* has five anal-fin pterygiophores inserted anterior to the first hemal spine (Fig. 3b). Other chaenopsids usually have 1 to 3 and rarely 4 (e.g., *Chaenopsis limbaughi,* see below) anal-fin pterygiophores inserted anterior to the first hemal spine. Finally, *Tanyemblemaria* has a high number, XXVII, of dorsal-fin spines; XXVII spines are known only in rare specimens of *Acanthemblemaria crockeri* (Stephens, 1963), while all other chaenopsids have fewer spines.

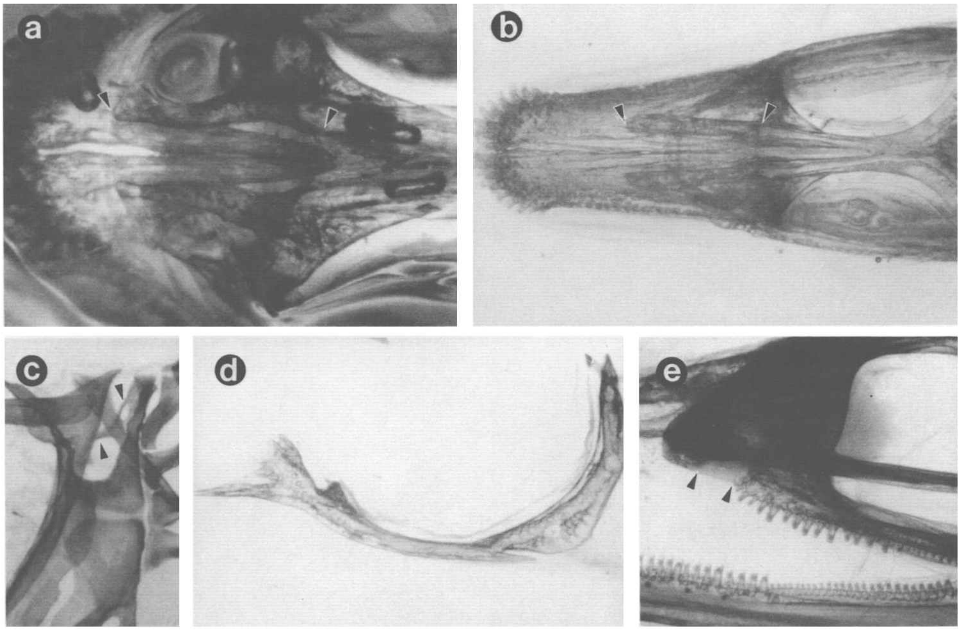

Figure 5. Osteology of selected cleared-and-stained chaenopsids illustrating hypothesized synapomorphies of various clades. a) Dorsal view of anterior portion of head of *Emblemaria atlantica* (UWF 2937); left and right arrows indicate, respectively, the anterior and posterior extent of the right nasal. b) Dorsal view of the anterior portion of the head of *Chaenopsis limbaughi* (UAZ uncat.); left and right arrows indicate, respectively, the anterior and posterior extent of the right nasal. In both a) and b), note that the nasals do not overlie the ascending premaxillary processes (character 1, Appendix Table 1). c) Lateral view of pectoral girdle of *Lucayablennius zingaro* (FMNH 96749); lower and upper arrows indicate, respectively, the scapular stay (38) and the foramen in the upper arm of the scapula (22). d) Lateral view of infraorbitals of *Chaenopsis alepidota* (UAZ 82-1); note the expanded, fanshaped anterior margin of the first infraorbital (7). e) Lateral view of the dentary, palatine, and anterior neurocranium of *C. alepidota* (UAZ 82-1); left and right arrows indicate, respectively, the posterior extent of the vomer and the anterior extent of the palatine (9).

Hemiemblemaria has two apparent autapomorphies. Its interorbit is broad and flattened, rather than narrow and concave as in other chaenopsids, and it has a unique color pattern and behavior, mimicking those of the bluehead wrasse (Longley and Hildebrand, 1940).

Lucayablennius has nine apparent autapomorphies, three of which may be paedomorphic. It has a fleshy projection on the anterior margin of the lower jaw, large foramina in the neural arches (Fig. 6a), the first basibranchial fused to the basihyal (Fig. 6b), the third hypobranchial unossified (also in some *Chaenopsis* species), a truncate pectoral fin, a unique coloration and behavior that may reflect aggressive mimicry of gobies of the genus *Coryphopterus* (Greenfield, 1972; Colin and Gomon, 1973), and the apparently paedomorphic characters of an interrupted supratemporal commissure, absence of muscles on the dorsal portion of the neurocranium, and a short jaw. The last two character states are also present in paedomorphic females of *Coralliozetus angelicus* (Hastings, 1991).

Not all species of the remaining two genera comprising this clade, *Chaenopsis* and *Emblemaria*, were examined. However, the representative species examined revealed potential autapomorphies for both genera. Three autapomorphies are hypothesized for *Chaenopsis*. The four species examined in this study have the first basibranchial fused to the urohyal (Fig. 6c; only weakly fused in *C. limbaughi*),

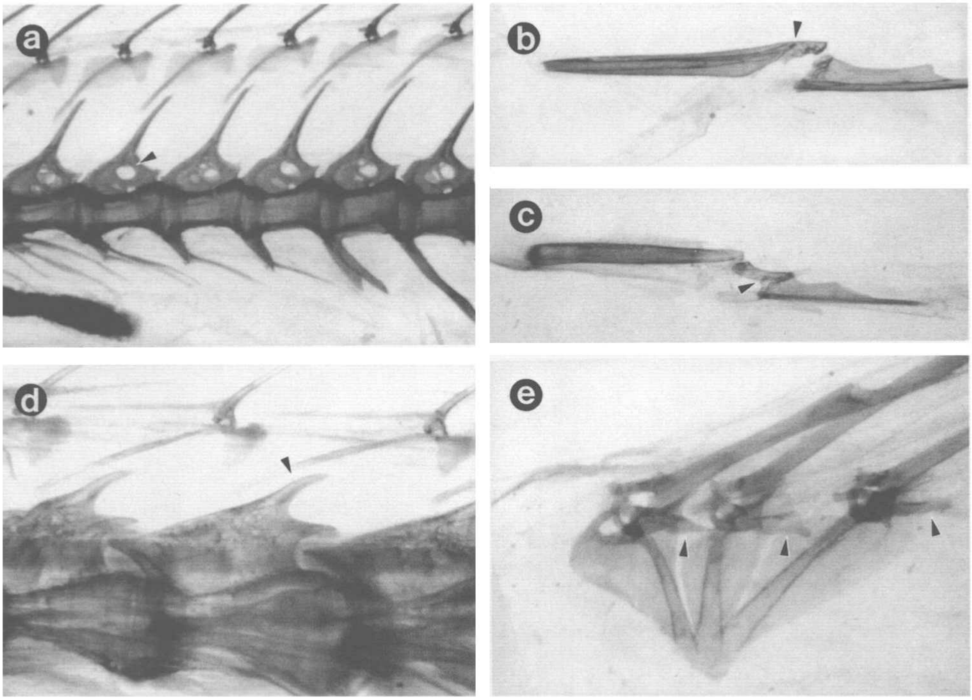

Figure 6. Osteology of selected cleared-and-stained chaenopsids illustrating hypothesized autapomorphies of three genera. a) Lateral view of posterior precaudal vertebrae of *Lucayablennius zingaro* (FMNH 96749); arrow indicates a large foramen in the lateral wall of the neural arch. b) Basihyal (left), first basibranchial, and urohyal (right) of *L. zingaro* (FMNH 96749); arrow indicates point of fusion between basihyal and first basibranchial. c) Basihyal (left), first basibranchial, and urohyal (right) of *Chaenopsis alepidota* (UAZ 82-1); arrow indicates point of fusion between first basibranchial and urohyal. d) Lateral view of posterior precaudal vertebrae of *C. alepidota* (UAZ 82-1); note short neural spine (arrow) relative to *L. zingaro* (Fig. 6a). e) Lateral view of anterior dorsal-fin pterygiophores of *Emblemaria hypacanthus* (UAZ 68-42); arrows indicate lateral ossified wings.

short neural spines on the precaudal vertebrae (Fig. 6d), and short ascending premaxillary processes (also in *Tanyemblemaria*).

A single autapomorphy is hypothesized for *Emblemaria.* The four species examined in this study have lateral winglike projections on the first three proximal dorsal-fin pterygiophores (Fig. 6e). In other chaenopsids, an ossified ridge may be present on the first proximal pterygiophore, but it does not project laterally, and is absent from the second and third pterygiophores. In *Emblemaria,* these projections may serve for insertion of muscles to support and manipulate the dorsal fin.

Outgroup substitution using as single outgroups *Ekemblemaria, Acanthemblemaria, Protemblemaria, Mccoskerichthys, Stathmonotus* or *Neoclinus* produced a single most parsimonious topology (Fig. 4a). Use of *Coralliozetus, Emblemariopsis* or *Protemblemaria lucasana* as single outgroups produced the same and a second equally parsimonious topology (Fig. 4b). These trees ranged from 47 to 54 steps and 0.78 to 0.84 in consistency index depending upon the outgroup used. Similar ingroup topologies were obtained using various combinations of outgroup taxa. The phylogenetic relationships supported by this analysis, excluding *Tanyemblemaria,* are similar to those proposed by Böhlke (1957; although he considered *Emblemariopsis* to be a part of *Emblemaria*) and supported by more recent workers (Stephens, 1970; Acero, 1984).

Hemiemblemaria, Lucayablennius and *Chaenopsis* share five unequivocal apomorphies (7–11). These include an expanded anterior margin of the first infraorbital (Fig. 5d), the lower jaw projecting anteriorly beyond the upper jaw, the palatine separated from the vomer by a space (Fig. 5e), long secondary canals on the sensory canals of the lower portion of the preopercle, and a long basihyal (Fig. 6b, c). These three genera also share derived states of four characters (12–15) that are also present in various other chaenopsids. These include loss of the supraorbital cirrus (also in some *Emblemariopsis* species), a thick orbital margin on the lateral ethmoid (also in two species of *Ekemblemaria,* see Hastings, 1992), an incised pelvic fin in males (also in *Emblemariopsis*), and no dorsal-fin flap (also in some *Emblemariopsis* species and outgroups of the Chaenopsidae sensu stricto).

Chaenopsis and *Lucayablennius* share five unequivocal apomorphies (16–20), including an interrupted upper lip, an elongate urohyal (Fig. 6b, c), the pectoral fin inserted high on the body, a broad, rectangular vomer, and a rudimentary mesopterygoid. They also share apparently derived states of eight characters that are present in other chaenopsids. They have two (rather than 3) dorsal-fin pterygiophores inserted anterior to the first neural spine (21; also in *Protemblemaria lucasana, P. bicirris* and outgroups of the Chaenopsidae sensu stricto), a prominent foramen in the dorsal arm of the scapula (22, Fig. 5c; also in *P. lucasana*), no anterofrontal pore two (23; also in *Coralliozetus, P. bicirris* and *Stathmonotus*) and derived states of four characters (29–32) in common with *Tanyemblemaria* (see below).

The relationships of *Tanyemblemaria* differ in the two trees. In the first (Fig. 4a), *Tanyemblemaria* is the sister group of *Emblemaria* with which it shares an elevated anterior dorsal fin in males (24), a hollow rather than chambered testicular accessory organ (25) and raised ridges on the nasals (26). An elevated dorsal fin, used by Stephens (1961) to diagnose *Emblemaria,* is seen sporadically in males of other chaenopsids, including some species of *Chaenopsis, Coralliozetus* and *Emblemariopsis.* Details of accessory organ morphology have yet to be studied for chaenopsids and the developmental and functional relationships of hollow and chambered accessory organs are unknown. A hollow accessory organ is also reported for a new species of *Ekemblemaria* (Hastings, 1992). *Protemblemaria lucasana* and *Emblemariopsis* also have ridged nasals, but their nasals differ from those of this clade in that they are not widely separate. *Tanyemblemaria* is also similar to *Emblemaria* in the number and distribution of cephalic sensory pores, and in the general appearance of the head.

In the second tree (Fig. 4b), *Tanyemblemaria* is the sister group of the clade comprising *Hemiemblemaria, Lucayablennius* and *Chaenopsis*; they share absence of a notch between the spinous and segmented-ray portions of the dorsal fin (27; also absent in *Mccoskerichthys, Ekemblemaria,* and some species of *Acanthemblemaria*) and a narrow sheet of bone anterior to the strut on the dorsal-fin pterygiophores (28; also in *Mccoskerichthys, Neoclinus* and some species of *Acanthemblemaria,* Hastings, 1990). Since the polarity assessment of both of these characters is questionable, this topology is not strongly supported.

Interestingly, *Tanyemblemaria* shares several derived character states with *Lucayablennius* and *Chaenopsis* but not *Hemiemblemaria.* These include absence of a nasal cirrus (29), a splintlike third pelvic-fin ray (30), an increased number of anal-fin pterygiophores inserting anterior to the first caudal vertebra (31; also in *Mccoskerichthys*) and no hypural five (32; also in a variety of chaenopsids). *Tanyemblemaria* and *Chaenopsis* share short ascending premaxillary processes

(33) and an elongate body (34; also in *Mccoskerichthys* and some species of *Stathmonotus*). While these characters appear to support a closer relationship of *Tanyemblemaria* with this clade than with *Emblemaria, Tanyemblemaria* lacks the nine synapomorphies of *Hemiemblemaria, Lucayablennius* and *Chaenopsis* (7–15). Homoplasy thus appears to be common in these fishes. Additional material of *Tanyemblemaria alleni,* especially females, may help in more fully resolving the relationships of this interesting chaenopsid.

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LITERATURE CITED

Acero, P. A. 1984. The chaenopsine blennies of the southwestern Caribbean (Pisces: Clinidae: Chaenopsinae) I. Systematic analysis and zoogeography. An. Inst. Inv. Mar. Punta de Betin. 14: 29–46.

Böhlke, J. 1957. A review of the blenny genus *Chaenopsis,* and the description of a related new genus from the Bahamas. Proc. Acad. Nat. Sci. Phil. 109: 81–103.

Colin, P. L. and M. F. Gomon. 1973. Notes on the behavior, ecology and distribution of *Lucayablennius zingaro* (Pisces: Clinidae). Carib. J. Sci. 13: 59–61.

Dingerkus, G. and L. D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Tech. 52: 229–232.

Donoghue, M. J. and P. D. Cantino. 1984. The logic and limitations of the outgroup substitution approach to cladistic analysis. Syst. Bot. 9: 192–202.

Fukao, R. 1980. Review of Japanese fishes of the genus *Neoclinus* with description of two new species and notes on habitat preference. Publ. Seto Mar. Biol. Lab. 25: 175–209.

———. 1987. Fishes of *Neoclinus bryope* species complex from Shirahama, Japan, with description of two new species. Jap. J. Ichthy. 34: 291–308.

Greenfield, D. W. 1972. Notes on the biology of the arrow blenny, *Lucayablennius zingaro* (Böhlke) from British Honduras. Copeia 1972: 590–592.

Hastings, P. A. 1990. Phylogenetic relationships of tube blennies of the genus *Acanthemblemaria* (Blennioidei). Bull. Mar. Sci. 47: 725–738.

———. 1991. The ontogeny of sexual dimorphism in the angel blenny, *Coralliozetus angelica* (Teleostei: Chaenopsidae). Copeia 1991: 969–978.

———. 1992. *Ekemblemaria lira,* a new blennioid fish from Ecuador, with comments on sexual dimorphism and relationships in *Ekemblemaria* (Teleostei: Chaenopsidae). Copeia 1992: 769–776.

Johnson, R. K. and D. W. Greenfield. 1976. A new chaenopsid fish, *Emblemaria hyltoni,* from Isla Roatan, Honduras. Fieldiana, Zool. 70: 13–28.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal and C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985: 802–832.

Longley, W. H. and S. F. Hildebrand. 1940. New genera and species of fishes from Tortugas, Florida. Pap. Tortugas Lab. 32 (Carnegie Instit. Washington Publ. 517): 223–285.

Rosenblatt, R. H. and J. E. McCosker. 1988. A new species of *Acanthemblemaria* from Malpelo Island, with a key to the Pacific members of the genus (Pisces: Chaenopsidae). Proc. Cal. Acad. Sci. 45: 103–110.

——— and J. S. Stephens. 1978. *Mccoskerichthys sandae,* a new and unusual chaenopsid blenny from the Pacific coast of Panama and Costa Rica. Los Angeles Co. Mus. Contr. Sci. 293: 1–22.

Smith-Vaniz, W. F. and F. J. Palacio. 1974. Atlantic fishes of the genus *Acanthemblemaria,* with description of three new species and comments on Pacific species (Clinidae: Chaenopsinae). Proc. Acad. Nat. Sci. Phil. 125: 197–224.

Stephens, J. S. 1961. A description of a new genus and two new species of chaenopsid blennies from the western Atlantic. Not. Nat. 349: 1–8.

———. 1963. A revised classification of the blennioid fishes of the American family Chaenopsidae. Univ. Calif. Publ. Zool. 68: 1–165.

———. 1970. Seven new chaenopsid blennies from the western Atlantic. Copeia 1970: 280–309.

Winterbottom, R. 1974. A descriptive synonymy of the striated muscles of the Teleostei. Proc. Acad. Nat. Sci. Phil. 125: 225–317.

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Appendix Table 1. List of characters and character states used in the phylogenetic analysis

1) Nasals: 0 = overlying ascending premaxillary processes; 1 = lateral to ascending premaxillary processes (Fig. 5a, b).
2) Vomerine and palatine dentition: 0 = contiguous; 1 = not contiguous, vomerine dentition reduced.
3) Neural spur (see Hastings, 1990): 0 = present on anteriormost vertebrae; 1 = absent from all vertebrae.
4) Frontal pore F2: 0 = present; 1 = absent.
5) Median frontal pores: 0 = present; 1 = absent.
6) Shape of pelvic fin of females: 0 = not prolonged, membranes extending to near distal tips of rays; 1 = rays prolonged and threadlike, membrane not extending to distal tips of rays.
7) Anterior end of first infraorbital: 0 = truncate; 1 = expanded, fanshaped (Fig. 5d).
8) Lower jaw: 0 = equal in length to upper jaw; 1 = longer than upper jaw.
9) Vomer and palatine: 0 = contiguous, bones abutting; 1 = not contiguous, space separating bones (Fig. 5e).
10) Secondary canals on ventral portion of preopercle: 0 = shorter than wide; 1 = longer than wide.
11) Basihyal: 0 = short, length less than half combined length of hypohyal, ceratohyal and epihyal; 1 = long, length greater than half combined length of hypohyal, ceratohyal and epihyal (Fig. 6b, c).
12) Number of supraorbital cirri: 0 = 1; 1 = none; 2 = 2 or more.
13) Orbital margin of lateral ethmoid: 0 = thin; 1 = thick and rugose.
14) Shape of pelvic fin of males: 0 = not prolonged, membrane extending to near distal tips of rays; 1 = rays prolonged and threadlike, membrane not extending to distal tips of rays.
15) Fleshy flap anterior to first dorsal-fin spine: 0 = present; 1 = absent.
16) Upper lip: 0 = continuous across snout; 1 = interrupted medially.
17) Urohyal: 0 = short, length much less than 5 times its greatest depth; 1 = elongate, length more than 5 times greatest depth (Fig. 6b, c).
18) Pectoral fin: 0 = inserted at or below midline of body; 1 = inserted above midline.
19) Shape of vomer: 0 = anterior margin angular, vomer triangular; 1 = anterior margin straight, vomer rectangular.
20) Mesopterygoid: 0 = present, well developed; 1 = rudimentary; 2 = absent.
21) Number of dorsal-fin pterygiophores anterior to first neural spine: 0 = 3; 1 = less than 3.
22) Foramen in upper scapular arm: 0 = absent or very small; 1 = large (Fig. 5c).
23) Anterofrontal pore 2: 0 = present; 1 = absent.
24) Dorsal fin of males: 0 = low, anterior spines even; 1 = elevated, anterior spine(s) elongate (Fig. 3e).
25) Testicular accessory organ: 0 = solid, with chambers; 1 = hollow.
26) Nasals: 0 = no ridges; 1 = ridges present, evident externally.
27) Junction of spinous and segmented-ray portion of dorsal fin: 0 = notch present; 1 = no notch, posteriormost spines equal in length to anteriormost rays.
28) Shape of proximal dorsal-fin pterygiophores (at level of mid spinous dorsal fin): 0 = no sheet of bone anterior to lateral strut; 1 = a narrow sheet of bone anterior to lateral strut.
29) Anterior nostril: 0 = cirrus present on posterior margin; 1 = no cirrus on posterior margin.
30) Third pelvic-fin ray: 0 = well developed, length greater than half that of second ray; 1 = reduced, length half that of second ray but greater than that of pelvic-fin spine; 2 = splintlike, length less than that of pelvic-fin spine. (ordered: 0-1-2).

Appendix Table 1. Continued

31) Number of anal-fin pterygiophores anterior to first hemal spine: 0 = less than 3; 1 = 3 or more (Fig. 3b).
32) Hypural 5: 0 = present; 1 = absent.
33) Ascending premaxillary processes: 0 = long, extending posterior to posterior margin of nasals; 1 = short, not extending posterior to posterior margin of nasals.
34) Body: 0 = not elongate, body depth at anal-fin origin less than 10 times in standard length; 1 = elongate, body depth at anal-fin origin 10 or more times in standard length.
35) Third basibranchial: 0 = ossified; 1 = not ossified.
36) Frontal ridge: 0 = absent; 1 = present (Fig. 3a).
37) Pits on frontal: 0 = absent; 1 = present (Fig. 3a).
38) Scapular stay to cleithrum: 0 = present (Fig. 5c); 1 = absent.
39) Suborbital region above upper jaw: 0 = composed of both first and second infraorbitals; 1 = composed of first infraorbital only (second displaced dorsally; Fig. 3c).
40) Second basibranchial: 0 = ossified; 1 = not ossified.