

***Protoblepharon rosenblatti*, a new genus and species of flashlight fish  
(Beryciformes: Anomalopidae) from the tropical South Pacific,  
with comments on anomalopid phylogeny**

Carole C. Baldwin, G. David Johnson, and John R. Paxton

(CCB, GDJ) Department of Vertebrate Zoology, MRC 159, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.; (JRP) Division of Vertebrate Zoology, The Australian Museum, Sydney, New South Wales, Australia

*Abstract.* — *Protoblepharon rosenblatti* is described from a single large specimen collected at 274 m off Rarotonga, Cook Islands. It differs from other anomalopids most notably in having a low number of gill rakers on the first arch (21 vs. 24 or more), high number of body scale rows (ca. 145 vs. 130 or fewer), no postorbital papillae, and a very small gap between the lacrimal and nasal for passage of the fibrocartilaginous stalk, which is twisted and not broadly exposed posteriorly. *Protoblepharon* is a primitive member of the lineage of flashlight fishes characterized by a shutter mechanism for light-organ occlusion.

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The Anomalopidae comprise a small group of nearly circumtropically distributed, marine beryciform fishes characterized most conspicuously by a subocular luminous organ in which symbiotic luminous bacteria are cultured (e.g., Harvey 1922, Haygood & Cohn 1986). Since a review of the family by McCosker & Rosenblatt (1987), in which five species were recognized in three genera, Johnson & Rosenblatt (1988) erected a new genus, *Phthanophaneron*, for the eastern Pacific *Kryptophanaron harveyi* Rosenblatt & Montgomery, and Rosenblatt & Johnson (1991) described a new genus and species from Tahiti, *Parmops coruscans*. With the exception of *Photoblepharon*, with two species, all genera are monotypic.

Using derived morphological features, including aspects of the occlusion mechanism of the light organ, Johnson & Rosenblatt (1988) hypothesized the following relationships (in phyletic sequence) among four anomalopid genera: *Anomalops*, *Phthanophaneron*, *Kryptophanaron*, *Protoblepharon*. Rosenblatt & Johnson (1991) placed *Parmops* as the sister group of the

*Phthanophaneron* + *Kryptophanaron* + *Photoblepharon* clade.

We have examined a very large (229 mm SL) flashlight fish from the preserved collections at the Australian Museum that cannot be assigned to any known species. The specimen was collected on hook and line in deep water off Rarotonga, Cook Islands. A comparison of the single known specimen of the new species with other anomalopids suggests that it is a primitive member of the group of flashlight fishes characterized by a shutter mechanism for light-organ occlusion, i.e., all anomalopid genera except *Anomalops* (Johnson & Rosenblatt 1988). Our phylogenetic placement of the new species is best served by erecting a new genus for it.

Flashlight fishes observed by divers and those preserved in fish collections typically are small (<100 mm SL), and thus the large size of the holotype of the new species is unusual. However, several large specimens (>200 mm SL) are known for *Anomalops* (McCosker & Rosenblatt 1987), and *Phthanophaneron harveyi* is known from a 20-mm SL juvenile, the 67.7-mm SL ho-

lotype, and a 204-mm SL specimen (Rosenblatt & Montgomery 1976, McCosker & Rosenblatt 1987, Allen & Robertson 1994). Large flashlight fishes typically are taken in deeper water than small ones (e.g., McCosker & Rosenblatt 1987), and may be more common than their poor representation in fish collections suggests. Further collecting efforts are needed to find small specimens of the new species, the holotype of which is from an area of the Cook Islands where small specimens of both *Anomalops* and *Photoblepharon* occur. Our purposes here are to describe the new species and discuss its relationships in the context of an existing phylogenetic hypothesis of anomalopid genera.

#### Methods

Measurements were made with needle-point dial calipers or an ocular micrometer to the nearest 0.1 mm. Terminology of structures associated with the light organ follows Johnson & Rosenblatt (1988). Gill-raker counts include all rudiments. Scale bars in illustrations represent 1 mm. We follow Johnson & Rosenblatt (1988) in using the name "Trachichthyoidei" for the clade comprising the Anomalopidae, Monocentridae, and Trachichthyidae, the monophyly of which was proposed by Zehren (1979) and Moore (1993). The Monocentridae and Trachichthyidae were considered the first and second outgroups, respectively, for the phylogenetic analysis of anomalopid genera based on the hypothesized monophyly of the Trachichthyoidei and a proposed sister-group relationship between the Monocentridae and Anomalopidae (Konishi & Okiyama 1997). Following Zehren (1979), Moore (1993) suggested a sister-group relationship between the Monocentridae and Trachichthyidae, but the single character cited as evidence involves the infraorbital series, which is modified in all anomalopids to accommodate the light organ. Further study is needed to test Konishi & Okiyama's (1997) Anomalopidae + Monocentri-

dae hypothesis, which also is based on a single character: presence of a separate spinous dorsal fin in monocentrids and all anomalopids except *Photoblepharon*. Recognizing that neither hypothesis of trachichthyoid interrelationships is well supported, we initially included the sister group of trachichthyoids, the Anoplogastridae + Dirremidae (Zehren 1979, Moore 1993, Baldwin & Johnson 1995), as an additional outgroup in our analysis, but this inclusion had no effect on the topology of the tree and will not be discussed further. All characters included in the phylogenetic analysis were weighted equally, and multistate characters were treated as unordered.

#### *Protoblepharon*, new genus

**Diagnosis.**—An anomalopid with 21 gill rakers on the first arch, about 145 body scale rows, a small (14.5% HL) rotatable light organ, no postorbital papillae, and a very small gap between the lacrimal and nasal for passage of the stalk, which is twisted and not broadly exposed posteriorly. The following combination of characters also is useful in distinguishing *Protoblepharon*: a separate spinous dorsal fin, a pelvic-fin spine, two anal-fin spines, 59–60 enlarged lateral-line scales, an elastic shutter, and a broad strap-like ethmomaxillary ligament with no groove or swelling.

**Type species.**—*Protoblepharon rosenblatti*, new species.

**Etymology.**—From the Greek *protos*, first, and *blepharon*, eyelid, in reference to the cladistic position of the genus as first in the lineage of flashlight fishes that occlude the light organ with an erectable shutter.

*Protoblepharon rosenblatti*, new species

Fig. 1

**Holotype.**—AMS I.24275-001. A 229-mm SL female specimen caught by hook and line northwest of Matavera, Rarotonga, Cook Islands (21°12'S, 159°45'W), at 274 m on 30 Nov. 1983, and donated by

N. Sims of the Cook Islands Fisheries Department.

Description. — Counts and measurements, in mm, of the holotype: Dorsal-fin rays VI-I, 14; anal-fin rays II, 11; pectoral-fin rays ii15i; pelvic-fin rays I,5; caudal-fin rays 10, 10+9, 9 (all procurent rays spinous except the posteriormost in the upper and lower caudal-fin lobes); branchiostegals 8; gill rakers on first arch 21 (5+12 rakers, plus two flat plates at dorsal end of epibranchial and two at anterior end of ceratobranchial); pored lateral-line scales 59 (60 on right side); scale rows above lateral line ca. 18; abdominal scutes 9; vertebrae 14+16. Head length 83.4; predorsal length 96.9; prepelvic length 112; body depth at origin of dorsal fin 81.9; caudal-peduncle depth 23.3; caudal-peduncle length 50.5; snout length 23.7; eye diameter 19.4; orbit diameter 20.5; light-organ length 12.1; pectoral-fin length 51.9; pelvic-fin length 41.2; first dorsal-spine length 12.2; third dorsal-spine length 17.0; sixth dorsal-spine length 6.8; seventh dorsal-spine length 20.0; first anal-spine length 5.8; second anal-spine length 12.3.

Body compressed (width 1.9 in depth) and deep (depth at origin of dorsal fin 1.8 in length without head). With mouth open, profile sloping gradually from occiput to snout, somewhat convex in region of mesethmoid, then dropping slightly to symphysis of upper jaw; upper-jaw symphysis at level of horizontal through middle of eye. Nostrils anterior and completely dorsal to eye with mouth open, the anterior with thickened posterior rim. With jaws forced closed, mouth oblique, lower jaw originating anteriorly near horizontal through middle of eye, and maxilla extending posteriorly to vertical through middle of eye. Posterior supramaxilla ovoid, anterodorsal surface with small pointed process extending anteriorly along posterodorsal edge of small anterior supramaxilla. Posterior supramaxilla covering most of posterior portion of maxilla, the posteroventral corner of maxilla exposed and covered with tiny black pa-

pillae. Distinct notch at symphysis of premaxillae, presumably accommodating small dentigerous knobs at symphysis of dentaries when mouth closed. Premaxillae, including most of lateral and medial surfaces, covered with bands of villiform teeth; no teeth at symphyseal notch. Each dentary with narrow band of villiform teeth posteriorly, patch of slightly larger teeth near symphysis extending onto lateral and medial surfaces. Vomer edentulous, palatines with well-developed bands of villiform teeth.

Bones of head and pectoral girdle covered with numerous, rugose to minutely serrate ridges. Cleithrum with large exposed surface posteriorly, margin smooth. Supracleithrum almost completely beneath opercle, only posterodorsal corner exposed, margin smooth. Anterior infraorbitals enlarged, covering anteroventral corner of orbit, and slightly flared laterally forming a medially sloping plate. Laterosensory canals of head appearing as channels of dark skin surrounded by bone, skin covered with small black papillae and perforated frequently by pores.

Eye small, diameter 4.1 in head. No fleshy papillae on posterior rim of orbit. Luminous organ below eye small, length 6.9 in head. Light organ free posteriorly, supported by fibrocartilaginous cup anteriorly, which is ligamentously bound to a fibrocartilaginous stalk. Organ capable of being rotated downward into pocket below eye and medial to infraorbitals. When occluded, dorsal margin of light organ well below infraorbital rim. Black elastic shutter membrane attached along outer margin of suborbital pocket.

Numerous small, spinoid scales (cf. Roberts 1993, = Ct' of Johnson 1984) covering body, about 145 lateral body rows but difficult to count because of irregular distribution of scales. Lateral line covered by enlarged scales, and abdomen with series of about 9 enlarged, keeled scutes. Head mostly scaleless, a few thick, heavily sculptured scales at anterodorsal corner of opercle, scales coalescing on cheek to form strong

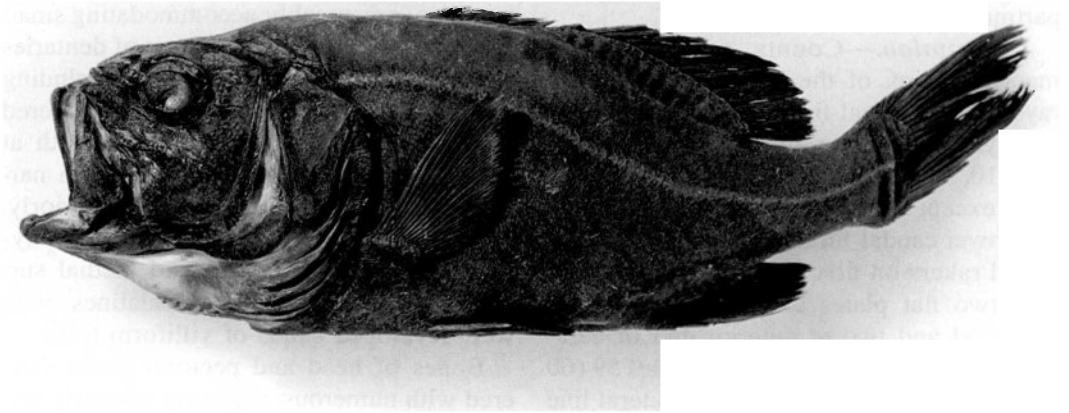


Fig. 1. Holotype of *Protoblepharon rosenblatti*, AMS I.24275-001, 229 mm SL. Photograph by C. Bento, AMS.

bony covering. Gular region naked, with low, pigmented, transverse ridges.

Most rakers on first gill arch long and lath-like, length of first raker below angle nearly two-thirds diameter of eye. Four anteriormost and two dorsalmost rakers on first arch and rakers on remaining arches less than half that long. Pseudobranch well developed, about 27 filaments.

Spinous dorsal fin lower than soft dorsal fin, the longest spine (seventh) 1.7 in length of longest unbroken soft ray (the fifth). Length of first spine 1.2 in second, second 1.1 in third and fourth, fifth 1.3 in first, sixth 1.7 in first, and seventh 0.6 in first. First anal spine shorter than any dorsal spine, second anal spine about equal in length to first dorsal spine. Longest anal soft ray (second) about equal to longest dorsal soft ray. Caudal fin deeply forked.

Pectoral-fin base nearly horizontal, fin directed posterodorsally. Pectoral-fin length about 1.6 in head, third through sixth rays the longest. Pelvic fin shorter than pectoral, 2.0 in head, and falling well short of anus. Color in alcohol dark brown to black; fins, posterior trunk, and cheek darkest. Lateral-line scales pale.

**Occlusion** mechanism (Fig. 2).—The cup

supporting the light organ is connected to a fibrocartilaginous stalk that is continuous with its contralateral member across the snout, with no attenuation at the commissure. Anteriorly, the stalk lies flat against the snout, with the broad surface facing outward; posteriorly, where the stalk passes through a small gap between the lacrimal and nasal, it twists such that its broad surface lies nearly in the horizontal plane (Fig. 2B). The posteroventral portion of the stalk and anteroventral corner of the cup each terminate in a short ventral process, and these are loosely joined dorsally by a short ligament. There is no ventral stalk hook. The shutter is slightly thickened near its anterodorsal corner, but there is no discrete shutter knob. The cup supports the anterior end of the light organ and extends posteriorly along about two-thirds of its ventral surface (Fig. 2B). A large section of it is exposed anterolaterally between the light organ and stalk; anteromedially, the cup forms a medially projecting shelf. The stalk muscle is not differentiated into dorsal and ventral bundles and inserts on the ligament connecting the stalk and cup. The Ligament of Diogenes originates on the rostral cartilage, curves around the ethmomaxillary lig-

ament as a broad strap, and then narrows posteriorly before inserting broadly on the ventral process and anteromedial shelf of the cup. The ethmomaxillary ligament descends anteroventrally from its origin on the mesethmoid to insert on the maxilla with a short branch to the palatine. This ligament is broad and flat, lacks a groove where it is crossed by the Ligament of Diogenes, has no pronounced forward flexure, and bears no swellings.

**Etymology.**—It is our pleasure to name this species in honor of Dr. Richard H. Rosenblatt, a mentor to one of us (GDJ), friend and valuable colleague to all of us. His contributions to the systematics and functional morphology of flashlight fishes have shed much light on the evolution and biology of the Anomalopidae.

**Remarks.**—States for *P. rosenblatti* of characters not associated with the light organ used by Johnson & Rosenblatt (1988) and Rosenblatt & Johnson (1991) to reconstruct the evolutionary history of anomalopid genera are given in Table 1, those associated with the light organ in Table 2. In Table 3, we list states of characters among anomalopids and outgroups not considered in previous publications that are useful in diagnosing *P. rosenblatti*: number and relative size of lateral-line scales, number of gill rakers, relative size of light organ, least distance between nasal and lacrimal, and orientation of fibrocartilaginous stalk. The relatively small size of the light organ of *P. rosenblatti* could be a function of the large size of the holotype, as comparisons with *Phthanophaneron haweyi* indicate an inverse relationship between relative size of light organ and body (31.2% HL in the 67.7-mm SL holotype and 22.7% HL in the 204-mm SL specimen). McCosker (1982) noted a similar trend in *Kryptophanaron alfredi* (44.7% HL in a 25-mm SL specimen, 34.9% HL in an 89-mm SL fish).

**Relationships.**—*Protolepharon* is most similar to *Parmops* in the primitive nature of the occlusion mechanism, especially the absence of a shutter knob and

stalk hook. These features are important in the erection of the shutter in *Phthanophaneron*, *Kryptophanaron*, and *Photoblepharon* (Johnson & Rosenblatt 1988), and it is thus unclear how the shutter mechanism operates in either *Parmops* or *Protolepharon*. *Protolepharon* lacks the primary diagnostic feature of *Parmops*, expansion of the first four infraorbital bones to form a medially sloping shelf that protrudes laterally well beyond the margin of the orbit (Rosenblatt & Johnson 1991). It shares with *Parmops*, *Phthanophaneron*, *Kryptophanaron*, and *Photoblepharon* many features recognized as synapomorphies of that lineage by Johnson & Rosenblatt (1988): two supra-maxillae, transverse ridges on the gular isthmus, large v-shaped lateral dentary tooth patches, over 100 lateral body scale rows, reflective lateral-line scales, an erectable (or at least elastic) shutter, and a stalk that is continuous across the snout. It lacks another derived feature of that group, a groove in the ethmomaxillary ligament (secondarily absent in *Phthanophaneron*). It is thus most parsimonious to hypothesize that *Protolepharon* is the sister group of *Parmops* + *Phthanophaneron* + *Kryptophanaron* + *Photoblepharon*. A previously undescribed character corroborating the placement of *Protolepharon* below *Parmops* involves the configuration of the lacrimal, nasal, and stalk. In most anomalopids, the stalk is broadly exposed at the commissure (Figs. 2B, C; 3B, C), and there is no attenuation where it joins its contralateral member. In *Protolepharon*, the lacrimal and nasal are separated by only a small gap (least distance between them ca. 1.6% HL; Fig. 3B), and the stalk twists before passing through this gap such that the broad surface is nearly in the horizontal plane, and the narrow margin formerly in a ventral position is exposed laterally (Fig. 2B). In the *Parmops* clade, the lacrimal is separated from the nasal by a large gap (4.0% HL or more, Fig. 3C), and the broad sur-

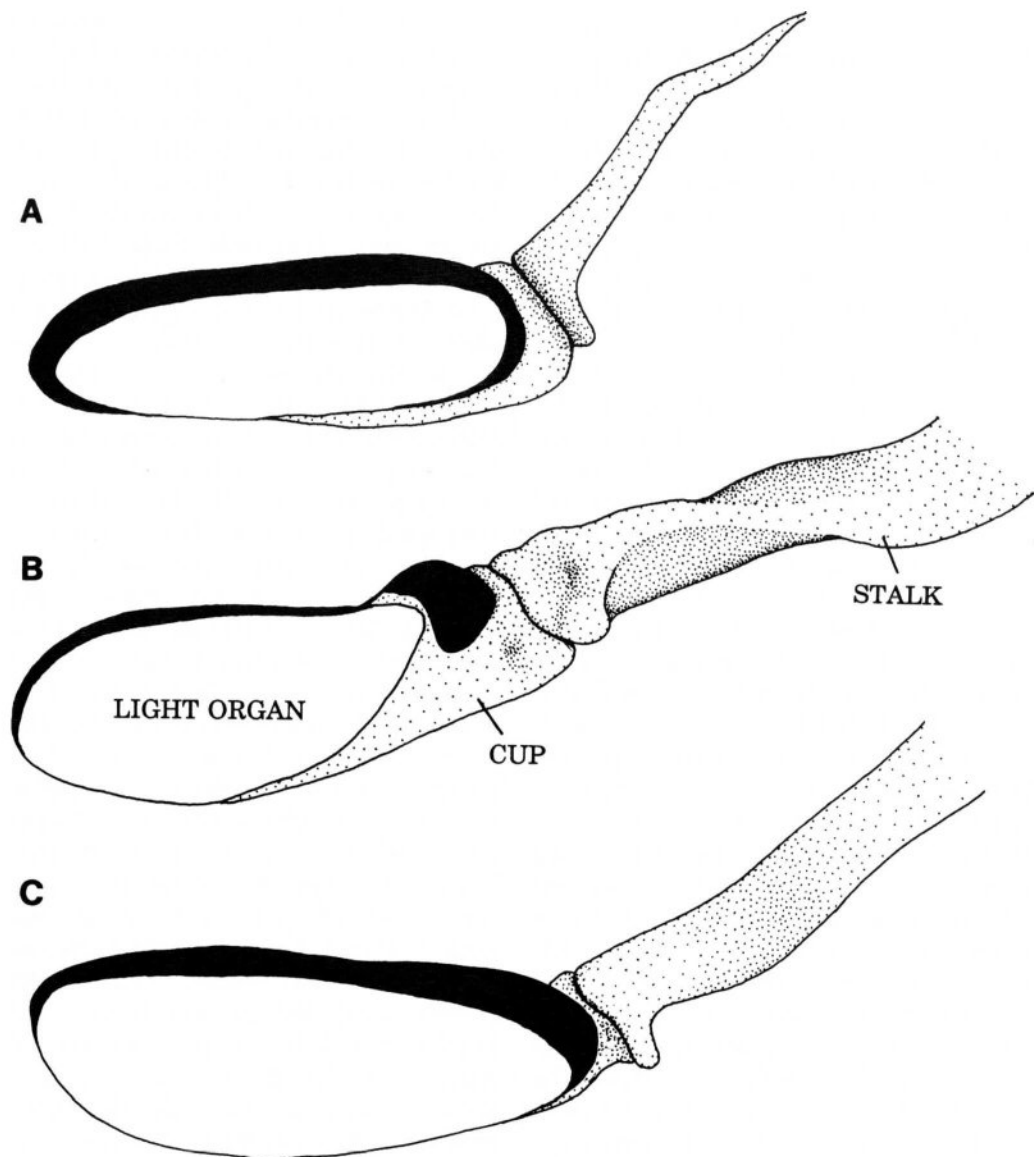


Fig. 2. Light organ and associated structures in (A) *Anomalops katoptron*, USNM 293340, (B) *Protoblepharon rosenblatti*, AMS 1.24275-001, (C) *Kryptophanaron alfredi*, USNM 343635. Right side.

face of the stalk is exposed along its entire length (Figs. 2C, 3C). *Anomalops* also has a very small gap between the lacrimal and nasal (ca. 1.0% HL, Fig. 3A), and the two bones are in contact with one another in the outgroups. A large gap between the lacrimal and nasal is thus an additional synapomorphy of *Parmops*, *Phthanophaneron*, *Kryptophanaron*, and *Photo-*

*blepharon*. A small gap is autapomorphic for the Anomalopidae. Although both have small gaps, the conditions in *Anomalops* (figs. 2A, 3A) and *Protoblepharon* (figs. 2B, 3B) are different in that the stalk is never broadly exposed in *Anomalops* (it is attenuated at the commissure) and does not twist posteriorly but nearly disappears from view in the region of the

Table 1.—States in *Protoblepharon rosenblatti* of Johnson & Rosenblatt's (1988) characters not associated with the light-organ complex.

1. Vertebrae bearing epineurals*	1, 2, 10–14
2. Branchiostegals	spiny
3. Openings in pars jugularis	?
4. Parasphenoid flanges	?
5. Swimbladder stay	—
6. Postorbital papillae	0
7. Cephalic sensory canal covering	Papillose
8. Lateral-line tubes	Closed
9. Midventral scutes	Continuous
10. <u>Dorsal Fin</u>	<u>VI-I,14</u>
Supraneurals	0/0/1 + 11
11. Supramaxillae	2
12. Transverse ridges on gular isthmus	+
13. Lateral dentary tooth patch	Large "V"
14. Body scale rows	ca. 145
15. Reflective or transparent lateral-line scales	+
16. Pelvic spine	+
17. Anal spines	II
18. Vertebrae	14 + 16
19. Corner of maxilla	Papillae

\* Epipleurals of Johnson & Rosenblatt (1988) are epineurals (Patterson & Johnson 1995).

small lacrimal/nasal gap as it turns abruptly ventrad (Johnson & Rosenblatt 1988). The different associations between the lacrimal and nasal possibly are also reflected in the morphology of the C-shaped process of the lacrimal (Zehren 1979),

which is probably smaller in *Proto-blepharon* than in the *Parmops* lineage because of the closer association of the lacrimal and nasal (and hence the lateral ethmoid). Additional specimens of *Proto-blepharon* that can be cleared and stained are needed to examine osteology.

A cladogram depicting relationships among the six anomalopid genera is shown in Figure 4. We constructed the tree using the Branch and Bound option of Swofford's (1991) PAUP 3.0 with the matrix in Table 4. All of the characters (Tables 1, 2) used by Johnson & Rosenblatt (1988) and Rosenblatt & Johnson (1991) initially were included in the analysis, but many are not informative and were eliminated from the matrix. Johnson & Rosenblatt (1988) and Rosenblatt & Johnson (1991) included all characters in Tables 1 and 2 on their cladograms, but noted that many features associated with the light organ could not be polarized by outgroup comparison because of the absence of comparable conditions in the outgroups. They surmised that the fully rotatable light organ of *Anomalops* and the complex shutter mechanism of the non-rotatable light organ of *Photoblepharon* represent highly specialized conditions within the family, and interpreted the less special-

Table 2.—States in *Protoblepharon rosenblatti* of Johnson & Rosenblatt's (1988) characters associated with the light organ.

I	Attachment of Ligament of Diogenes on cup	Medial
II	Attachment of Ligament of Diogenes anteriorly	Rostral Cartilage
III	Cup with medial shelf	Moderate
IV	Insertion of stalk muscle dorsally	Ligament
V	Stalk with inward flexure at cup articulation	—
VI	Rotation pad	—
VII	Postocular skin flap	—
VIIIa	Erectile shutter	+
VIIIb	Shutter knob	—
IX	Stalk hook	—
X	Stalk continuous across snout	+
XIa	Ethmomaxillary ligament with groove	—
XIb	Ethmomaxillary ligament with medial swelling	—
XII	Hook and shutter knob intimately associated	NA
XIII	Cup process attached to stalk hook by ligament	NA
XIV	Organ rotatable	+

Table 3.—Comparison of some diagnostic features of *Protolepharon rosenblatti* among anomalopids and other trachichthyoids. Data are from the literature or specimens examined in this study (single values represent counts or measurements of a single individual). For light organ length and least distance between nasal and lacrimal, range of values given only for taxa where data from a wide range of adult sizes was available. HL = head length, ant. = anteriorly, NA = not applicable.

Taxon	Lateral-line scales	Gill rakers on 1st arch	Light organ length (% HL)	Least distance between nasal & lacrimal (% HL)	Orientation of stalk
<i>Anomalops</i>	57–59 (Not enlarged)	28–32 <sup>f</sup>	35.4	1.0	Not broadly exposed
<i>Protolepharon</i>	59–60 (Enlarged)	21 <sup>b</sup>	14.5	1.6	Broadly exposed ant., twisted posteriorly
<i>Parmops</i>	30 (Enlarged)	30	35.6	4.8	Broadly exposed
<i>Phthanophaneron</i>	38 (Enlarged)	22–24 <sup>b</sup>	22.7–31.2	4.0–4.6	Broadly exposed
<i>Kryptophanaron</i>	32–34 <sup>c</sup> (Enlarged)	24–28 <sup>f</sup>	36.3–44.7 <sup>d</sup>	5.7	Broadly exposed
<i>Photoblepharon</i>	39 (Enlarged)	25–30 <sup>f</sup>	48.6	5.6	Broadly exposed
Monocentridae	12–15' (Not enlarged)	19–21 <sup>f</sup>	NA	0	NA
Trachichthyidae	25–63 <sup>e</sup> (Enlarged in some)	15–44 <sup>b</sup>	NA	0	NA

<sup>a</sup> Shimizu (1984), this study.

<sup>b</sup> Counts include flat plates at dorsal end of epibranchial, anterior end of ceratobranchial, or both.

<sup>c</sup> Colin et al. (1979), this study.

<sup>d</sup> McCosker (1982).

<sup>e</sup> Abe & Haneda (1973).

<sup>f</sup> Smith (1986).

<sup>g</sup> Gomon (1994).

<sup>h</sup> Kotlyar (1980).

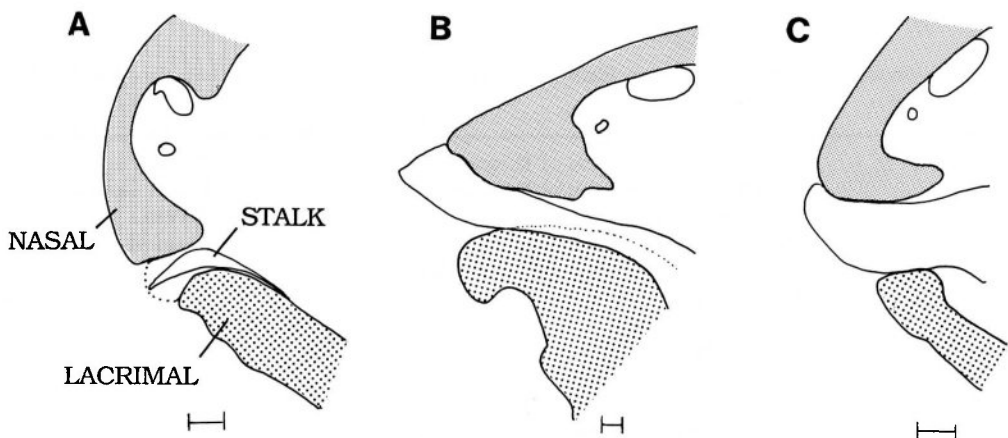


Fig. 3. Diagrammatic illustrations of the anterior snout region in three anomalopids, showing different configurations of the nasal, lacrimal, and fibrocartilaginous stalk. (A) *Anomalops katopteron*, USNM 293340, (B) *Protolepharon rosenblatti*, AMS I.24275-001, (C) *Kryptophanaron alfredi*, USNM 343635. Dotted line in *Anomalops* shows anterior extent of skin covering stalk, that in *Protolepharon* represents region where stalk is twisted.



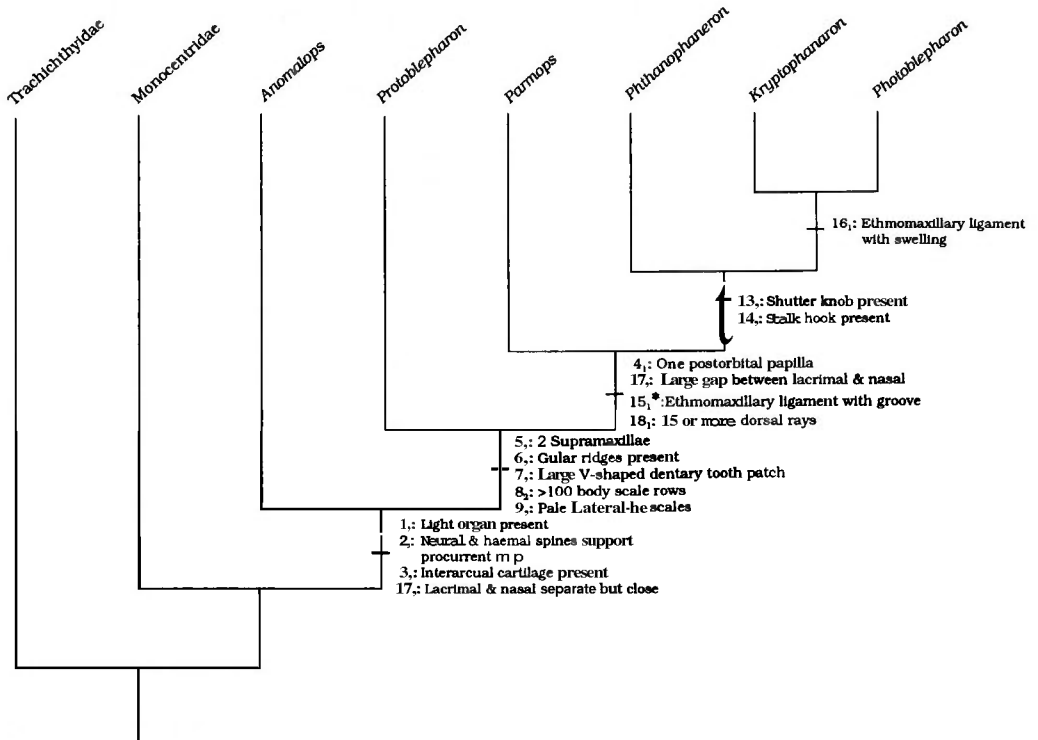


Fig. 4. Cladogram showing hypothesized relationships among anomalopid genera. \* = ambiguous character resolved using ACCTRAN. Treelength = 29 CI = 0.83 RI = 0.83.

ized states in *Trachichthyidae* and *Monocentridae* as ancestral for the family. They polarized features of the light organ based on these assumptions.

The PAUP analysis did not make such assumptions, and recognized that the occlusion mechanisms in either *Anomalops* or cladistically primitive members of the *Protoblepharon* lineage could be ancestral for the family. Nevertheless, the phylogeny of Johnson & Rosenblatt (1988) and Rosenblatt & Johnson (1991) emerged as the single most parsimonious tree based on 18 informative characters (Table 4). We concur with Johnson & Rosenblatt (1988) that the occlusion mechanisms of *Anomalops* and *Photoblepharon* probably represent the most derived conditions within the family and that the occlusion mechanism of *Protoblepharon*, which lacks a well defined shutter knob, a stalk hook to engage the shutter knob, and a groove and swelling in

the ethmomaxillary ligament, is ancestral. Relative to outgroups *Monocentridae* and *Trachichthyidae*, other features of *Protoblepharon* that might corroborate a *Protoblepharon-like* anomalopid ancestor include the small size of the light organ (14.5% HL vs. 22.7–48.6% HL in all other anomalopid genera), absence of postorbital papillae (eight in *Anomalops*, one in other anomalopids, none in the outgroups), and low number of gill rakers (21 or fewer in *Protoblepharon*, monocentrids, and some trachichthyids, 24 or more in other flashlight fishes).

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Table 4.—Character matrix used in constructing cladogram in Figure 4, followed by brief description of character states. See text and Johnson & Rosenblatt (1988) for further descriptions of characters. ? = missing data, 9 = not applicable, % = polymorphism.

	1-5	6-10	11-15	16-18
Trachichthyidae	00000	00100	1%999	90%
Monocentrinae	00000	00000	00999	900
<i>Anomalops</i>	11120	00101	11000	010
<i>Protoblepharon</i>	11?01	11210	00000	010
<i>Parmops</i>	11?11	11210	21001	021
<i>Phthanophaneron</i>	11?11	11210	01110	021
<i>Kryptophanaron</i>	11111	11210	01111	121
<i>Photoblepharon</i>	11111	11211	11111	121

1. Light organ absent (0), present (1).
2. Neural and haemal spines of fourth preural vertebra do not support procurent caudal rays (0), support procurent caudal rays (1).
3. Interarcual cartilage absent (0), present (1).
4. Postorbital papillae zero (0), one (1), eight or nine (2).
5. Supramaxillae one (0), two (1).
6. Transverse gular ridges absent (0), present (1).
7. Lateral dentary tooth patch small (0), large v-shaped (1).
8. Lateral body scale rows <50 (0), 50–100 (1), >100 (2).
9. Pale (reflective?) lateral-line scales absent (0), present (1).
- \*10. Pelvic-fin spine present (0), absent (1).
- \*11. Corner of maxilla papillose (0), with bony ornamentation (1), smooth (2).
- \*12. Gill rakers 21 or fewer (0), 24 or more (1).
13. Shutter knob absent (0), present (1).
14. Stalk hook absent (0), present (1).
- \*\*15. Ethmomaxillary ligament without groove (0), with groove (1).
16. Ethmomaxillary ligament without swelling (0), with discrete swelling (1).
17. Nasal connected to lacrimal (0), not connected but close (least distance between bones 1.0–1.6% headlength)—(1), separated by large space (least distance between bones >4.0% headlength)—(2).
18. Dorsal-fin rays 14 or fewer (0), 15 or more (1).

\*Informative only as autapomorphy of one or more genera; \*\* ambiguous character.

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