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Mechanisms of light organ occlusion in flashlight fishes, family Anomalopidae (Teleostei: Beryciformes), and the evolution of the group

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The circumtropical, nocturnal, shore-fish family Anomalopidae is characterized by a subocular luminous organ containing symbiotic luminous bacteria. The five known species are placed in four genera, one of which is new. ***Phthanophaneron*** is restricted to the eastern Pacific, ***Kryptophanaron*** to the western Atlantic, ***Photoblepharon*** is Indo-West Pacific in distribution and ***Anomalops*** is west Pacific. The symbiotic bacteria emit light continuously, and two superficially different mechanisms of occluding the glowing face of the organ are found. In ***Photoblepharon*** a black shutter of elastic skin is drawn up over the face of the organ, whereas in ***Anomalops*** the organ is rotated downward, so that only the heavily pigmented back of the organ is exposed. In ***Phthanophaneron*** and ***Kryptophanaron,*** both rotational and shutter mechanisms are present. Elucidation of the structures and linkages involved in light-organ occlusion reveals that the superficially different mechanisms are based on a common functional complex. In all four genera, the light organ is supported by a cartilaginous cup that articulatrs anteriorly with a cartilaginous stalk. Motive power for both the shutter and rotational mechanisms is supplied by the adductor mandibulae through a complex biomechanical linkage involving the ethmomaxillary ligament and a ligament unique to anomalopids, the Ligament of Diogenes. The structures involved in shuttrr erection and organ rotation are illustrated and described in detail for ***Photoblepharon*** and ***Anomalops*** and are compared with those in the other two forms; a functional hypothesis is advanced. Extrafamilial relationships of the Anomalopidae are discussed, and a hypothesis of the phylogenetic relationships of the four genera is derived from a cladistic analysis involving 19 non-light-organ characters and corroborated by some light-organ characters. Most characters associated with the light-organ complex cannot be polarized by conventional outgroup comparison, and the evolution of the light organ occlusion mechanisms is interpreted in light of the hypothesized phylogeny and a hypothesized ancestral mechanism. We propose that the common ancestor of anomalopids possessed a forced rotational mechanism like that of ***Phthanophaneron*** and ***Kryptophanaron.*** This was refined to a more efficient flipping rotational mechanism in ***Anomalops,*** the sister group of the lineage comprising the other three genera, within which the shutter mechanism was progressively refined. The ostensibly unnecessary complexity of the shutter mechanism is apparently a result of functional-morphological constraints imposed on the system by the pre-existence of a rotational mechanism. A brief zoogeographic scenario is proposed.

KEY WORDS: — Anomalopidae – Beryciformes – bioluminescence – functional morphology – phylogeny.

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CONTENTS

INTRODUCTION

The family Anomalopidae is a small circumtropical group of nocturnal shore fishes belonging to the primitive acanthopterygian order Beryciformes. The most conspicuous characteristic of the family is a subocular luminous organ containing symbiotic luminescent bacteria. Current knowledge of the taxonomy and distribution of the group has been summarized by McCosker & Rosenblatt (1987). There are five known species, referable to four genera, with three in the Indo-Pacific, one in the eastern tropical Pacific and one in the western tropical Atlantic (Figs 1, 2).

The Indo-Pacific species, ***Anomalops katoptron*** (Bleeker, 1856) and ***Photoblepharon palpebratus*** (Boddaert, 1781), have long been known. Springer (1982) gives Philippine and Pacific Plate records for both genera. ***Anomalops*** is known from the Indo-Australian region, the Philippines, Taiwan, Guam and Japan to the north, and as far east as Rarotonga and the Tuamotus and possibly Tahiti. It appears to be abundant only at Banda, Indonesia and the Philippines. ***Photoblepharon*** is known in the Pacific from Banda, New Guinea, the Philippines, the Marshall, Caroline and Cook Islands and northern Australia, and has been taken at the Comoro Islands, Indian Ocean and at the north end of the Red Sea. It is common at all of these localities. The Red Sea population was named as a subspecies, P. ***p. steinitzi***, by Abe & Haneda (1973) based on its possession of fewer pelvic-fin rays. Our observations indicate that P. ***p. steinitzi*** also differs in lacking scales on the gular isthmus, having non-imbricate cheek scales and in having more strongly ornamented head bones. McCosker & Rosenblatt (1987) regard the Indian Ocean and Red Sea populations as distinct at the species level. ***Kryptophanaron alfredi*** Silvester & Fowler 1926, was described from a single specimen found floating at the surface at Jamaica in 1907 and was not collected again until 1977, when a single specimen was taken at Puerto Rico. It has since been discovered at Grand Cayman Island, Puerto Rico, Curacao (Colin, Arneson & Smith-Vaniz, 1979) and the Bahamas (McCosker, 1982).

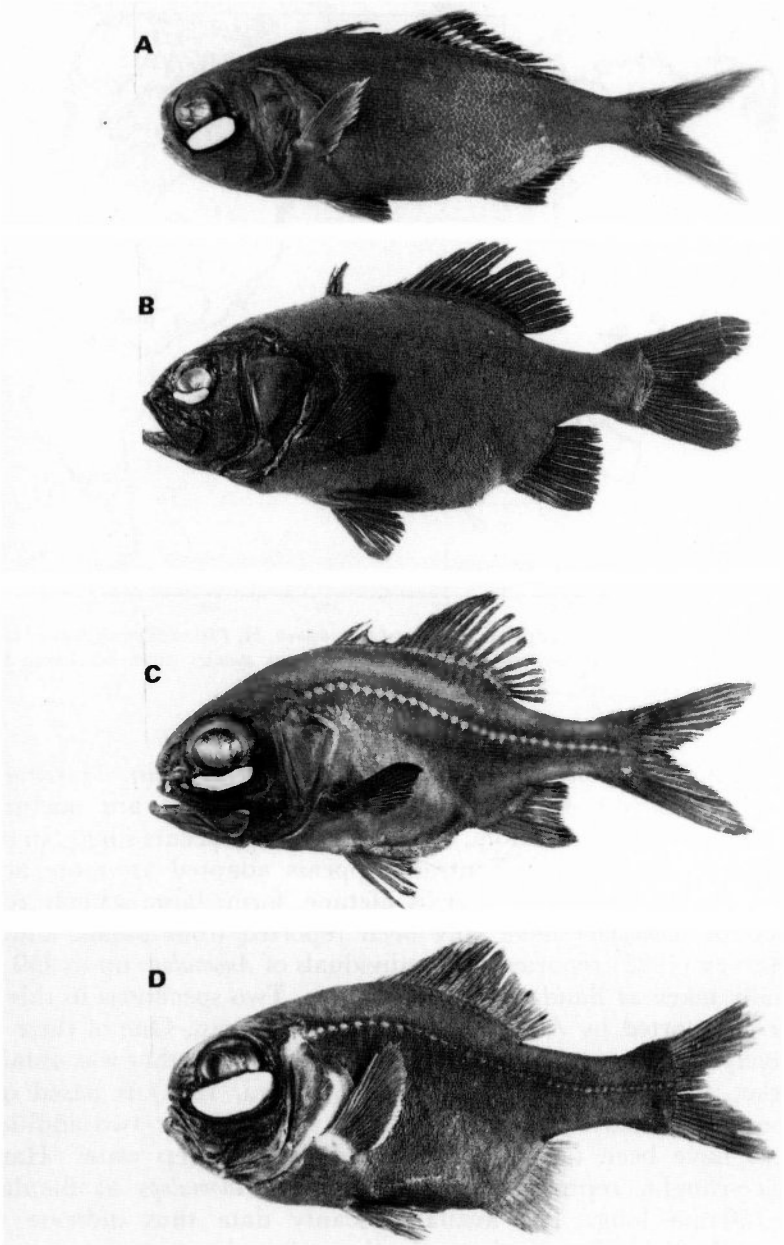

Figure 1. The genera of the Anomalopidae, A, ***Anomalops katoptron. B, Phthanophaneron harveyi*** **(spinous dorsal aberrant). C,** ***Kryptophanaron alfredi. D, Photoblepharon palpebratus.***

The remaining species, *K. harveyi* Rosenblatt & Montgomery, 1986. was described from a single specimen taken in the Gulf of California. A second specimen has since been taken at Thetis Bank, Lower California (Marine Vertebrate Collection, Scripps Institution of Oceanography, SI078–299).

Aspects of the anatomy, physiology and natural history of *Anomalops* and *Photoblepharon* have been studied at Banda (Steche, 1909; Harvey, 1922; Haneda

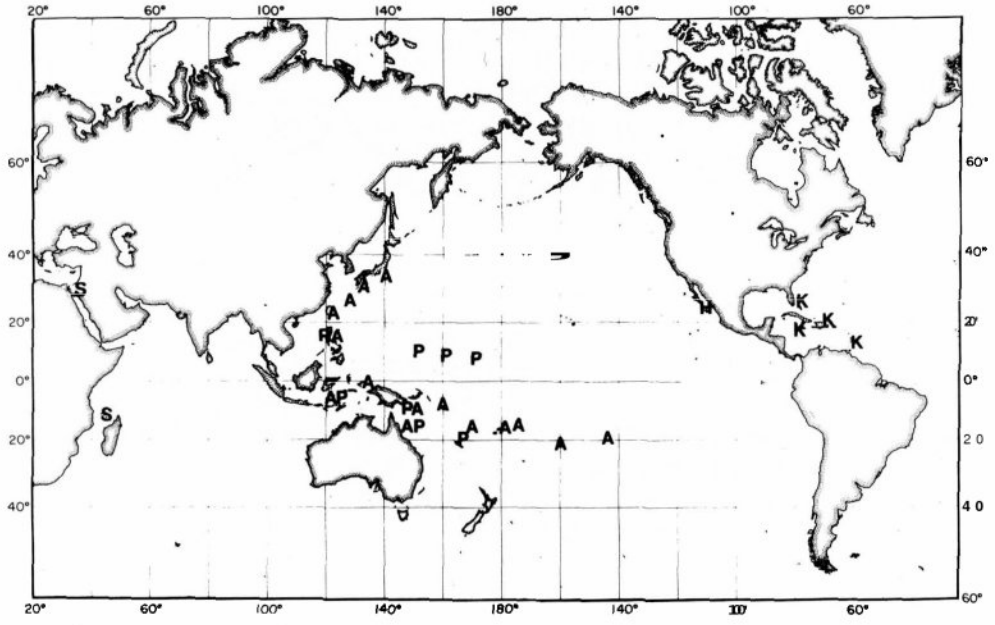

Figure 2. Distribution of the Anomalopidae. A, *Anomalops katoptron. H, Phthanophaneron harveyi. K, Kryptophanaron aljredi. P, Photoblepharon palpebratus.* **S,** *Photoblepharon steinitzi* **(from McCosker & Rosenblatt, 1987).**

& Tsuji, 1971) and of ***Photoblepharon*** in the Red Sea (Morin, Harrington, Nealson, Krieger, Baldwin & Hastings, 1975). Both forms are nocturnal. ***Photoblepharon*** is found near the bottom, close to cover, and occurs singly, in pairs or in small groups. ***Anomalops,*** in contrast, appears adapted for more active swimming, and, during at least part of its lifetime, forms large schools at the surface. Schools of ***Anomalops*** have only been reported from Banda and the Philippines. Harvey (1922) reported that individuals of ***Anomalops*** up to 250 mm were occasionally taken at Banda on hook and line. Two specimens in this size range have been reported by Abe (1942, 1951) from Japan. One of these was taken in relatively deep water (300 m) on hook and line, the other was obtained in a fish market. The published Guam record (Kami, 1971) is based on a 240 mm SL specimen taken by hook and line in about 100 m; two additional large specimens have been taken by hook and line in deep water. Harvey reported surface-caught, reproductive individuals of ***Anomalops*** at Banda as being about 100 mm long. The available scanty data thus indicate that although mature ***Anomalops*** live for time near the surface, large adults move into deeper water. Rosenblatt & Montgomery (1976) reasoned that the apparent rarity of ***K. alfredi*** and ***K. harveyi*** is related to a deep-water habitat. The rediscovery of ***K. alfredi*** in the Caribbean at depths of 25–200 m supports this surmise.

Leisman, Kohn & Nealson (1980) and Haygood, Tebo & Nealson (1984) have shown conclusively that light production in anomalopids is due to symbiotic luminescent bacteria that are cultured within tubes of the subocular organ. Because light is emitted continually by the bacteria, control of light emission can only be effected by occlusion of the luminous face of the organ. It

has been known for some time that ***Anomalops*** and ***Photoblepharon*** are capable of rapidly occluding the light, and this has now been confirmed for *K. alfredi* (J.Morin, personal communication; and R.H.R., personal observation). Aspects of bioluminescence in the family were summarized by Herring (1982). Morin *et al.* (1975) discussed several functions of the light organ in ***Photoblepharon.*** These include predator avoidance, intraspecific communication, and feeding. Direct evidence was mainly available for the last function. ***Photoblepharon*** was observed "capturing prey (adult *Artemia*) by the light of their own luminescent organs, which was also adequate for vision by the human eye." ***Anomalops*** with intact light organs are able to feed on adult ***Artemia*** in total darkness and individuals with non-functional light organs cannot (R.H.R., unpublished data). Most nocturnal reef planktivores feed mainly on the large nocturnal meroplankton (Emery, 1968). Anomalopids, however, feed to a large extent on transparent small holoplankton. The subocular light organ has apparently made available a resource that cannot be utilized by other nocturnal particulate plankton feeders.

Although the structure of the light organ is exceedingly similar in ***Anomalops*** and ***Photoblepharon*** (Steche, 1909; Harvey, 1922), mechanical control of light emission is achieved by very different means (Fig. 3). In ***Anomalops*** the light organ is rotated downward, so that only the heavily pigmented back of the organ is exposed. In ***Photoblepharon*** a black shutter of elastic skin is drawn up

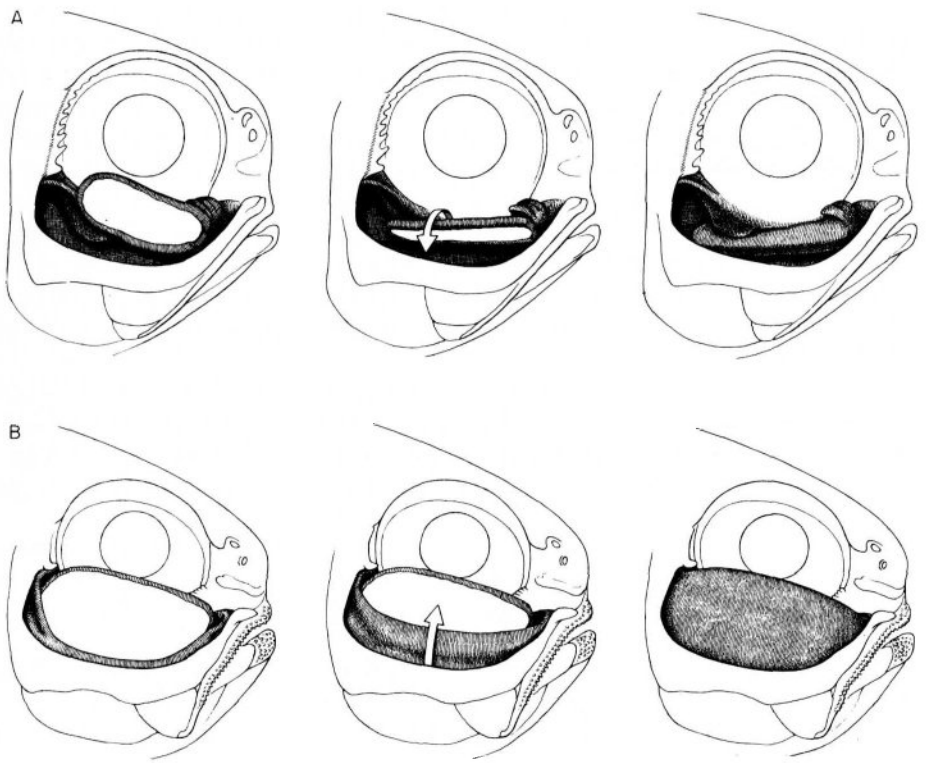

Figure 3. Method of occlusion of light organ in: A, *Anomalops katoptron*; B, *Photoblepharon palpebratus* (from McCosker, *1977*).

over the luminous face of the organ. Harvey (1922) pointed out the obvious enigma: "Why two such closely allied genera, similar in other respects and almost exactly alike in the general structure of the light organ, should have developed such totally different mechanisms for obscuring the light is a great mystery." Despite considerable subsequent work on the histology and biochemistry of the organs (e.g. Watson, Thurston & Nicol, 1978; Haneda & Tsuji, 1971), the anatomy of the occlusion mechanism and its bearing on Harvey's conundrum has remained uninvestigated. Steche (1909) briefly attributed the rotation of the organ of Anomalops to muscles associated with the stalk on which it is borne, although he referred to his understanding as ". . . nicht vollkommen klar geworden". No suggestions have ever been made concerning the mechanism by which the shutter is drawn up in Photoblepharon.

The observation that the species of Kryptophanaron appear to possess both a shutter and rotational capability (Rosenblatt & Montgomery, 1976), and the availability of fresh material of *K. alfredi*, Anomalops and Photoblepharon, gave impetus to the present comparative study of the functional anatomy of light organ control mechanisms in the genera of the Anomalopidae. Our study has revealed that these control mechanisms have a number of common features. The light organ is supported by a variously developed cartilaginous basal cup that articulates with a supporting cartilaginous stalk. A shutter is present in all but Anomalops, and the light organ can be rotated to some degree in all but Photoblepharon.

Motive power for both the rotational and shutter mechanisms is supplied by the adductor mandibulae through a complex mechanical linkage. Essential to the operation of the mechanism is a ligament, unique to anomalopids, that inserts posteriorly on the basal cup of the light organ, passes forward around a flexure in the ethmomaxillary ligament and inserts anteriorly on the rostral cartilage or on the cartilaginous pad between the head of the maxilla and the vomer. This ligament is here named the Ligament of Diogenes. Rotation of the organ and raising of the shutter are both achieved by a pull on the organ cup, but in the latter action the pull is translated into a rotation of the stalk, a projection of which flips the shutter up. The enigma posed by Harvey (1922), then, is at least partially resolved. The two superficially distinct mechanisms are not "totally different" but share a functional complex indicative of their common origin.

Similarities and differences in the light organ control mechanisms led us to investigate other morphological features of the five known anomalopids in an attempt to formulate hypotheses about their interrelationships. The results of this analysis require the introduction of a new genus for Xryptophanaron *harveyi*.

TAXONOMY

Phthanophaneron gen. nov.

Diagnosis: An anomalopid with a separate spinous dorsal fin, a pelvic spine, a single postorbital papilla, lateral-line scales not enlarged, belly scutes in a continuous series but not enlarged and thornlike, no reflective markings on fins or body, a fully rotatable light organ and an erectile shutter.

Type species: Kryptophanaron *harveyi* Rosenblatt & Montgomery 1976.

Etymology: From the Greek *phthanos* early, and ***phaneron*** evident or shining, in reference to the apparent primitiveness of the light occlusion mechanism.

Gender: Masculine.

Justification: Our hypothesis of the cladistic relationships within the Anomalopidae (Phylogeny) is best served by placement of *K. harveyi* in a distinct genus. *Kryptophanaron aljredi* and the species of *Photoblepharon* share at least two specializations, reflective lateral-line scales and a swelling and groove on the ethmomaxillary ligament, but we have identified no synapomorphies between *K. alfredi* and *K. harveyi. Kryptophanaron harveyi* is therefore the sister species to ***Kryptophanaron*** *alfredi* and *Photoblepharon* spp. Because *Kryptophanaron* would be paraphyletic if ***K. harveyi*** were included, we recognize a distinct genus for *K. harveyi.*

MATERIAL AND METHODS

Fresh and preserved specimens of ***Anomalops***, *Photoblepharon,* and *Kryptophanaron alfredi* were available for dissection and clearing and staining. These specimens are housed in the collections of the Scripps Institution of Oceanography, La Jolla and the National Museum of Natural History, Washington, D.C. The holotype and second specimen of ***Kryptophanaron*** *harveyi* were examined by radiography and partial dissection. Material of *Photoblepharon* included specimens of both *P.* ***palpebratus*** and *P. steinitzi.*

Vertebral counts include the second ural centrum. The first caudal vertebra is the first vertebra with a haemal spine. Drawings were made with the aid of a camera lucida. Histological sections of stalk, cup, shutter knob and postorbital tubercle were examined by light microscopy, and stalk tissue was examined by electron microscopy, to confirm their cartilaginous structure.

MORPHOLOGY

Photoblepharon ***palpebratus***
(Figs 4–6)

Skeletal elements (Figs 4–6). The bones associated with the light organ and supporting structures are the lateral ethmoid, nasal, infraorbitals, palatine, maxilla and rostral cartilage.

The nasal, lacrimal, and lateral ethmoid are modified to accommodate the light organ and stalk. The anterior end of the lacrimal is displaced laterally and ventrally but retains contact with the lateral ethmoid through a narrow posteromedial extension (the C-shaped process of Zehren, 1979). The C-shaped process arises at the anteromedial end of the lacrimal. It runs medially, then abruptly curves upward to form a laterally directed upper limb (Fig. 6B, C). The lower part is tightly bound along the dorsal surface of the maxillary process of the palatine, and the upper along the ventrolateral surface of the lateral ethmoid. A small bony nubbin projects dorsally from the anterior end of the lower limb of the lacrimal process.

The upper jaw bones are also displaced ventrally to accommodate the stalk, and the ascending processes of the premaxillae are elongated, so that the normal relationship with the rostral cartilage is maintained (Fig. 4). At its anterior end,

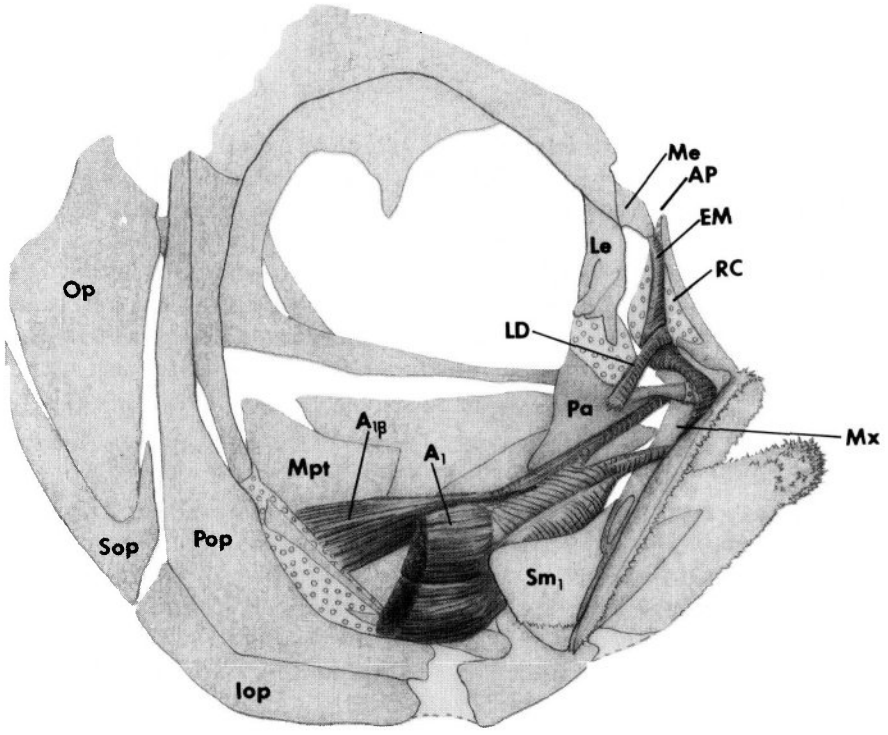

Figure 4. Head bones, ligaments and muscles associated with the light organ and supporting structures in Photoblepharon palpebratus; light organ, supporting structures and infraorbitals removed, see Fig. 5, below. Abbreviations: A_1, $A_{1\beta}$, sections of adductor mandibulae; AP, ascending process of premaxilla; EM, ethmomaxillary ligament; Iop, interopercle; LD, Ligament of Diogenes, cut anterior to usual point of insertion on cup; LE lateral ethmoid; ME, mesethmoid; Mpt, metapterygoid; Mx, maxilla; Op, opercle; Pa, palatine; Pop, preopercle; RC, rostral cartilage; Sm,, posterior supramaxilla; Sop subopercle.

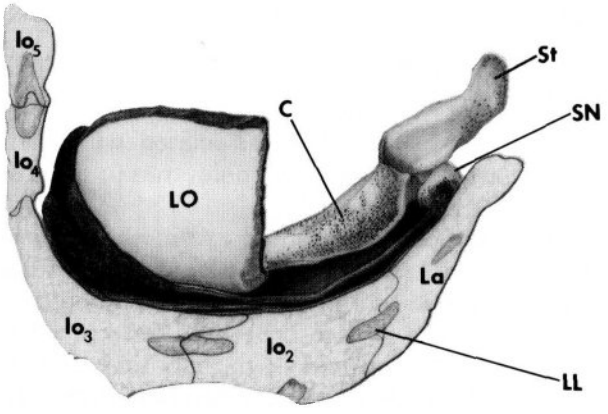

Figure 5. Light organ and supporting structures in normal association with infraorbitals in Photoblepharon palpebratus Abbreviations: C, cup; Io_2–Io_5, infraorbitals; La, lacrimal; LL, pore in lateral-line canal; LO, light organ, anterior half removed; SN, shutter nodule; St, stalk.

the nasal (not shown) bears a lateral process that curves across the snout and attaches to the lateral ethmoid. The ventral surface of this process provides a firm attachment for the connective tissue anchoring the stalk across the snout.

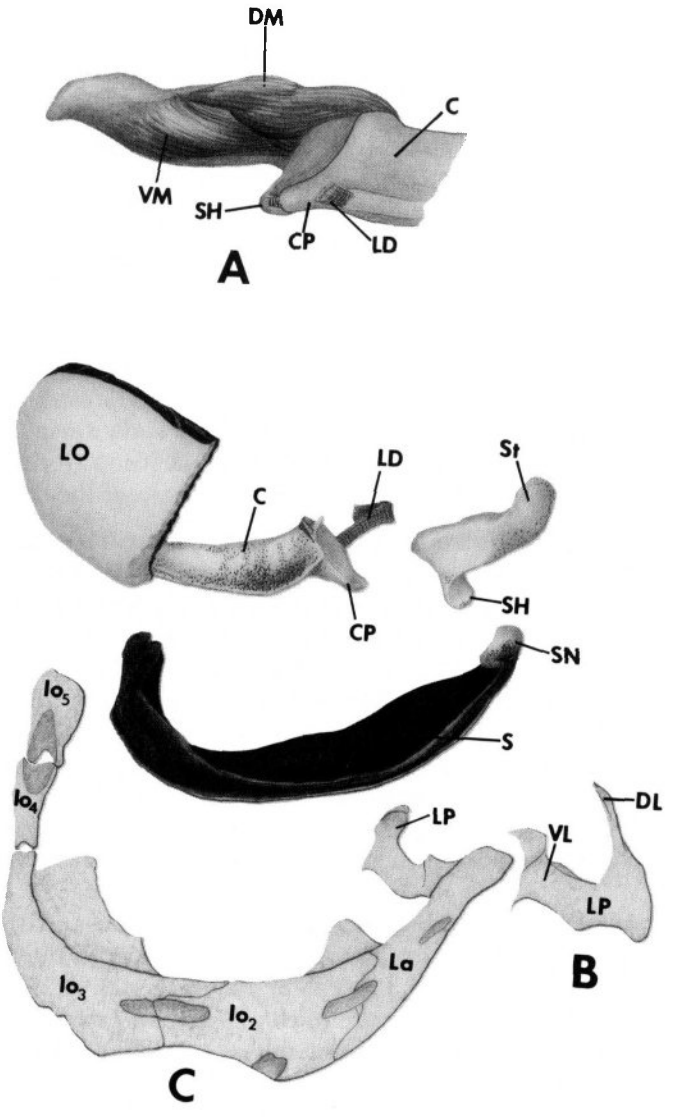

Figure 6. Expanded view of light organ, and associated structures, in *Photoblepharon palpebratus*, right side. A, Medial view of stalk and cup articulation and associated muscles. B, Ventral view of medial process of lacrimal. C, Infraorbitals, shutter, cup and stalk. Abbreviations: C, cup; CP, ventral process of cup; DL, dorsal limb; DM, dorsal stalk muscle; Io_2–Io_5, infraorbitals; La, lacrimal; LD, Ligament of Diogenes; LO, posterior half of light organ; LP, medial (C-shaped) process of lacrimal; S, shutter; SH, stalk hook; SN, shutter nodule; St, stalk; VL, ventral limb; VM, ventral stalk muscle.

Stalk and cup (Figs 5, 6). A thick, cartilaginous (fibrocartilage) stalk (St), continuous across the front of the snout with its contralateral member, extends posteriorly to articulate movably, near the anteroventral corner of the orbit, with a cartilaginous (fibrocartilage), cup-like structure (cup, C) that supports the organ proper. At this point the stalk bears a ventrally projecting, hook-like process (stalk hook, SH) that passes along the medial side of, and then under, a movable nodule of cartilage (SN, see description of shutter) at the anterior

margin of the elastic shutter membrane (S). The stalk is firmly bound to the snout by connective tissue for most of its length. The anterior and ventral margins of the organ are tightly bound to the cartilaginous cup. Anteriorly, the ventral part of the cup is expanded into a medially projecting shelf that runs about one-third of the way along the organ and continues backward as a posteriorly tapering rod (see Steche, 1909: figs **5,** 6).

The anterior margin of the cup is dorsoventrally expanded to form a concave articular surface for reception of the posterior end of the stalk. Dorsally and ventrally the cup and stalk are connected by short ligaments (not shown). The ventrolateral corner of the cup extends forward as a short process (CP) that passes behind, and is tightly bound to, the medial side of the stalk hook.

Two muscles are associated with the stalk (Fig. 6A). The dorsal stalk muscle originates about halfway along the stalk, near the anterior end of the lacrimal and inserts on the ligament that connects the cup and stalk dorsally. The ventral stalk muscle originates on the medial side of the stalk just anterior to the origin of the dorsal muscle, and inserts ventrally near the base of the stalk hook.

Ligaments (Fig. *4).* The stout, cord-like ethmomaxillary ligament (EM) extends from the mesethmoid ventrally to about the dorsal margin of the head of the maxilla, where it bends and continues obliquely forward to insert on the ventrolateral margin of the maxilla. Near its insertion, the ligament spreads laterally to wrap around the ball-like cartilaginous tip of the maxillary process of the palatine. The EM bears a posterior bulbous expansion at the point of its forward flexure; its anterolateral surface is grooved at this point.

The Ligament of Diogenes (LD) arises from the posterolateral margin of the rostral cartilage, extends anterolaterally to curve around the forward flexure of the EM (lying in the EM groove at that point) and then continues posteroventrally to insert on the medial edge of the shelf-like expansion of the cup.

In other beryciforms, a ligament arises on the palatine and extends to the premaxilla. In all anomalopids this ligament arises instead at the anterior tip of the upper limb of the C-shaped process of the lacrimal. A small, cord-like ligament originates on the inner flexure of the C-shaped process of the lacrimal and extends anterodorsally to insert on the dorsal surface of the stalk; anteriorly this ligament is suspended from the ventral surface of the upper limb of the C-shaped process where some fibres join the ligament that extends to the premaxilla. Another anchoring ligament arises at the inner surface of the C-shaped lacrimal process and extends posterolaterally to insert broadly on the medial expansion of the cup, near the insertion of the LD. These three ligaments are not illustrated.

Shutter (Figs 5, 6). The shutter (S) is an elastic membrane that originates on the lower anterior corner of the orbit, extends along its ventral rim and terminates at a fleshy papilla about halfway up the posterior margin (see Fig. **3B).** The shutter is complexly folded at the posteroventral corner of the orbit, creating a medially projecting pocket. When retracted, the shutter folds downward below the organ in a single accordion-like fold, with the free margin directed outward. Anteriorly the shutter arises from a discrete cartilaginous nodule that is movably attached to the bony nubbin on the anterior end of the C-shaped process of the lacrimal. This nodule (SN) is composed of fibrocartilage

and approximates a kidney bean in shape, with the concave medial surface wrapping around the stalk hook. The hook and nodule are tightly bound together by connective tissue and skin. The SN bears a wing-like expansion posteriorly (covered by shutter membrane in illustration) that stiffens the upper margin of the shutter.

Adductor mandibulae (Fig. 4). The configuration of the adductor mandibulae is essentially identical in all five anomalopids. It comprises four major sections, A_1, $A_{1\beta}$, A_2 and A_3. Only $A_{1\beta}$ and the anterior portions of A_2 and A_2 are illustrated. A_2 and A_3 originate on the preopercle and insert on the medial side of the lower jaw. A_1 originates on the preopercle, above the origin of A_2, and lies dorsolateral to it. A_2 gives rise dorsally to a tendon that extends anterodorsally to join the tendon of $A_{1\beta}$. Ventrally a tendon joins the A_2–A_3 aponeurosis. $A_{1\beta}$ is a triangular muscle lying medial to A_2. It originates on the metapterygoid and quadrate and gives rise to a strong, strap-like tendon that passes below the maxillary arm of the palatine to insert on the dorsal margin of the maxillary shaft, just posterior to the maxillary head.

Anomalops *katoptron*
(Figs 7–9)

Skeletal elements (Fig. 7). The configuration of the bones associated with light organ accommodation in Anomalops is similar to that described for Photoblepharon, with two notable differences. There is no knob-like dorsal process on the lower limb of the C-shaped process of the lacrimal, and there is an anterodorsal process of the lateral ethmoid, with which the nasal articulates.

Stalk and cup (Figs 8, 9). The configuration of the cup and stalk differs trenchantly from that of Photoblepharon. The stalk is not continuous with its opposite member but attached to it by a ligament across the snout. This ligament merges with the lacrimal-premaxillary ligaments where it passes beneath the insertion of the latter. As in Photoblepharon, the stalk is bound to the snout by connective tissue along most of its length. Just posterior to the anterior margin of the eye, the stalk bends abruptly, forming a rounded posterior surface with which the cup articulates (Fig. 9A, B). The cup and stalk are loosely articulated and attached by short ligaments (Fig. 9A, not shown in 9B) dorsally and ventrally, in such a way that the cup can rotate freely ventrolaterally, with respect to the stalk. When the cup is so rotated, the rounded butt of the stalk fits into a broad depression along the backside of the cup. The cup itself is a crescentic structure that curves around, and is tightly affixed to, the anteromedial end of the light organ. The lower limb of the cup extends about two-thirds of the way along the ventral margin of the organ. Anteriorly the ventral surface of the cup is expanded medially as a small horizontal shelf. This expanded, anteroventral surface of the cup rests on a thick rectangular pad of fibrocartilage and connective tissue in the floor of the orbit (RP, Fig. 9C). The cup slides along this pad when rotated.

Two muscles are associated with the stalk and organ (Fig. 9A). Both lie on the medial surface of the stalk, one dorsal to the other. Both originate on the stalk at the level of the EM. The dorsal muscle inserts by a strap-like extension

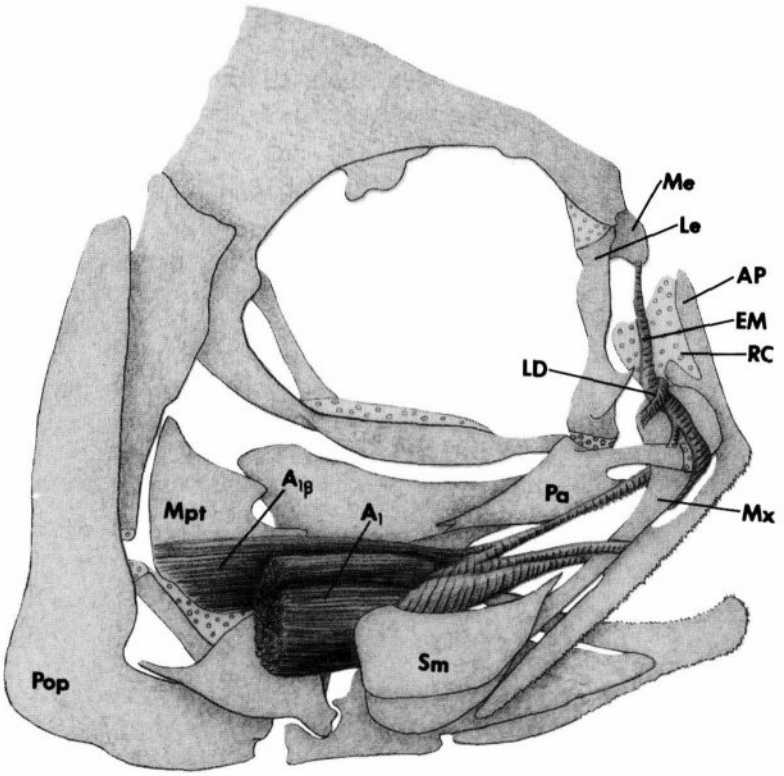

Figure 7. Head bones, ligaments and muscles associated with the light organ and supporting structures in *Anomalops katoptron*; light organ, supporting structures and infraorbitals removed, see Fig. 8 below. Abbreviations as in Fig. 4.

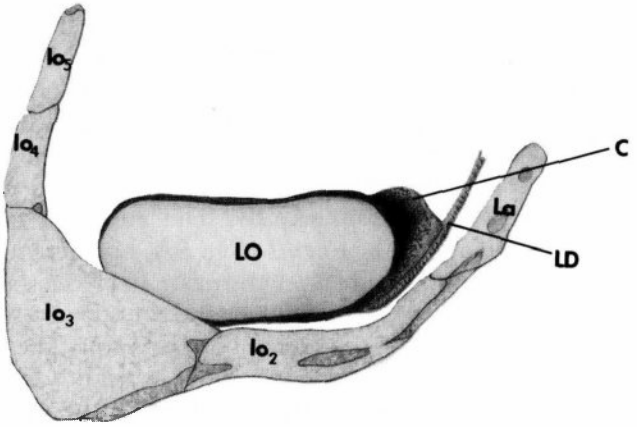

Figure 8. Light organ and supporting structures in normal association with infraorbitals in *Anomalops katoptron*. Abbreviations as in Fig. 5.

directly on the anterodorsal corner of the cup; the ventral muscle inserts on the medial surface of the medial flexure of the stalk.

Postorbital region (Fig. 3A). There is a small free rim of skin along the ventrolateral margin of the orbit. Along the posterior margin of the orbit there

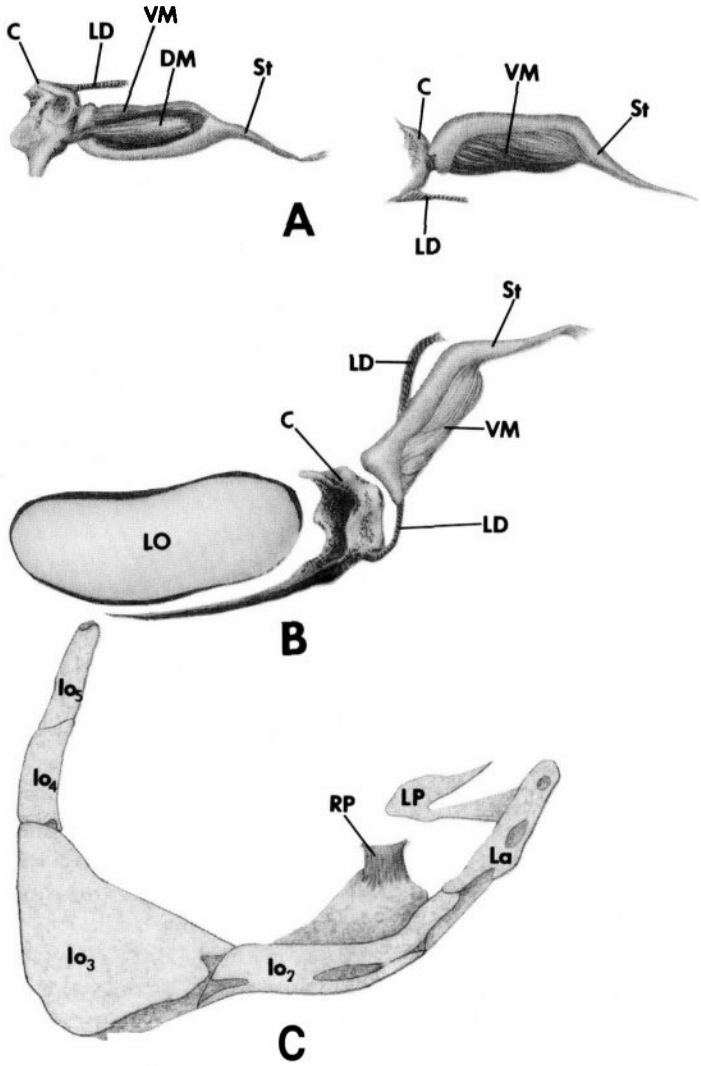

Figure 9. Expanded view of light organ and associated structures in *Anomalops katoptron*, right side. A, Dorsal and ventral views of stalk and cup articulation and associated muscles. B, Orgn, cup and stalk. C, Infraorbitals. Abbreviations: LO, entire light organ; RP, rotation pad; others as in Fig. 6.

is a series of eight to 11 fleshy tubercles that continue posterior to the orbital rim as fleshy ridges. The next to ventralmost tubercle gives rise to a fold of skin that runs down and forward along the posteroventral corner of the eyeball. This skin fold forms a free triangular flap enclosing a pocket at the posteroventral corner of the orbit. The ventral margin of the flap is rolled inward and considerably swollen and forms a pad-like horizontal surface that rests on the back of the organ when it is rotated down. The flap does not extend to the orbital margin, and the enclosed pocket thus has a large posterior opening.

Ligaments (Fig. 7). As in *Photoblepharon* the EM passes ventrally from its origin on the mesethmoid to about the level of the dorsal margin of the maxillary head where it bends obliquely forward to pass around the cartilaginous tip of the

rostral cartilage, the result is a forward pull on its posterior attachment to the cup, which is thus moved forward and rocked outward slightly. As the cup moves forward and out, the short process at its anteroventral corner is brought to bear on the medial side of the stalk hook, rotating it outward and upward. Rotation of the stalk hook forces the intimately associated shutter nodule to swing upward and forward, placing tension on the shutter and drawing it upward as well. Because the shutter is folded under the organ, it remains closely applied to the luminous face of the organ as it is erected. Upon relaxation of the adductor mandibulae, elasticity of the shutter causes it to return to its original position. The precise function of the stalk muscles is unknown. They may aid in moving the stalk hook when the shutter is erected or allowed to relax, they may aim the light by bending the stalk slightly, or they may perform both functions. We have been able to pull the shutter up in both fresh and cleared and stained specimens by pulling back on the maxilla and have observed the stalk hook and shutter knob to move as described without the assistance of the stalk muscles.

Anomalops
(Figs 7–9)

As in *Photoblepharon,* contraction of the adductor mandibulae pulls the maxilla posteriorly. Because the EM passes around the cartilaginous tip of the palatine, as if over a pulley, the EM is straightened and moved forward. Forward movement of the EM is limited, because it is anchored by a short ventral branch to the palatine. Movement of the EM would thus seem to be less important than in *Photoblepharon.* However, because the LD is attached to the head of the maxilla, a posterior movement of the maxilla will still be translated into a forward pull at the point where the LD passes tightly around the forward flexure of the EM, just as in *Photoblepharon.* Because the LD inserts posteriorly on the ventrolateral (outer), rather than ventromedial, corner of the cup, the forward pull on LD results in a rotation of the organ, bringing its luminous face down against the floor of the orbit. Rotation of the organ is facilitated by the configuration of the posterior articular end of the stalk and by the manner in which the cup is counterbalanced on the fibrocartilage pad on the floor of the orbit. Only a slight force is needed to flip the organ up or down. Upward rotation of the organ is accomplished by contraction of the dorsal stalk muscle, which attaches to the anterodorsal corner of the cup.

Anomalops is capable of an additional movement of the organ. Contraction of the ventral stalk muscle, which inserts on the medial flexure of the stalk, results in a lateral bowing of the stalk. The configuration of the cup-stalk articulation (Fig. 9A) and the anchoring ligaments is such that the bending of the stalk causes the entire organ to swing out and forward, so that it may lie almost at right angles to the head. Manipulation of fresh and cleared and stained. specimens bears this out. Lateral and anterior movement of the stalk has been observed in live specimens by James Morin (Department of Biology, University of California, Los Angeles, personal communication) and is mentioned by Burgess & Axelrod (1975).

Steche (1909) suggested that the postocular skin flap of *Anomalops* (Fig. 3A) might serve as an elastic spring assisting the return of the light organ to the upright (light-exposed) position. However, when the organ is rotated

Shutter. The shutter is attached as in Photoblepharon but is considerably smaller. As in Photoblepharon, the shutter folds downward in an accordion-like fold, so that the free margin is directed laterally. At the anterior origin of the shutter there is a movable nodule of fibrocartilage, the shutter nodule. It is smaller and less firm than that of Photoblepharon and straight rather than crescentic in shape.

Phthanophaneron *harveyi*

Skeletal elements. The configuration of the bones associated with the light organ and supporting structures are basically like those of Photoblepharon.

Stalk and cup. The stalk is continuous with its opposite member, but the commissure across the snout is even thinner than in Kryptophanaron. The configuration of the cup and stalk is similar to that of Kryptophanaron, but the stalk hook is smaller and less strongly curved. As in *Kryptophanaron*, the hook can be lifted free of the shutter nodule. The cup is smaller, but does not differ markedly in configuration from that of Kryptophanaron.

The stalk muscles are similar to those of Kryptophanaron and Photoblepharon.

Shutter. The shutter nodule is similar to, but smaller than, that of Kryptophanaron. The shutter attaches as in Photoblepharon and Kryptophanaron, but does not form a free fold between the posteroventral corner of the eye and the fleshy papilla marking its posterior attachment to the orbit. As in Photoblepharon and Kryptophanaron, the shutter folds downward on itself when retracted.

Ligaments. The EM is as in Anomalops. There is a short branch to the palatine and no posterior swelling at the point of forward flexure. As in Kryptophanaron and Photoblepharon, the LD arises from the posterolateral border of the rostral cartilage, passes laterally around the EM at its forward flexure and extends posteriorly to insert on the medial shelf of the cup.

The anchoring ligaments are as in Kryptophanaron.

FUNCTION

The following accounts, which should be read in conjunction with the figures, represent our hypotheses, based on manipulation of fresh material as well as inferences from structural relationships, for the function of the light organ occlusion mechanism in each genus:

Photoblepharon
(Figs 4–6)

With the mouth closed, contraction of $A_{1\beta}$ of the adductor mandibulae pulls the maxilla posteriorly, carrying the ventral end of the EM with it. Because the EM is stretched over the cartilaginous tip of the palatine, this backward pull is translated into straightening and slight lateral rotation of the EM at its forward flexure. The palatine thus acts as a pulley. Rotation of the EM swings its posterior swelling laterally, bringing it to bear on the LD, placing tension on it and carrying it slightly outward. Concurrently, straightening of the EM produces a forward pull on the **LD.** Because the **LD** is firmly anchored to the

maxillary process of the palatine and insert on the ventrolateral margin of the maxilla just posterior to its head. Unlike Photoblepharon, the EM gives rise to a short ventral branch, just below its forward flexure, that inserts on the shaft of the maxillary process of the palatine. The LD arises anteriorly from a biconcave meniscus of fibrocartilage on the posteromedial border of the head of the maxilla (not visible in illustration), passes laterally around the EM at its forward flexure and runs posteriorly to insert on the ventrolateral corner of the anterior end of the cup.

Two thin, strap-like ligaments arise from the posterior end of the maxillary arm of the palatine. One runs anteriorly to attach to the stalk, passing lateral to the LD; the other runs dorsally to the lateral ethmoid. Another ligament runs posteriorly from the inner surface of the flexure in the C-shaped process of the lacrimal, sends a short branch to the anteromedial corner of the connective tissue pad on the floor of the orbit and continues back to attach to the midline of the back of the light organ. These ligaments are not illustrated.

Kryptophanaron alfredi

Skeletal elements. The bones involved in accommodation of the light organ and associated structures are similar to those of Photoblepharon.

Stalk *and* cup. The light organ is proportionally smaller than that of Photoblepharon. The stalk is continuous across the snout, as in Photoblepharon, but the commissure is somewhat thinner. At its articulation with the cup, the stalk bears a ventral hook-like process that passes along the medial side of and then under, a movable shutter nodule. The configuration of this stalk hook is similar to that of Photoblepharon, but it is relatively smaller and less intimately associated with the shutter nodule. There is no connective tissue attaching the two, and the hook can be lifted free of the nodule without dissection.

The cup differs from that of Photoblepharon only in being relatively somewhat smaller and in being less tightly bound to the stalk. Dorsally the cup and stalk are attached by a short ligament, as in Photoblepharon. The anteroventral process of the cup, which passes behind the stalk hook, is not tightly attached to the medial side of the hook as in Photoblepharon, but moves freely with respect to it; this freedom allows partial rotation of the cup.

The muscles of the stalk are similar to, but smaller than, those of Photoblepharon; the dorsal muscle inserts on the ligament that connects the cup and stalk and the ventral muscle inserts on the articular termination of the stalk.

Ligaments. The EM is like that of Anomalops in having a short branch to the palatine below its forward flexure. It is like that of Photoblepharon, however, in having a posterior swelling and groove for the LD at this forward flexure. The swelling and groove are somewhat less well-developed than in Photoblepharon. As in Anomalops and Photoblepharon, the EM passes around the cartilaginous tip of the palatine to insert on the ventrolateral margin of the maxilla just ventral to its head. As in Photoblepharon, the LD attaches anteriorly to the posterolateral border of the rostral cartilage, passes laterally around the forward flexure of the EM and extends posteriorly to insert on the medial shelf of the cup. The anchoring ligaments are similar to those of Photoblepharon.

downward, its posterior end fits snugly under the fleshy pad of this flap. The flap thus holds the posterior portion of the organ firmly against the floor of the orbit. This would not interfere with abduction (downward rotation) of the organ, because the organ can easily slip under the flap. It is possible that the original function of the skin fold was hydrodynamic. The lower part of the orbit is deeply excavated, exposing the curve of the eyeball. The excavation forms a deep posterior pocket that would seemingly cause turbulence as the fish swims, and the skin fold may act as a fairing to streamline the eyeball. If the skin fold were completely attached to the rim of the orbit posteriorly (like an adipose eyelid), water displaced by the light organ as it rotated into a closed pocket would be forced out around the organ, perhaps slowing its movement. Instead, a posterior opening should allow water displaced by the organ to escape.

Kryptophanaron

In Kryptophanaron, there is both a rotational capability and a functional shutter. As in Photoblepharon, tension is placed on the **LD** by the **EM.** The EM is swollen near its forward flexure, forming a discrete but smaller bulbous projection than that of Photoblepharon. There is also a shallow groove and a slight bulge above the flexure that may serve to prevent the LD from sliding upward along the EM when placed under tension. Because the LD is attached to the medial shelf of the cup, a forward pull on it does not flip the organ over as in *Anomalops.* Instead the cup is pulled forward and its anterior end is rocked outward slightly.

As in Photoblepharon, rotation of the cup brings the process at its anteroventral corner to bear on the medial side of the stalk hook. Kryptophanaron differs, however, in that the ventral process of the cup is not tightly bound to the stalk hook but can move in relation to it. Thus as the cup is pulled forward, the process, which is tapered, slides along the medial side of the stalk and because the surface of the process is inclined, the forward movement is translated into a downward rotation of the cup. This rotational mechanism, which requires translation of forces and consequent frictional losses, is not as efficient as that of Anomalops. Anatomically it does not seem possible that the face of the organ could be tightly appressed to the floor of the orbit. Observations on living and fresh material indicate that the organ can be rocked downward, but that the outer face cannot assume a completely horizontal position.

The mechanism of the shutter is fundamentally like that of Photoblepharon, but the stalk hook and particularly the shutter nodule are less well developed and are not bound together.

As described above, a forward pull on the cup brings its anterior process to bear on the stalk hook, pressing it outward and upward, as in Photoblepharon (but here, at the same time, forcing a downward rotation of the cup). This brings the stalk hook to bear on the shutter nodule, the posterior end of which is rocked outward and upward, producing tension on the shutter nodule and thereby raising it.

According to our proposed mechanism there should be some coupling of organ rotation and shutter movement. Observations of living Kryptophanaron indicate that the organ is in fact tilted down during a shutter blink. Manipulation of fresh material shows that the movements described above occur when the maxilla is pulled backward or when the **LD** is pulled forward.

The stalk musculature is simpler than in Photoblepharon but probably serves similar functions.

Phthanophaneron

The relationships of the cup stalk and LD are similar to those of Kryptophanaron and the postulated forces and motions should be the same. Manipulation of the second specimen of Phthanophaneron, which had been frozen and thawed, indicates that the organ is capable of full rotation, confirming the surmise of Rosenblatt & Montgomery (1976). We presume that the small size of the organ allows its complete downward rotation in Phthanophaneron, whereas the larger organ of Kryptophanaron cannot be completely rotated. As in Kryptophanaron, a forward pull on the cup pushes the stalk hook outward and upward against the shutter knob, bringing the shutter out and up. The shutter is smaller than in Kryptophanaron, but it is large enough when fully erected to cover the face of the organ. Although it appears that the rotational and shutter mechanisms are closely coupled, only observations on living material can establish whether the shutter mechanism can operate independent of movement of the organ, via the ventral stalk muscle.

PHYLOGENY

Extrafamilial relationships

Rosenblatt & Montgomery (1976) followed others in regarding the Anomalopidae as closely allied to the Trachichthyidae and listed several characters common to both. In his study of beryciform intrarelationships, Zehren (1979) noted that the Anomalopidae, Trachichthyidae and Monocentridae probably form a monophyletic assemblage, herein referred to as the trachichthyoids. In both dendrograms of beryciform relationships presented and discussed by Zehren, the interrelationships of these three families are the same. Trachichthyoids share a number of derived features, including the presence of mid-ventral scutes and absence of the basihyal and ventral postcleithrum, but none of these are unique among beryciforms. According to Zehren (1979), the strongest evidence for trachichthyoid monophyly is the shared absence of the fourth upper pharyngeal tooth plate. Among beryciforms, Zehren noted this element to be absent elsewhere only in *Stephanoberyx*, where he considered it a probable homoplasy; however, Rosen (1973: fig. 91) indicated that it is present in that genus.

Within the trachichthyoids, the Trachichthyidae and Monocentridae share 26 of Zehren's 94 derived character states. Although none of these is unique among beryciforms Zehren noted that two additional, apparently unique synapomorphies, frontal pattern and a reduced, hook-like subocular shelf, corroborate his hypothesis that monocentrids and trachichthyids are most closely related and thus together form the sister group of the Anomalopidae.

Anomalopids differ most notably from all other beryciforms in their possession of a subocular light organ and the associated bony and soft tissue modifications; this complex specialization confirms the monophyly of the family. Other important differences from the other trachichthyoids are found in the caudal skeleton and dorsal gill arches. In trachichthyoids and other beryciforms we

have examined, the neural and haemal spines of the third preural centrum extend backward to support the anterior procurrent caudal rays and the anteriormost radial cartilages, which lie at the anterodistal margins of the spines. Anomalopids are apparently unique within the Beryciformes in that the neural and haemal spines of the fourth preural centrum also support procurrent rays; thus, the anteriormost radial cartilages lie anterior to these spines.

The gill arches of anomalopids are unusual among beryciforms in having a small interarcual cartilage between the uncinate process of the first epibranchial and a process on the second infrapharyngobranchial. Rosen & Greenwood (1976) regarded the interarcual cartilage as a unique specialization of perciform fishes. More recently, Travers (1981) has reported the presence of the interarcual cartilage in some members of non-perciform groups including myctophoids, ophidioids, atherinomorphs and scorpaeniforms. Rosen & Parenti (1981) reported that it is primitively present in every major group of acanthopterygians that have an uncinate process or its equivalent on the first epibranchial; however, in most beryciforms, including non-anomalopid trachichthyoids, there is no interarcual cartilage.

Aside from anomalopids, an interarcual cartilage has also been observed among beryciforms in *Melamphaes macrocephalus* (R. *K.* Johnson, Field Museum of Natural History, personal communication; G.D.J., personal observations) but (Travers (1981) reported it to be absent in M. *beani.* Presence of the cartilage in anomalopids and *Melamphaes macrocephalus* raises the possibility that an interarcual cartilage was present primitively in beryciforms and has been lost numerous times within the group, but morphological evidence does not favour this hypothesis. Those beryciforms lacking the interarcual cartilage exhibit an articulation identical to that of more primitive euteleosts, in which the cartilaginous tip of the uncinate process of the first epibranchial articulates directly with a process of the second infrapharyngobranchial. (In those perciforms that appear to have lost the interarcual cartilage, either there is usually a decided gap between the uncinate process of the first epibranchial and the second infrapharyngobranchial, or the uncinate process is absent.) A second, more plausible hypothesis is that a small interarcual cartilage arose independently in *Melamphaes* and the common ancestor of the anomalopids. In any case, homology of the small cartilage in anomalopids with the larger, rod-shaped interarcual cartilage of perciforms seems unlikely and is inconsistent with other morphological evidence that supports trachichthyids and monocentrids (not perciforms or any perciform subgroup) as the sister group of the Anomalopidae.

Intrafamilial relationships

Our analysis of the cladistic relationships of the anomalopid genera is based on characters involving morphological features not obviously associated with the light organ complex. Although the resultant hypothesis is corroborated by some characters of the light-organ complex, phylogenetic interpretation of most of the characters associated with light organ occlusion is problematic, and the evolution of occlusion:mechanisms is discussed separately below, in light of the hypothesized phylogeny.

States of characters used in constructing the phylogeny are given for the four anomalopid genera and the two outgroup families in Table 1. The number of characters comparable among all four genera was limited because only two specimens of *Phthanophaneron* are known and osteological material was not available. Polarity of characters listed in Table 1 was determined by outgroup comparison with character states in the first outgroup, the Trachichthyidae plus Monocentridae, based on Zehren's (1979) hypothesis (discussed above) that these two families constitute the sister group of the Anomalopidae. For characters exhibiting two states within the Anomalopidae, the ancestral state is most parsimoniously hypothesized to be the one expressed faithfully in this first outgroup. Where both states occur in the outgroup, the primitive state for the outgroup was hypothesized based on Zehren's hypothesis of generic relationships, and this was considered the ancestral state for anomalopids.

We chose to limit our comparisons to the first outgroup because identity of the second and subsequent outgroups was uncertain in Zehren's (1979) analysis. In his most parsimonious dendrogram No. 1 (Zehren, 1979: fig. 4), holocentrids, berycids and diretmids constitute the second outgroup and *Polymixia* the third. In his discussion, however, Zehren agreed with Rosen (1973) that there is little evidence to relate holocentrids to other beryciforms, and presented evidence to support the removal of *Polymixia* from the Beryciformes. More recently Stiassny (1986) has given evidence to support the placement of *Polymixia* as the sister group of all other acanthomorphs. Zehren's preferred, but less parsimonious, dendrogram No. 2 (Zehren, 1979: fig. 5) places *Anoplogaster* and *Diretmus* as the second outgroup and stephanoberycoids as the third. This second hypothesis is apparently no stronger than the first and, in addition, we question the wisdom of using character states in highly specialized meso- and bathypelagic forms to assess the ancestral state in the primarily benthic trachichthyoids. In view of the questionable identity of additional outgroups for the Anomalopidae, we see little value in attempting to include the various possibilities in our character analysis. Maddison, Donoghue & Maddison (1984) demonstrated that the first outgroup has considerably more influence on parsimonious assessment of ancestral states for the ingroup than do more distant outgroups, which can never ". . . . completely shift the assessment away from the state in the first outgroup." In our analysis, the polarity of 16 of 19 characters is resolvable by reference to the first outgroup; reference to additional outgroups could only corroborate the hypothesized polarity or make it equivocal.

Derived character states are designated by an asterisk in Table 1. For characters also considered by Zehren (1979), our analysis assigned polarities opposite those assigned by him. For example, Zehren considered the presence of ventrolateral flanges on the parasphenoid as primitive for beryciforms, and the absence of these flanges as derived. Because his combinatorial method did not allow character reversals, absence of the flanges was interpreted as a derived feature at all levels of his dendrograms, resulting in eight independent derivations in the preferred dendogram No. 2. A more parsimonious solution (requiring seven fewer steps) would treat the loss of parasphenoid flanges as a specialization of all beryciforms except holocentrids, and allow for reacquisition of the flanges in *Anomalops*. The latter interpretation is in accord with our polarization of the character for anomalopids, based on the absence of flanges in trachichthyids and monocentrids. Zehren apparently recognized that similar

TABLE 1. Comparison of characters not associated with light-organ complex among anomalopids and other trachichthyoids

Characters	*Anomalops*	*Phthanophaneron*	*Kryptophanaron*	*Photoblepharon*	*Monocentridae*	*Trachichthyidae*
1 Epipleural ribs	12*	2	2	2	0	2
2 Branchiostegals	Smooth*	Spiny	Spiny	Spiny	Spiny	Spiny
3 Openings in pars jugularis	4*	3	3	3	2	3
4 Parasphenoid flanges	+*	+	–	–	–	–
5 Swimbladder stay	+*	–	–	–	–	–
6 Postorbital papillae	8–9*	1	1	1	0	0
7 Cephalic sensory canal covering	Papillose	Papillose	Smooth*	Papillose	Papillose	Smooth or Papillose
8 Lateral-line tubes	Closed	Closed	Closed	Open*	Closed	Closed
9 Midventral scutes	Continuous	Continuous	Continuous	Reduced, discontinuous*	Continuous	Continuous
10 Dorsal Fin / Predorsals	V—I, 14 / 0/0/1+1/	IV—I, 15 / 0/0/1+1/	IV—I, 15 / 0/0/1+1/	II, 18–19* / 0/0/1+1/	VI—11 / 0/0/1+1/	III–VIII, 12–16 / 0/0/1+1/
11 Supramaxillae	1	2*	2*	2*	1	1
12 Transverse ridges on gular isthmus	–	+*	+*	+*	–	–
13 Lateral dentary tooth patch	Small	Large "V"*	Large "V"*	Large "V"*	Small	Small
14 Body scale rows	50	110*	150*	130*	15	50–100
15 Reflective lateral line scales	–	–	+*	+*	–	–
16 Pelvic spine	–*	+	+	–*	+	+
17 Anal spines	II	II	I	I	0	II–III
18 Vertebrae	14+ 16	14+16	15+15	13+17	12+15	11–13+14–17
19 Comer of maxilla	Bony ornamentation	Papillae	Papillae	Bony ornamentation	Papillae	Bony ornamentation

* Hypothesized derived state.

reasoning applies to many of his characters. He discussed the possibility of reversals in three characters (presence of dorsal, anal and pelvic spines), but did not alter his dendrograms. Re-analysis of Zehren's data using a methodology that allows character reversal would be worthwhile and could result in a new phylogenetic hypothesis for the Beryciformes. However, it is unlikely that this would refute the hypothesized monophyly of the trachichthyoids or alter the proposed interrelationships of the three component families; i.e. character polarity hypotheses for the Anomalopidae would not be affected.

Below, we briefly describe the 19 characters listed in Table 1 and discuss their polarization. Because most of these features are not described elsewhere in this paper, characters of unresolvable polarity and autapomorphies, as well as synapomorphies, are discussed; all three provide comparative information about the four genera. The cladistic hypothesis is based only on the six characters shown to be synapomorphies (shared by two or more genera).

1. Trachichthyids have epipleural ribs only on the first two vertebrae and monocentrids lack them altogether. Twelve epipleural ribs in Anomalops is hypothesized to be derived.

2. In trachichthyids and monocentrids, the ventral margin of several branchiostegals is spinulose. Absence of spines on the branchiostegals in Anomalops is hypothesized to be derived.

3. The pars jugularis is the outer portion of the trigemino-facialis chamber of the prootic bone. Its lateral wall may have from two to four openings for passage of the orbital artery, jugular vein and branches of the trigeminal and facial nerves. Three openings is primitive for acanthopterygians (Patterson, 1964) and beryciforms (Zehren, 1979). Trachichthyids have three and monocentrids only two openings; the presence of four openings in Anomalops is hypothesized to be derived.

4. Zehren (1979) treated the presence of ventrolateral flanges on the shaft of the parasphenoid as a primitive feature of beryciforms. These flanges are absent in trachichthyids and monocentrids; their presence in Anomalops is most parsimoniously hypothesized as derived (reversal).

5. The swimbladder stay is a unique, derived feature of Anomalops, absent in all other beryciforms. It is a stout, L-shaped strut of cartilage projecting forward from the first anal pterygiophore; the tapered posterior end of the swimbladder is bound into a trough along the anteroventral side of the stay.

6. A graduated series of eight to nine fleshy papillae along the posterodorsal margin of the orbit is a unique, derived feature of Anomalops. Similar structures are found in several unrelated, small, planktivorous percoids (e.g. the serranid *Schultzea* and the pomacentrid *Lepidozygus*) and may channel water flow over the eyeball to maintain laminar flow. The relationship of these papillae to the more ventrally located one associated with the shutter and postocular skin flap is not clear. The latter papilla is present in all four anomalopid genera.

7. The skin roofing the cephalic sensory canals is smooth in Kryptophanaron and papillose in the other three anomalopid genera. Both conditions are found in trachichthyids, but in monocentrids this skin is always papillose. The papillose condition is thus hypothesized to be primitive for anomalopids, and smooth latero-sensory canal roofing is a derived feature of Kryptophanaron.

8. In Photoblepharon, tubes of the posterior lateral-line scales are not roofed by

bone, as they are in other anomalopids, trachichthyids, and monocentrids. Instead they are covered by darkly pigmented skin, a unique, derived feature of Photoblepharon.

9. A continuous series of mid-ventral scutes (enlarged keeled scales) is present in all anomalopids except Photoblepharon, which has only a few weak scutes. A well developed series of scutes occurs in trachichthyids (reduced in a few species of Hoplostethus) and monocentrids. A discontinuous series of reduced mid-ventral scutes is considered a unique, derived feature of Photoblepharon.

10. The following dorsal fin-ray counts are found in anomalopids: II, 18–19 in Photoblepharon; IV—I, 15 in Kryptophanaron and Phthanophaneron; and V—I, 14 in Anomalops. (A rule, —, indicates a separate spinous dorsal fin in the latter three genera.) In trachichthyids the spinous and soft portions are continuous (III–VIII, 12–6) and in monocentrids they are separate (VI–II). Based on this information alone, the ancestral state of the dorsal fin of anomalopids (separate or continuous) cannot be resolved. However, the interdigitation of the anteriormost pterygiophores and neural spines in Photoblepharon is 0/0//1+1/, which is unique among trachichthyoids and clearly derived. In all other anomalopids, trachichthyids and monocentrids, this configuration is 0/0/1+1/. Loss of two pterygiophores and the associated three spines from the third interneural space in Photoblepharon would explain the absence of a separate spinous dorsal and the difference in total number of spines between Photoblepharon (two) and Phthanophaneron and Kryptophanaron (five). Consequently, we hypothesize that the dorsal fin of Photoblepharon is derived.

11. Primitively, beryciforms have two supramaxillae (Zehren, 1979). Extant trachichthyids and monocentrids have only one. The ancestral state for anomalopids is hypothesized to be one, found only in Anomalops, and reversion to the two supramaxillae found in more primitive beryciforms is thus interpreted here as a synapomorphy of the other three anomalopid genera. It should be noted that certain fossil genera referred to the Trachichthyidae are reported to have two supramaxillae (Patterson, 1967; Guyet, 1982). It is possible then, that the common ancestor of the living forms had two supramaxillae and that the loss in Anomalops represents an apomorphy, but this cannot be resolved without a more complete phylogeny of fossil and extant trachichthyids.

12. In trachichthyids, a naked gular isthmus is usually smooth but bears large papillae in *Trachichthys*. Monocentrids also have large papillae on the naked isthmus. In Anomalops, a few small papillae are found on the naked anterior tip of the gular isthmus. In Phthanophaneron the naked anterior portion of the isthmus bears small papillae arranged in transverse rows on slightly raised fleshy ridges. In Photoblepharon the anterior portion of the isthmus bears large papillae that gradually coalesce posteriorly into well-defined transverse ridges. In Kryptophanaron, thick fleshy transverse ridges, some slightly papillose, cover the entire gular isthmus. A papillose gular isthmus, without transverse fleshy ridges, is hypothesized to be the ancestral state for anomalopids. The presence of transverse ridges is a synapomorphy of Phthanophaneron, *Kryptophanaron* and Photoblepharon.

13. In trachichthyoids, the anterior tip of each dentary is somewhat knoblike at the symphysis and bears teeth on its anterolateral surface. In trachichthyids and monocentrids, this tooth-bearing surface is relatively small and does not extend ventrally below the point of insertion of the maxillodentary ligament.

This condition also occurs in Anomalops and is hypothesized to be the ancestral state for anomalopids. In the other three anomalopids the dentary knob is somewhat enlarged and the tooth bearing surface is notably more extensive, extending ventrally and then posteriorly, so that it essentially forms a "V" around the insertion of the maxillodentary ligament.

14. Although body scales are difficult to enumerate in anomalopids and some trachichthyids due to their small size, irregular arrangement and spinescence, an approximate count can serve as a reasonable indicator of relative scale size. Among trachichthyids our counts of body scales range from 50–100. The highly specialized armour-like scales of monocentrids number only about 15. Anomalops has relatively large scales (50 rows along the body), whereas in the other three anomalopids scales are quite small (100–150). The ancestral condition for anomalopids is most parsimoniously hypothesized to be large scales (< 100 rows along the body). Smaller, more numerous scales (> 100) are considered a synapomorphy of Phthanophaneron, Kryptophanaron and Photoblepharon.

15. Kryptophanaron and Photoblepharon share enlarged, reflective lateral-line scales, which are lacking in other anomalopids, monocentrids and trachichthyids. Although there are some differences in structural detail (they are more delicate and not roofed by bone posteriorly in Photoblepharon), we consider reflective lateral-line scales a unique synapomorphy of Kryptophanaron and Photoblepharon.

16. In anomalopids, the first pelvic ray may be spinous (Phthanophaneron and Kryptophanaron) or soft (Anomalops and Photoblepharon). This element is spinous in all trachichthyids and monocentrids. Presence of a pelvic spine is hypothesized to be the ancestral state for anomalopids. Anomalops and Photoblepharon share the derived state.

17. Anomalopids have one or two (Anomalops and Phthanophaneron) anal spines. Trachichthyids have two or three, and monocentrids have none. Assuming that anal spines are gained or lost one at a time, the ancestral state for trachichthyids and monocentrids could be zero, one, two or three spines. Polarity for the Anomalopidae is unresolvable.

18. Anomalopids have 30 total vertebrae (including the free U2) in the following caudal/precaudal combination: $14+16$ in Anomalops and Phthanophaneron, $15+15$ in Kryptophanaron, and $13+17$ in Photoblepharon. Trachichthyids have 27–30 ($11–13+14–17$) and monocentrids have 27 ($12+15$). The ancestral state for trachichthyids and monocentrids is most parsimoniously hypothesized to be $12+15$. Polarity for the anomalopids is unresolvable.

19. In Anomalops and Photoblepharon the lateral surface of the posteroventral corner of the maxilla (area just below supramaxilla) is ornamented with small spines and/or serrate ridges. In Phthanophaneron and Kryptophanaron this area bears no bony ornamentation and is covered with relatively thick, papillose skin. Only the first condition is found in trachichthyids, and the latter characterizes, monocentrids. Polarity for the Anornalopidae is unresolvable.

Of the 19 characters described above, the first six are autapomorphies of Anomalops, one (7) is an autapomorphy of Kryptophanaron, and three (8–10) are autapomorphies of Photoblepharon. Polarity of three (17–19) of the remaining nine is unresolvable. Only six characters are synapomorphic. Four of these

(11–14) are shared by *Phthanophaneron, Kryptophanaron* and *Photoblepharon* and one *(15)* is shared by *Kryptophanaron* and *Photoblepharon.* These five synapomorphies corroborate the relationships expressed in the cladogram shown in Fig. 10. The sixth apparent synapomorphy (16) is shared by *Anomalops* and *Photoblepharon* and thus conflicts with the hypothesized relationships. It is most parsimonious to assume that character 17 (loss of the pelvic spine) evolved independently in *Anomalops* and *Photoblepharon.*

Anomalops, as the sister group of the other three genera, is primitive with respect to them in possessing a single supramaxilla, having a smaller lateral tooth patch on the dentary, and lacking fleshy transverse ridges on the gular isthmus. *Anomalops* exhibits several unique specializations: 12 epipleural ribs, smooth branchiostegals, four openings in the pars jugularis, and the presence of parasphenoid flanges, a swimbladder stay and postorbital tubercles. Several of these may be functionally correlated with the more active swimming habits of the terete-bodied *Anomalops.*

Phthanophaneron is the sister group of *Kryptophanaron* and *Photoblepharon* and shares with them the following derived characters: two supramaxillae, transverse fleshy ridges on the gular isthmus, a large, V-shaped lateral tooth patch on the dentary and smaller, more numerous scales. *Phthanophaneron* is the most generalized anomalopid and we were unable to identify any autapomorphic features.

Kryptophanaron is unique in having large, reflective belly scutes, reflective scales at the base of the dorsal fin and smooth skin covering the cephalic laterosensory canals. It shares uniquely with *Photoblepharon* large, reflective, lateral-line scales, Unique specializations of *Photoblepharon* are a modified predorsal pattern together with fewer dorsal spines, tubes in posterior lateral-line scales not roofed by bone, and a reduced, discontinuous series of belly scutes.

EVOLUTION OF OCCLUSION MECHANISMS

The subocular light organ and all modifications associated with its physical accommodation and mechanical control form a complex of functionally related characters not present in other beryciforms (Table 2). Many of these characters cannot be polarized by conventional outgroup comparison because they involve modifications of structures for which there are no homologues among non-anomalopid beryciforms; i.e. neither of the states occurs within the outgroup. As an example, although the presence of an erectible shutter can be hypothesized to be derived based on its absence among outgroups, the polarity of different points of attachment of the Ligament of Diogenes cannot, because no comparable structure exists in other beryciforms. Of 14 characters listed in Table 2, only four represent new structures not present in the outgroups and can be unequivocally polarized. Two, the rotation pad (VI) and postocular skin flap (VII), are unique to *Anomalops* and provide no phylogenetic information. The remaining two are synapomorphies congruent with our hypothesized phylogeny. The shared presence of an erectible shutter and shutter nodule (VIII) corroborate the monophyly of the *Phthanophaneron–Kryptophanaron–Photoblepharon* line, and presence of a swelling and groove on the ethmomaxillary ligament corroborates the sister-group relationship between the latter two genera.

TABLE 2. Comparison of characters associated with the light organ among anomalopid genera

	Characters	*Anomalops*	*Phthanophaneron*	*Kryptophanaron*	*Photoblepharon*
I	Attachment of LD on cup	Lateral*	Medial	Medial	Medial
II	Attachment of LD anteriorly	Maxilla*	Rostral cart.	Rostral cart	Rostral cart.
III	Cup with medial shelf	Small*	Moderate	Moderate	Large
IV	Insertion of dorsal stalk muscle	Directly on cup*	Ligament to cup	Ligament to cup	Ligament to cup
V	Stalk with inward flexure at cup articulation	+*	−	−	−
VI	Rotation pad	+**	−	−	−
VII	Postocular skin flap	+**	−	−	−
VIII	Erectible shutter with moveable shutter nodule	−	+**	+**	+**
IX	Stalk with ventral hook	−	+*	+*	+*
X	Stalk continuous across snout	−	+*	+*	+*
XI	EM with swelling and groove	−	−	+**	+**
XII	Hook and shutter nodule intimately associated and attached by ligament	NA	−	−	+*
XIII	Cup process attached by ligament to stalk hook	NA	−	−	+*
XIV	Organ rotatable	+	+	+	−*

*Hypothesized derived state based on assumption of ancestral mechanism.
**Hypothesized derived state based on outgroup comparison.

We see nothing circular in interpreting the evolution of occlusion mechanisms in light of a phylogeny that is corroborated by characters of the light-organ functional complex. Schaefer & Lauder (1986), in a study of the evolution of feeding mechanisms in loricarioid catfishes, excluded from their phylogenetic analysis characters that were functionally correlated with feeding, arguing that interpretation of the evolution of function based on a phylogeny that includes in its construction characters associated with that function is circular. We disagree and maintain that the underlying philosophy in construction of a phylogeny based on parsimony argumentation requires inclusion of all available information, unless there is independent evidence to suggest that certain characters are phylogenetically capricious; the latter can really be determined only after construction of the cladogram. We see no justification (nor did Schaefer & Lauder offer any) for the assumption that functional characters are less informative phylogenetically. It may be necessary to exclude functional characters due to inability to polarize shape or positional differences in neomorph structures for which homologues do not exist among outgroups (as is the case with most of the functional characters in our study). However, so long as the outgroup information exists to polarize them, a phylogeny constructed using functional as well as all other available characters provides the most rigorous hypothesis of evolutionary transformation. The interpretation of the evolution of function is nothing more than an explication of the transformation sequences on the most parsimonious cladogram, and is not circular. To exclude functional characters and interpret them only with respect to some other suite of characters could result, without justification, in a less parsimonious explanation of overall character distribution and thus bring about a misleading representation of functional transformation sequences.

The remaining characters associated with light-organ occlusion cannot be polarized based on outgroup comparison, and although the various states can be mapped onto the existing cladogram, this does not resolve their polarity. Full interpretation of the evolutionary transformations involved in the evolution of light-organ control in anomalopids still requires assumptions about the ancestral control mechanism. Based on its relative simplicity and on overall parsimony we propose that the primitive occlusion mechanism (the one present in the common ancestor) was a forced rotation like that of Phthanophaneron and Kryptophanaron, wherein downward rotation of the organ is forced by sliding the cup forward. The forced rotational mechanism is the simplest and apparently least refined of the occlusion mechanisms. It involves fewer structures and linkages than the shutter mechanism or the highly refined flipping mechanism of Anomalops, and it seems reasonable to assume, in the absence of evidence to the contrary, that the least complex mechanism was primitive.

Furthermore, the hypothesis that the ancestral anomalopid possessed only a forced rotational mechanism requires fewer transformations from the outgroup condition (no organ-associated structures) to explain the distribution of the remaining occlusion-associated characters. Rosenblatt & Montgomery (1976) suggested that both rotational and shutter mechanisms were present in the common ancestor as in Phthanophaneron and Kryptophanaron. There is indeed a free rim of skin along the lateral border of the floor of the orbit in Anomalops that could represent the remnant of a once functional shutter. Alternatively, this rim of skin was never a functional shutter ancestrally, but may have served as a

shield that assisted an imperfect rotational mechanism in occlusion of the light. Of the two possibilities, the latter is preferred because it does not require the loss in Anomalops of the structures associated with an erectile shutter.

Based on the premise that all character states associated with a forced rotational mechanism are primitive for anomalopids, polarity was determined for the problematic light-occlusion characters (see Table 2). Derived states of these and the other four occlusion characters are mapped on the hypothesized phylogeny (Fig. 10), with which they are fully congruent.

From the common ancestor of extant anomalopid genera, evolution of light organ occlusion proceeded along two divergent mechanical pathways. In the line leading to Anomalops, the rotational mechanism was modified and refined to produce a mechanically more efficient flipping mechanism. The large medial shelf on the cup, important in forced rotation, was reduced (111), allowing greater rotational freedom. Insertion of the LD was shifted from the medial shelf to the anterolateral corner of the cup (I), providing for a direct rotation of the cup and organ by the ligament. Origin of the LD was shifted from the rostral cartilage to the head of the maxilla (11), increasing the efficiency of translation of the posterior movement of the maxilla to a forward pull on the LD as it passes around the EM. The origin of a cartilaginous rotation pad on the floor of the orbit (VI) on which the cup is counterbalanced further increased the ease with which the organ could be rotated or, essentially, flipped over. The dorsal stalk muscle encroached on its ligamentous insertion on the cup to attach directly (IV), providing a direct means of counter rotation. Additional specializations included the advent of a postocular skin flap (VII), providing a spring to retain the organ in an occluded position without muscle tetanus and the development of a medial flexure of the stalk (V) on which the ventral stalk muscle inserts, providing a means for lateral extension of the cup and organ.

In the lineage comprising the other three genera a shutter mechanism for occlusion of the light arose and was refined. The free rim of skin along the ventrolateral border of the orbit was expanded to form an elastic, erectible shutter that could be drawn up over the face of the organ by means of a cartilaginous nodule movably attached to the palatine (VIII). Development of

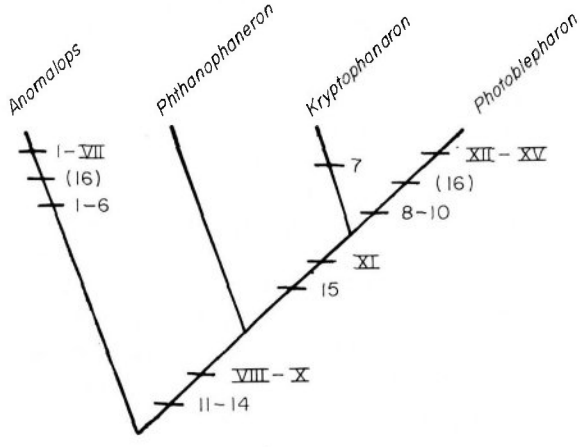

Figure 10. Cladogram of the Anomalopidae. Numbers designate derived states of characters listed in Tables 1 and 2 and discussed in text. Numbers in parentheses indicate hypothesized homoplasy.

a ventral hook on the stalk (IX), embracing the nodule anteriorly and abutting the cup posteriorly, provided the mechanical linkage between shutter nodule, stalk and cup necessary to translate the forward pull on the cup by the LD into shutter erection. Concomitantly, the stalk was enlarged and became continuous across the snout (X). In Phthanophaneron and *Kryptophanaron* the primitive forced rotation was retained and functions in conjunction with the shutter mechanism. In the common ancestor of *Kryptophanaron* and Photoblepharon the light organ became slightly larger, and the shutter, shutter nodule and stalk hook better developed. Additionally, the advent of a cam-like posterior swelling and anterior groove on the EM (XI) increased efficiency of translation of the posterior movement of the maxilla to a forward pull on the LD.

The ultimate refinement of the shutter mechanism was realized in Photoblepharon in which the much greater size of the organ and the ligamentous attachment of the anteroventral process of the cup to the stalk hook (XIII) completely precludes rotation (XIV). Erection of the considerably larger shutter is facilitated by a more intimate embrace and ligamentous connection between the well-developed stalk hook and shutter nodule (XIII). Exclusion of forced rotation and refinement of the shutter mechanism in Photoblepharon suggests the potential capability for finer and more rapid control of occlusion than might be available to Phthanophaneron and *Kryptaphanaron*, which rely on two seemingly less efficient mechanisms to achieve complete occlusion. This conjecture remains to be tested by experimental and behavioural observations. Morin et al. (1975) documented a varied behavioural repertoire associated with rapid and diverse patterns of blinking in Photoblepharon, but such extensive behavioural observations have not been made on the other genera.

From the standpoint of biomechanical efficiency, the number and complexity of linkages involved in the operation of the shutter mechanism seems extravagant. One can easily conceive of a simpler means of erecting the shutter that would apply the motive force more directly, e.g. a small muscle extending from the palatine to the shutter nodule. The pre-existence of an integrated rotational mechanism undoubtedly imposed functional–morphological constraints on the light-organ occlusion system. We postulate that such constraints account for a shutter apparatus that seems excessively complicated.

ZOOGEOGRAPHY

The distribution of the Anomalopidae is shown in Fig. 2. The lack of sympatry is striking. One species is eastern Pacific, another Caribbean, one is Indian Ocean, and two are western Pacific. Anomalops and Photoblepharon are known to co-occur at Banda, New Guinea, eastern Australia and the Philippines, the western and eastern limits of their respective distributions. It is likely, however, that all of the forms have wider distributions than shown and that undescribed taxa remain to be collected. The recent collection history of the group bears this out. The discovery of the Indian Ocean and Philippine populations of Photoblepharon, the Philippine occurrence of Anomalops, the Grand Cayman and Puerto Rican records of *Kryptophanaron* and the discovery of Phthanophaneron are all relatively recent.

In light of this, an in depth analysis of the historical biogeography of the

Anomalopidae would be premature. Instead, we propose the following brief scenario for the evolution of the anomalopid fishes:

The ancestral anomalopid was probably, like most trachichthyoids, bottom-associated. The common ancestor, with a forced rotational occlusion mechanism, probably had a general physiognomy similar to that of Phthanophaneron, and, like most trachichthyoids, was bottom-associated, The ancestral population was distributed circumtropically. Anomalops, as the initial divergent, was isolated early in the west Pacific. The East Pacific Barrier (Ekman, 1953) could have isolated east and west Pacific populations. To the east, a land connection between Australia and Asia may have provided a barrier. Ecologically, the Anomalops line became specialized for pelagic feeding, and rotation of the light organ was refined to the more efficient flipping mechanism. In the other lineage, feeding remained bottom-orientated, and rotation of the light organ became less important with the advent of a shutter apparatus. Phthanophaneron has the least developed shutter apparatus and may represent a relict population in the eastern Pacific. Its early isolation is puzzling in view of the relatively recent closure of the Panamanian seaway in the late Pliocene; however, it is conceivable that the deeper habitat of Phthanophaneron could have effectively isolated it from the western Atlantic long before the final elevation of the Panamanian isthmus. The full early life history of anomalopids is unknown; however, preliminary observations of aquarium spawnings indicate that anomalopid eggs and larvae may spend little or no time in the plankton (Patrick Colin, personal communication; Meyer-Rochow, 1976).

Evolution of the **Kryptophanaron–Photoblepharon** line, as discussed above, took place in central Tethys. The light organ was enlarged, so that rotation was incomplete; the shutter was enlarged and the ventral fold became better developed, so that the shutter fit tightly over the face of the organ. Following isolation of the Indian Ocean from the Mediterranean and Atlantic, refinement of the shutter mechanism continued in the Indian Ocean form, which led to Photoblepharon. The light organ and shutter were enlarged, and the stalk hook became tightly attached to the shutter nodule and cup, eliminating forward motion and rotation of the organ. Isolation of the western Indian Ocean (P. *steinitzi*) and West Pacific (P. palpebratus) populations occurred subsequently.

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