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Egg Attachment Systems in the Family Cichlidae (Perciformes: Labroidei), with Some Comments on Their Significance for Phylogenetic Studies

MELANIE L. J. STIASSNY¹ AND JASON G. MEZEY²

ABSTRACT

Among substrate-spawning cichlids two quite distinct egg attachment systems are described using scanning electron microscopy. In the phylogenetically primitive Asian and Madagascan cichlids examined, the eggs are nonadhesive and are attached to the substrate, or to one another, by a tuft of filaments arising from the pole opposite the micropyle. A different system appears to characterize the Afro-Neotropical clade; in these fishes the eggs are highly adhesive with attachment to the substrate facilitated by a thick mucus layer and numerous surface filaments.

Outgroup data from the Pomacentridae are equivocal and do not permit conclusive assignment of polarity for variation within the Cichlidae. However, while we are unable to determine the plesiomorphic cichlid attachment system, the presence of a distinct mucus-filament attachment system is unique among percomorph taxa examined to date and is interpreted here as further support for the monophyly of the Afro-Neotropical Cichlidae.

INTRODUCTION

Recent investigations of the reproductive biology of a phylogenetically primitive cichlid fish from Madagascar, *Paratilapia polleni* Bleeker, 1868, have revealed an unusual egg attachment system in this taxon (Stiassny and

Gerstner, 1992). It is this finding, and our attempts to interpret such an attachment system within a phylogenetic framework, that has stimulated this review of cichlid egg ultrastructure (Mezey, 1992). Wickler (1956a,

¹ Associate Curator, Department of Herpetology and Ichthyology, American Museum of Natural History.

² Undergraduate student intern.

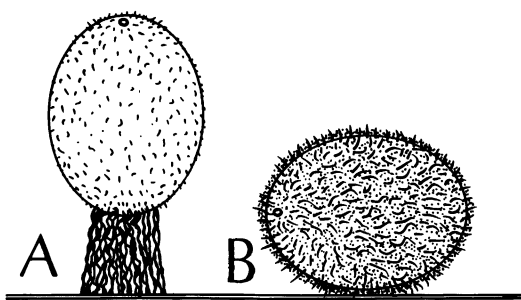


Fig. 1. Schematic representation of Wickler's (1956a, b) (A) "p"-type and (B) "l"-type eggs.

1956b) provided a baseline light microscopy study of cichlid eggs in a review of egg attachment systems in a range of Asian, Neotropical, and African taxa. While Wickler's study was essentially ecological in orientation, he noted that among the Cichlidae two quite distinct egg types are recognizable (fig. 1). In Wickler's "p"-type, as represented in the Asian genus *Etroplus*, the eggs are attached to the substrate by a filament tuft at one pole, the egg surface is without a mucus coat, and is nonadhesive. Wickler's "l"-type eggs, common to most African and Neotropical species, lack the filament tuft and instead are attached along their longitudinal axes by an encasing mucus/filament layer. Although he presented no phylogenetic argument, Wickler believed that the "l"-type egg is characteristic of "genuine cichlids," while "p"-type eggs are found in forms only "marginally considered as cichlids" (Wickler, 1956a).

There is little published information on egg ultrastructure among labroid fishes (Kaufman and Liem, 1982). The embiotocids are viviparous (Wourms, 1981) and therefore of limited utility in the present context. Some data on the egg morphology of various pomacentrid species are available (e.g., Shaw, 1955; Swerdloff, 1970; Ré, 1980; Thresher, 1984; Mooi, 1990), but detailed information on labrid egg structure, particularly that of the demersal eggs of the nest building European Labrinae, are virtually nonexistent (Richards and Leis, 1984; Russell, 1976). Somewhat surprisingly given the vast literature on their reproductive behavior and biology (e.g., Baerends and Baerends Van Roon, 1950; Breder and Rosen, 1966; Keenleyside, 1991; Barlow, 1991), there is little detailed information on substrate-spawning cichlid egg

ultrastructure beyond that provided by the light microscopy studies of Wickler (1956a, 1956b, 1962).

The recent papers of Mooi (1990) and Mooi et al. (1990) provide excellent detailed data on egg ultrastructure in some demersal spawning perciforms. Comparative data of a similar quality are scarce, but Mooi's analyses highlight the potential for additional studies of egg surface structure in other percomorph taxa.

PREPARATION AND MATERIALS

PREPARATION TECHNIQUES

All eggs were obtained immediately post fertilization from aquarium stocks. After careful removal from the substrate, the eggs were fixed in 0.2M glutaraldehyde solution for a 24 hr period. Ovarian eggs of a gravid formalin preserved female *Paratilapia poleni* were carefully cleaned of excess ovarian tissue and refixed in glutaraldehyde solution for 24 hr. Our protocol involved successive washings with 0.2M Na Cacodylate buffer, immersion in osmium tetroxide, dehydration through a graded series of alcohols, and final immersion in a 50% ethyl alcohol/50% amyl acetate solution. Treated eggs were then immersed in amyl acetate for 24 hr before critical-point drying and splutter coating with gold for SEM viewing.

MATERIAL EXAMINED

Cichlidae

Asian: *Etroplus maculatus* (Bloch, 1795); Madagascan: *Paratilapia poleni* (Bleeker, 1868); Neotropical: "*Cichlasoma (Archocentrus)*" *nigrofasciatus* (Günther, 1869), *Herotilapia multispinosa* (Günther, 1866), "*Cichlasoma (Amphilophus)*" *citrinellum* (Günther, 1864); African: *Tilapia zillii* (Gervais, 1848), *Pelvicachromis pulcher* (Boulenger, 1901), *Lamprologus mustax* Poll, 1978.

Pomacentridae: *Amphiprion* sp.

METHODS

Throughout this study we have attempted to determine character polarity using the out-group method (Maddison et al., 1984). However, in the absence of a well-supported scheme of labroid interrelationships, selec-

tion of appropriate perciform outgroups for the present study is highly problematical. Based on similarities in pharyngeal anatomy, Stiassny (1981) suggested a possible relationship between the labroids and two perciform families; the Sparidae and the Gerreidae. Unfortunately, what little information that is available on egg structure in these families indicates that their eggs, like those of the great majority of marine perciforms (Breder and Rosen, 1966; Leis and Trnski, 1989; Mooi et al., 1990) are pelagic and typically without any attachment structures or surface ornamentation (Lo Bianco, 1956; Breder and Rosen, 1966; Thresher, 1984), and are therefore of little utility in helping to polarize variation in attachment structures of the demersal eggs of labroids.

Equally problematical are the precise intrarelationships of the labroid families themselves. Stiassny and Jensen (1987) reviewed the morphological data bearing on this question and favored the most parsimonious scheme in which the Cichlidae form the sister group to a clade containing the Embiotocidae and a pomacentrid-labrid subclade (Stiassny and Jensen, 1987: fig. 19). However, previous hypotheses of labroid intrarelationships differ from this scheme and place the Pomacentridae as the basal labroid clade forming the sister group to the Cichlidae and a labrid-embiotocid subclade (Stiassny, 1980; Kaufman and Liem, 1982). Given the uncertainty of labroid intrarelationships (Stiassny and Jensen, 1987), coupled with the absence of pertinent information in other labroids, it seems reasonable to treat the demersal spawning Pomacentridae as an operational outgroup for polarity assessment of egg structure variation within the family Cichlidae. Information on the egg structure in the demersal spawning labrid subgroup Labrinae might bear on this question, but until we are able to examine spawned eggs of these fishes little more can be added. Our assumption of outgroup relationships is admittedly tentative, but is open to further testing and refinement as more data become available.

ACKNOWLEDGMENTS

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pomacentrid eggs for use in this study. Cynthia Gerstner's preliminary studies of the eggs of *Paratilapia* laid the foundation for the present study, and we are grateful to her for all of her help. Thanks also to Carlos Rodriques, William Barnett, Jennie Ono, and Peling Fong for their patience and skill in the SEM laboratory. Jackie Lazzaro ably cared for aquarium fish stocks and successfully goaded *Etroplus maculatus* into spawning. Klaus Kallman kindly helped with the German translation of a number of important papers. For many helpful comments on earlier drafts of this paper we thank Randy Mooi, Mario de Pinna, and Tony Gill. This work was supported by NSF Research Experiences for Undergraduates (REU) Site Awards to the senior author. Funding from the NSF REU awards supported the summer research of Jason Mezey (DIR 9001058), Cynthia Gerstner (DIR 9001058), and Jackie Lazzaro (DIR 9200351).

RESULTS

POMACENTRIDAE

Pomacentrids lay a plaque of adhesive demersal eggs which are guarded by the male, sometimes assisted by the female, usually until hatching as pelagic larvae some 2 to 7 days after spawning. The eggs, which are typically elliptical, range in size from 0.49 to 4.50 mm along the highest dimension (Thresher, 1984) and are attached to the substrate by a dense tuft of filaments. Most descriptions of pomacentrid eggs are based on field observations or light microscopic examination, and consequently, details of attachment filament structure and surface ornamentation are lacking.

Mooi (1990) examined ovarian eggs from three pomacentrid species, *Paraglyphidodon nigroris*, *Chromis weberi*, and *Amphiprion clarki*. He noted the presence of a complex two-layered sheet that partially or totally encases the eggs. The outer layer is an anastomosing network of filaments while the inner layer consists of longer filaments closely apposed to, or continuous with, those of the outer layer. He suggested that both of these layers peel off the egg surface to form an adhesive disc or cup which attaches the egg to the substrate (Mooi, 1990: 465).

We have been unable to confirm the pres-

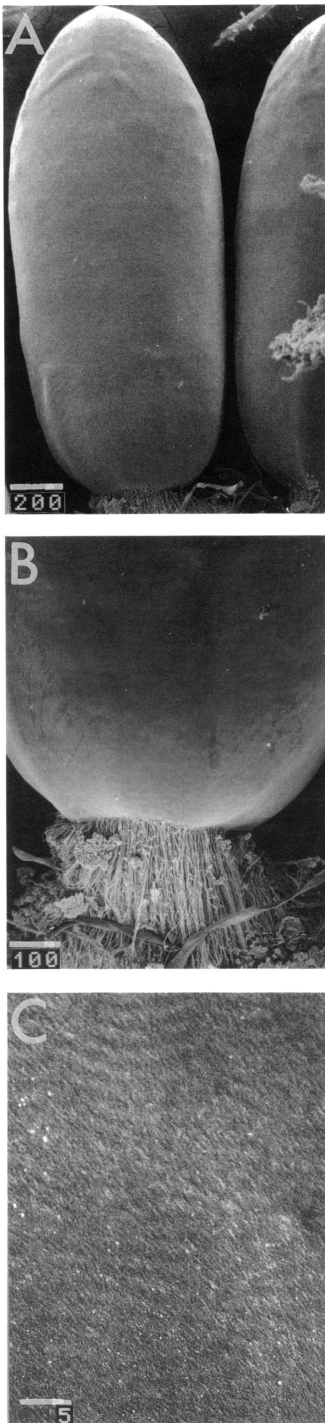


Fig. 2. Egg morphology of *Amphiprion* sp. (A) Single egg, micropyle obscured by attachment filaments; (B) filament tuft surrounding micropyle; (C) surface of the chorion with no filaments. Scale bars are in micrometers.

ence of a complex two-layered network in spawned pomacentrid eggs (fig. 2). Rather, as reported by other authors who illustrate spawned pomacentrid eggs (e.g., *Abudefduf*: Shaw, 1955; Ré, 1980. *Chromis*: Swerdloff, 1970; Thresher, 1984. *Amphiprion*: Thresher, 1984, and *Glyphidodontops*: Thresher, 1984) we find a single filament tuft arising from around the micropyle that attaches each egg to the substratum (fig. 2A, B). The remaining egg surface is smooth, nonadherent, and without surface filaments or mucus coating (fig. 2C). A similar, though less well-defined, meshlike network encases the ovarian eggs of *Paratilapia pollenii* (fig. 4D). As this encasing network is not present in spawned *Paratilapia* eggs (fig. 4C), we suggest that the outer layer described in pomacentrids by Mooi (1990) is possibly ovarian in origin and may be shed at or prior to spawning leaving the inner filament layer, originating around the micropyle, as the attachment structure.

CICHLIDAE

Cichlids are often divided into two polyphyletic behavioral groups: substrate-spawners and mouthbrooders (e.g., Baerends and Baerends van Roon, 1950; Fryer and Iles, 1972; Noakes and Balon, 1982; Keenleyside, 1991; Barlow, 1991). Substrate-spawning is the plesiomorphic cichlid condition and mouthbrooding, a derived condition, has arisen independently at least three (and probably many more) times within the Afro-Neotropical cichlid radiation (Stiassny and Gerstner, 1992). Wickler (1956a, 1956b) did not include mouthbrooding cichlid lineages in his initial studies. However, some details of the surface structure of mouthbrooded eggs are given in a later paper (Wickler, 1962), as well as in Kraft and Peters (1963) and Bern and Avtalion (1990). Mouthbrooded eggs are all characterized by an increase in size, a loss of the adhesive mucous coat, and a reduction or loss of surface filaments (Fryer and Iles, 1972).

Here we restrict our review to the eggs of substrate-spawning taxa representing each of the major geographical cichlid clades (Stiassny, 1991: fig. 1.3).

Asian Cichlidae: Eggs of the Orange Chromide, *Etrophus maculatus*, bear a marked superficial similarity to those of pomacentrids. They are elliptical and measure 1.5 mm

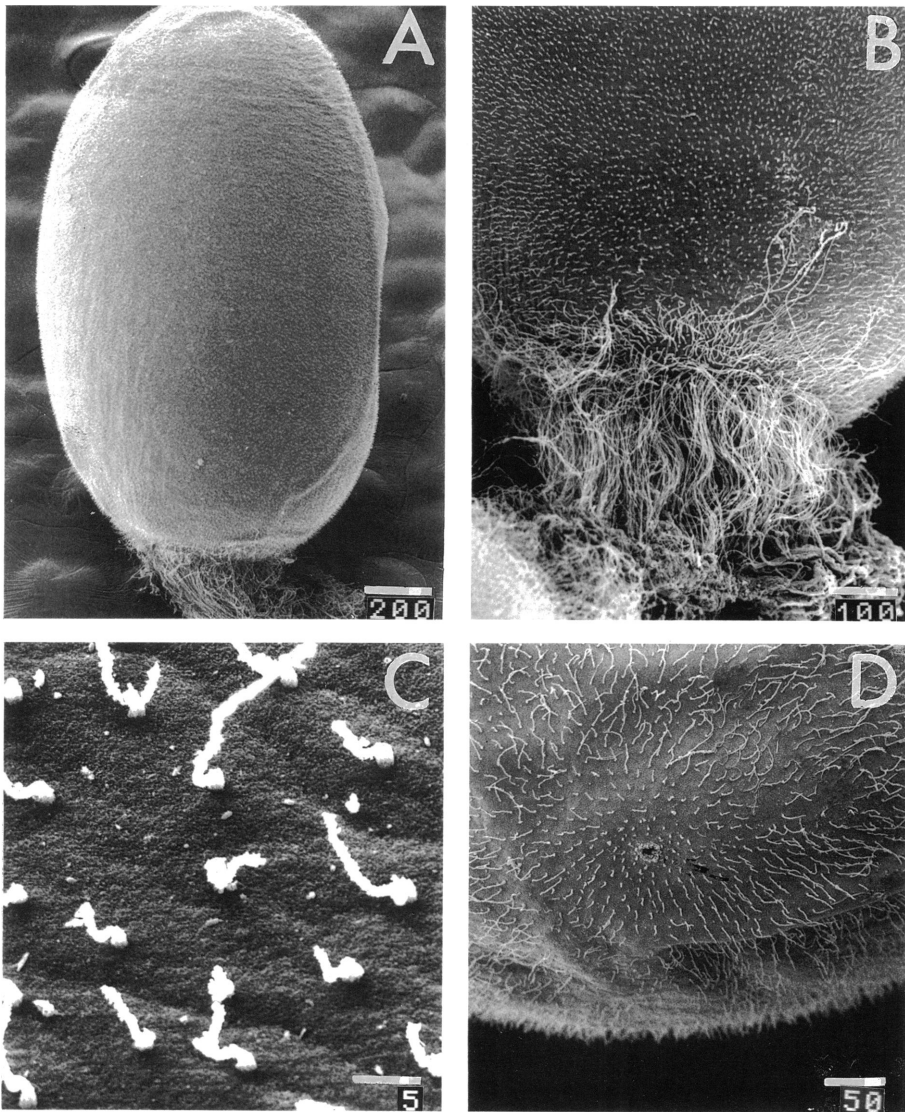


Fig. 3. Egg morphology of *Etroplus maculatus*. (A) Single egg; (B) filament tuft at pole opposite micropyle; (C) surface of chorion studded with short filaments; (D) micropylar pole. Scale bars are in micrometers.

along the longest dimension (fig. 3). Each egg is attached to the substrate by a thick filament tuft but, unlike the situation in the Pomacentridae, the etropline attachment tuft arises from the pole opposite the micropyle (fig. 3A, B, D). The remaining egg surface is nonadherent, but is studded with short filaments (fig. 3C). These surface filaments increase slightly in length around the micropyle (fig. 3D). No trace of an encasing mucus layer is present. Wickler's (1956a) light microscopy

study revealed a similar filament tuft attachment system in the Green Chromide, *Etroplus suratensis* (Bloch, 1790).

Madagascan Cichlidae: Eggs of the Madagascan cichlid, *Paratilapia polleni*, are slightly elliptical and measure 1.2 mm along the longest dimension (fig. 4). A tuft of elongate filaments arises from the pole opposite the micropyle (fig. 4A, B), very much as in the manner of the etropline cichlids. However, this filament tuft does not attach the

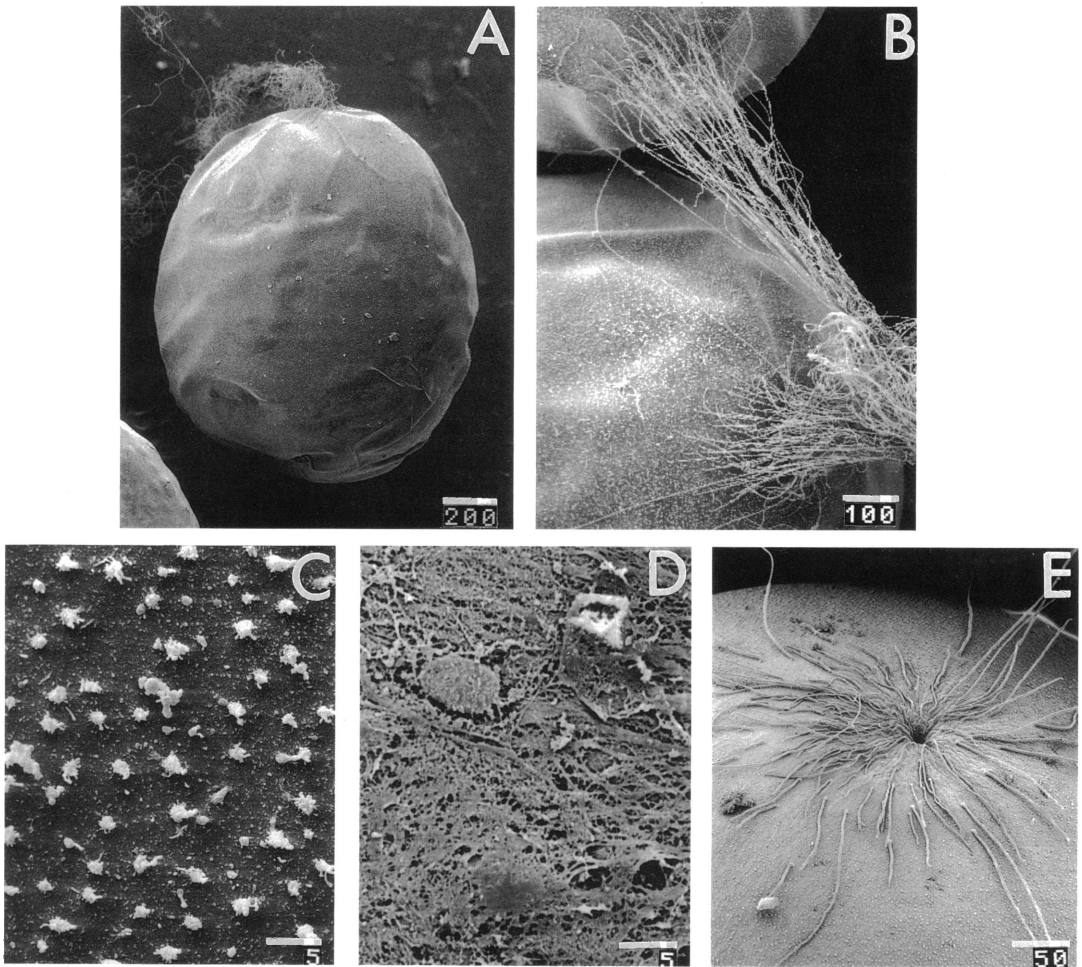


Fig. 4. Egg morphology of *Paratilapia polleni*. (A) Single egg; (B) filament tufts of two eggs entwined; (C) surface of chorion studded with extremely short filament stubs; (D) surface of chorion of an ovarian egg; (E) micropylar pole. Scale bars are in micrometers.

Paratilapia eggs to the substrate. Instead, the tufts of individual eggs entangle with one another resulting in a moveable egg mass (Stiassny and Gerstner, 1992; fig. 4B). The remaining egg surface is nonadherent and is studded with very short filaments which are little more than filament stubs (fig. 4C). The micropyle is ringed by somewhat more elongate filaments (fig. 4E). No trace of an encasing mucus layer is present.

Afro-Neotropical Cichlidae: In this large clade the eggs are typically somewhat elliptical and vary in size usually between 1.0 and 1.5 mm along the longest dimension (see also Wickler, 1956a; Noakes and Balon, 1982; fig.

5A). The eggs are extremely “sticky” and adhere, most often along their longitudinal axes, to the substrate by a distinctive mucus/filament layer (fig. 5B). At points of contact between eggs, egg to egg attachment is also facilitated by the glutinous mucus coating and fine filament threads (Kraft and Peters, 1963). No attachment tuft is present and the entire surface of the egg is covered with relatively elongate filaments (e.g., fig. 5C) which are encased in a dense mucus layer (fig. 5B). According to Kraft and Peters (1963), glutinous ovarian secretions adhere to the egg surface just prior to spawning. These highly adhesive eggs will attach wherever they contact the

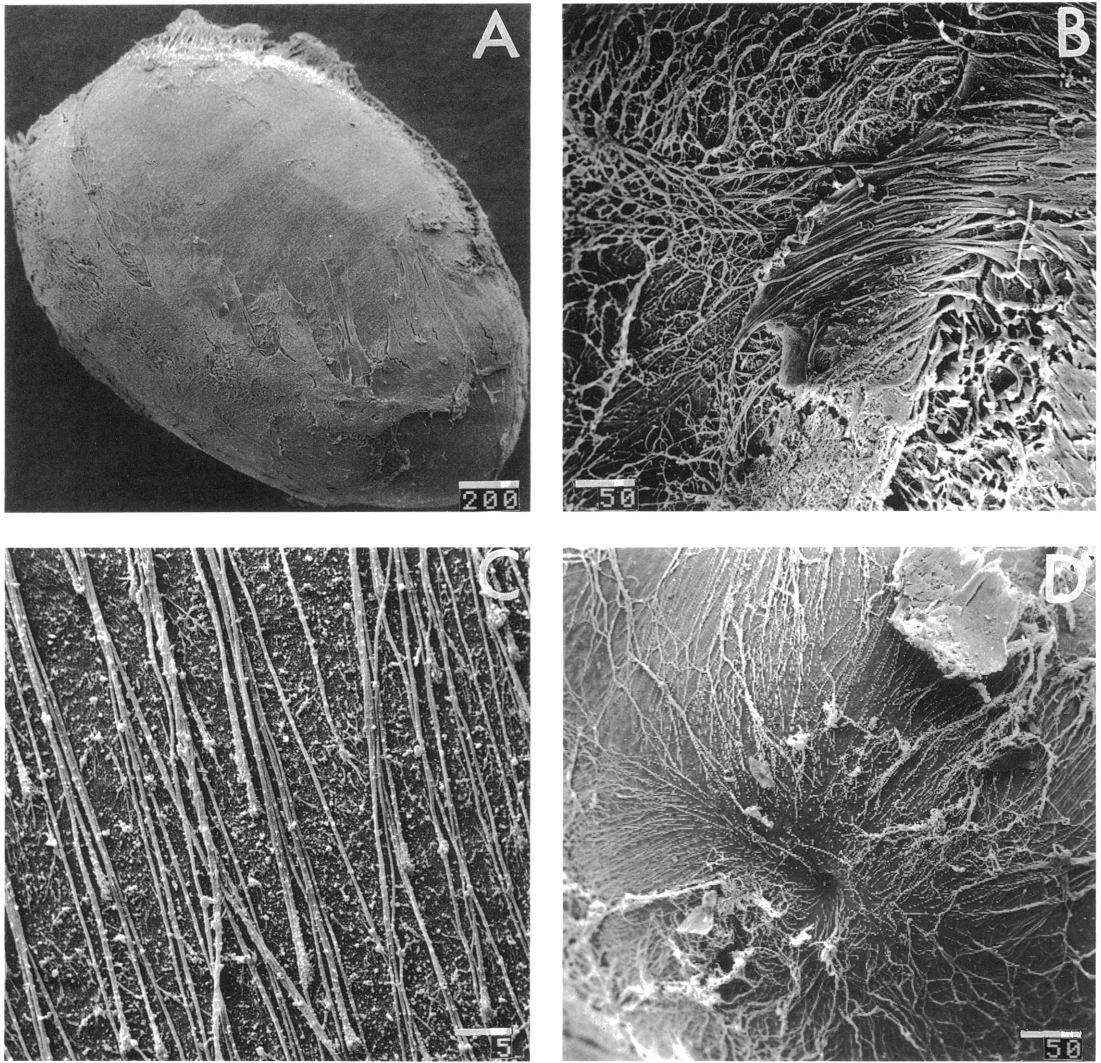


Fig. 5. Egg morphology of *Tilapia zillii*. (A) Single egg; (B) mucus layer and mucus-encrusted filaments on surface of egg; (C) surface of chorion covered with elongated filaments; (D) micropylar pole. Scale bars are in micrometers.

substrate or each other. When the eggs are removed from the substrate their point of attachment is usually evident as a smooth area from which most of the mucus and filaments are absent from the eggs and remain adherent to the substratum (fig. 5A).

Among the Neotropical and African taxa we examined, variation in egg structure is minimal and manifest only in the amount of mucus adherent to the eggs and in the length of the surface filaments. For example, the eggs of the African chromidotilapine *Pelvicachro-*

mis pulcher are extremely sticky and covered with a thicker layer of mucus and have longer surface filaments than those of other species. Clearly, our sampling of Neotropical and African lineages is limited; however, Wickler's (1956a) study incorporated three additional African species [*Hemichromis fasciatus* Peters, 1858, *Hemichromis bimaculatus* Gill, 1862, and *Nanochromis nudiceps* (Boulenger, 1899)] and nine additional Neotropical species [*Aequidens curviceps* [= *Laeticara curviceps* (Ahl, 1924)], *Aequidens portalegreensis*

[= *Cichlasoma portalegrensis* (Hensel, 1870)], *Apistogramma ramirezi* [= *Papiliochromis ramirezi* (Meyers and Harry, 1948)], *Cichlasoma severum* [= *Heros severus* Heckel, 1840], *Cichlasoma festivum* [= *Mesonauta festivus* (Heckel, 1840)], *Pterophyllum scalare* (Lichtenstein, 1832), *Symphysodon discus* Heckel, 1840, *Geophagus brasiliensis* (Quoy and Gaimaird, 1824), and *Geophagus cupido* [= *Biotodoma cupido* (Heckel, 1840)]. Within that sample, Wickler (1956a) also noted similar variation in the thickness of the mucus covering and in filament dimensions and their distribution over the egg surface. For example, *Symphysodon* and *Pterophyllum* apparently share a specialized configuration in which the mucus and surface filaments are arranged in a broad "belt" around the girth of the egg.

Interestingly, he also found that the eggs of one African chromidotilapine (*Nanochromis nudiiceps*) and one Neotropical geophagine (*Biotodoma cupido*) differed from the rest of the group. In these two species Wickler (1956a, 1956b) recorded the presence of a filament tuft by which the eggs are hung from the roof of caves. We have been unable to obtain spawned eggs of either of these two taxa, however Linke (1989) illustrated the eggs of an undescribed species of *Nanochromis*. In this species the eggs are suspended from the roof of the spawning tube by an adhesive filament up to 1.5 mm in length. According to Linke (1989: 105) the adhesive filament is composed of several individual fibers which enclose the egg in "a sort of net resembling an inverted parachute."

DISCUSSION

The monophyly of the family Cichlidae is well supported by data from a wide range of anatomical systems (Stiassny, 1981, Zihler, 1982; Gaemers, 1984) and Stiassny (1991) provided a recent discussion and summary of intrafamilial relationships. While her conclusions are tentative, at least at the more inclusive levels, a hypothesis of cichlid intrarelationship is now available, and variation in egg attachment systems can be explored within that phylogenetic framework (Stiassny, 1991: fig. 6).

With respect to the determination of the

polarity of variation in egg attachment systems within the Cichlidae, outgroup data from the Pomacentridae are equivocal. The apparent similarity of the filament tuft attachment system in pomacentrids and in the basal cichlid clades is probably spurious. In pomacentrids the attachment tuft arises from around the micropyle, while in etroplines and *Paratilapia* the attachment tuft originates from around the pole opposite the micropyle. Mooi (1990) noted similar variation in filament location with respect to the micropyle in the various demersal spawning "pseudochromoid" taxa he investigated. For example, in most pseudochromid subfamilies, filaments originate in the region opposite the micropyle, while in opistognathids, grammatids, and plesiopids, the filaments arise around the micropyle, as they do in apogonids and pomacentrids (Mooi, 1990). Eggs of two other demersal spawning percomorph families, the Gobiidae and Blenniidae, apparently also bear an attachment tuft or disc located around the micropyle (Lo Bianco, 1956; Wickler, 1956a, 1956b; Russell, 1976; Thresher, 1984). Wickler (1956a) suggested that the position of the micropyle in substrate-attached eggs is closely matched by spawning behavior. In fishes where the attachment tuft encircles the micropyle, the micropyle is functionally closed to sperm entry after attachment and fertilization and egg extrusion must be closely synchronized. In cichlids, fertilization can occur after egg attachment has taken place.

While outgroup data from the Pomacentridae do not permit conclusive assignment of polarity for variation within the Cichlidae, the presence of a polar tuft of filaments attaching the eggs to the substrate is not uncommon among demersal spawning percomorphs. However, as the homology of these systems in different families remains obscure (see also Mooi, 1990), we are unable to determine with any certainty the plesiomorphic cichlid attachment system. For the time being we are able to do little more than speculate that the ancestral cichlid egg attachment system was probably similar to that of the etropline cichlids (the "p"-type egg of Wickler, 1956a). The configuration in the Madagascan genus, *Paratilapia*, in which the polar attachment tuft of each egg entwines to form

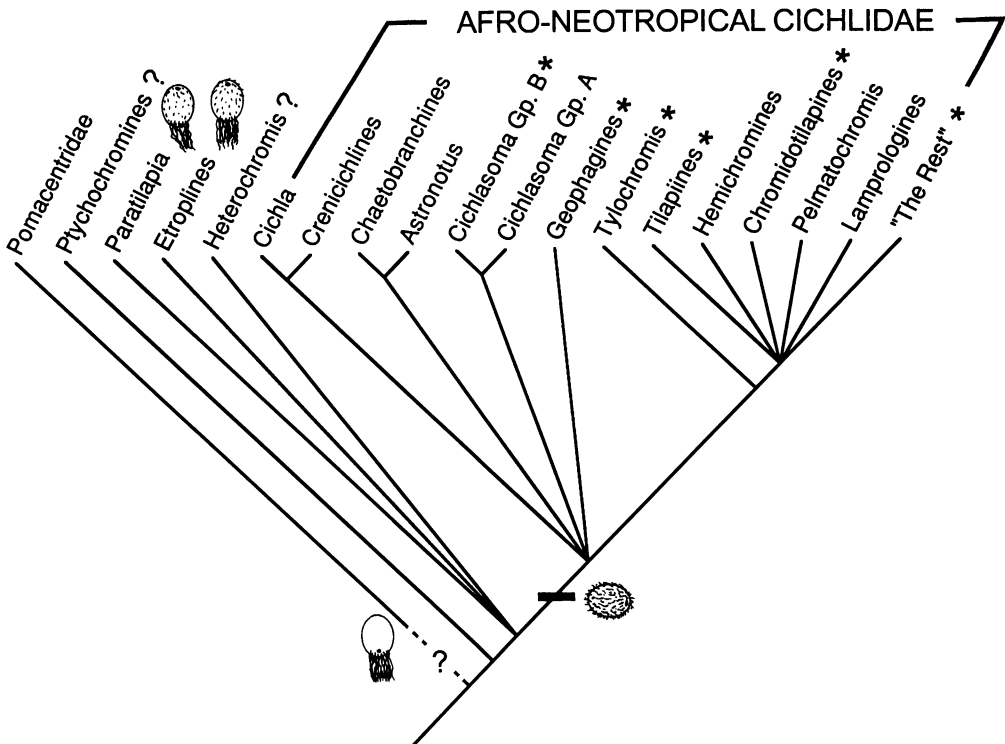


Fig. 6. Strict consensus tree of cichlid intrarelationships. Modified after Stiassny (1991). The asterisks indicate lineages in which the occurrence of mouthbrooding in some members has been documented. Cross-bar indicates hypothesized level of origin of the derived "l"-type egg. For a list of the genera included in each named lineage, and characters supporting the various clades, see Stiassny (1991).

an interconnected and mobile egg mass (Stiassny and Gerstner, 1992: fig. 4B), is a unique system within the family. It is of interest to note that a number of other perciform taxa have similar moveable egg masses. For example, Mooi (1990) described the egg balls of pseudochromids, plesiopids and opistognathids as being formed by the entanglement of filaments of adjacent eggs. In opistognathids the egg ball is formed of filament threads entangled to form braided ropelike strands (Mooi, 1990), a condition seemingly very similar to that observed in *Paratilapia*. However, as noted previously, the filaments in these taxa originate from around the micropyle rather than from the opposite pole as in *Paratilapia* and other basal cichlids. Despite the superficial similarities between the attachment system of *Paratilapia* and that of some of the "pseudochromoids" described by Mooi (1990) we interpret the system in *Paratilapia* as an autapomorphy of that ge-

nus, probably representing a modification of the tuft-to-substrate attachment system present in etroplines.

Further information on the attachment system of eggs in the remaining basal cichlid clades, in particular the ptychochromines and in the aberrant African genus, *Heterochromis*, would be of great interest (fig. 6). Although we have been unable to obtain spawned eggs from these basal cichlid taxa, de Rham (in litt.) reported that the eggs of *Ptychochromis oligacanthus* (Bleeker, 1868) are unlike those of *Paratilapia* and are attached individually to the substrate in a manner similar to that observed in the etropline genus *Paretroplus*. We anticipate that *Paretroplus*, like its sister genus *Etroplus* (Stiassny, 1991) will attach its nonadhesive eggs individually to the substrate via single filamentous attachment tufts.

The cichlid egg attachment system in which an adhesive mucus layer encases a filament-

covered egg (the "I"-type egg of Wickler, 1956a) is unique among percomorph taxa examined to date and as such is reasonably interpreted here as an innovation of the Afro-Neotropical Cichlidae (fig. 6). The apparent similarity between the eggs of the Neotropical geophagine *Biotodoma* and the African chromidotilapine *Nanochromis*, with those of the etroplines (Wickler, 1956a, 1956b) requires further investigation. However, until spawned eggs from these taxa become available for study, it is not possible to determine whether the similarities noted are more than superficial. Linke's (1989) description of the attachment tuft in *Nanochromis* as "a sort of net resembling an inverted parachute" certainly suggests nonhomology with the etropline tuft system. It is the case, however, that whatever the morphological similarities, parsimony requires an assumption of homoplasy for the egg attachment systems of *Biotodoma* and *Nanochromis* as both of these taxa are embedded within monophyletic Neotropical

and African subclades (Stiassny, 1991) in which the other clade members, and taxa basal to them, exhibit the derived mucus/filament adhesion system.

Prior to this study, Stiassny (1991) identified two derived anatomical characters supporting the monophyly of the Afro-Neotropical Cichlidae (excluding the Zairian genus, *Heterochromis*). The recognition of a derived egg morphology at this level of the cichlid tree adds further support for the monophyly of this extensive cichlid radiation (fig. 6).

The results of this preliminary study highlight the potential utility of egg ultrastructure variation in studies of cichlid phylogenetic intrarelationships. More data from additional taxa are necessary before the precise distribution, extent, and homology of variation in egg structure within the family can be determined, but our preliminary observations suggest that this system is potentially rich in phylogenetically informative variation.

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