

Evolution of Reproductive Behaviors in Percid Fishes

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Percid fishes are freshwater derivatives of a marine perciform, perhaps an anadromous serranid (McCully 1962; Collette & Banaresecu 1977). They appear to be relatively recent (i.e., most evolved during the Pliocene or later) but have undergone a tremendous radiation in North America, where they now comprise about 151 species in five genera. Among North American freshwater fishes, only minnows (Cyprinidae), with about 225 species, are more diverse. Together, percids and minnows constitute almost half of the temperate North American freshwater fish fauna. In addition to being diverse groups, these fishes often occur in large populations and are important in determining the ecological characteristics of North American streams and lakes. Elsewhere, percids are present only in temperate Eurasia, where there are 14 species in six genera. Two genera, *Stizostedion* and *Perca*, occur in both North America and Eurasia (Table 1).

Several reasons exist for studying the reproductive habits of organisms. Among these are that (1) reproductive habits are inherently interesting; (2) reproduction is that activity toward which all life processes ultimately are directed and, therefore, understanding its variations is important if we wish to protect or manage species; and (3) reproductive characteristics provide information useful in estimating evolutionary (phylogenetic) history. Percids are especially interesting in this last regard because, as a recent and diverse group, transitions among their various types of reproductive behaviors remain evident today. Reconstructing the evolutionary history of reproductive behav-

iors of percids results in a better understanding of the relationships among species.

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TYPES OF REPRODUCTIVE BEHAVIORS

Accompanying the evolution of a large diversity of percids has been the evolution of a variety of reproductive

Table 1. — Percid taxa and their distributions.

Taxa	Number of Species	Distribution
Etheostomatinae		
Luciopercini		
<i>Stizostedion</i>	5	Holarctic
Etheostomatini		
<i>Percina</i>	ca. 38	Nearctic
<i>Ammocrypta</i>	7	Nearctic
<i>Rhinostoma</i>	ca. 103	Nearctic
Romanichthyini		
<i>Zingel</i>	3	Palaearctic
<i>Romanichthys</i>	1	Palaearctic
Percinae		
<i>Percarina</i>	1	Palaearctic
<i>Perca</i>	3	Holarctic
<i>Gymnocephalus</i>	4	Palaearctic

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strategies, and in the most advanced states, parental care of the eggs. Among the 76 species of percids for which spawning behaviors are known, six types of behavior are recognized, some of which can be subdivided further, as discussed below. These six types, named for the mode of egg-deposition, are termed (1) broadcasting, (2) stranding, (3) burying, (4) attaching, (5) clumping, and (6) clustering.

Broadcasting

Broadcasting is the primitive mode of reproductive behavior among fishes and is retained in primitive percids. Eggs and sperm are discharged in large numbers, often in a frenzy of activity involving several individuals. A coarse substrate, usually composed of rocks or plants, is chosen to provide crevices and other hiding places for the fertilized eggs. In its most primitive state, broadcasting makes no other behavioral provisions for the eggs, either before or after spawning.

Stizostedion vitreum (Mitchill) and *S. canadense* (Smith) broadcast their eggs between March and June in streams and in areas of lakes with sufficient water movement to ventilate the eggs (Eschmeyer 1950; Nelson 1968). Spawning usually occurs in the evening (Ellis & Giles 1965) or at night (Eschmeyer 1950), and territories are not established (Ellis & Giles 1965).

Courtship consists of an individual of either sex approaching another individual from behind or from the side and pushing against it. The approached fish either withdraws or, if sexually responsive, makes quick darts forward and upward. This increased activity often elicits the attention of other individuals, and soon a compact group forms, which periodically rushes forward and upward. Eggs and sperm are released during a forward rush of activity (Ellis & Giles 1965). Spawning groups vary from two individuals to several individuals of both sexes (Fig. 1). Eggs are adhesive for a few hours, and they may adhere to rocks or plants for a short time; ultimately they fall to the bottom and into interspaces among the components of the substrate (Fig. 2), where they presumably are less exposed to predation (Colby et al. 1979). *S. marinum* (Cuvier) and *Percarina demidoffi* Nordmann appear to exhibit similar, perhaps identical, behavior (Berg 1949) although descriptions of spawning are vague.

Stizostedion lucioperca (Linnaeus) exhibits a modification of this behavior in that eggs and sperm are broadcast over a circular pit previously constructed by the male. The pit is lined with gravel, shells, or plant material (often roots) and is guarded before and after spawning by the male, who also fans the fertilized eggs (Kryzhanovshy et al. 1953). Mating in this more special-

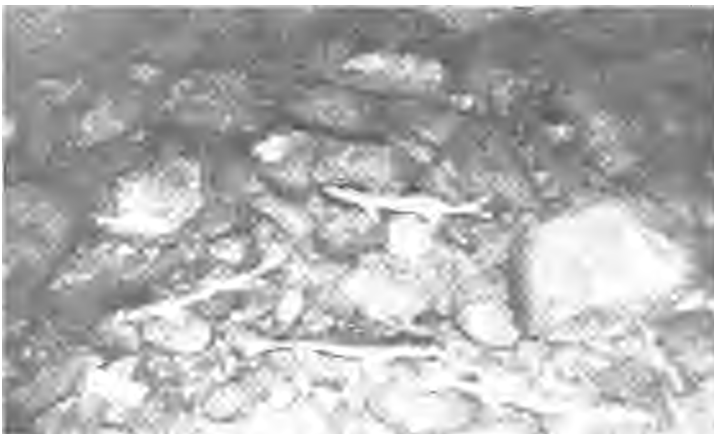
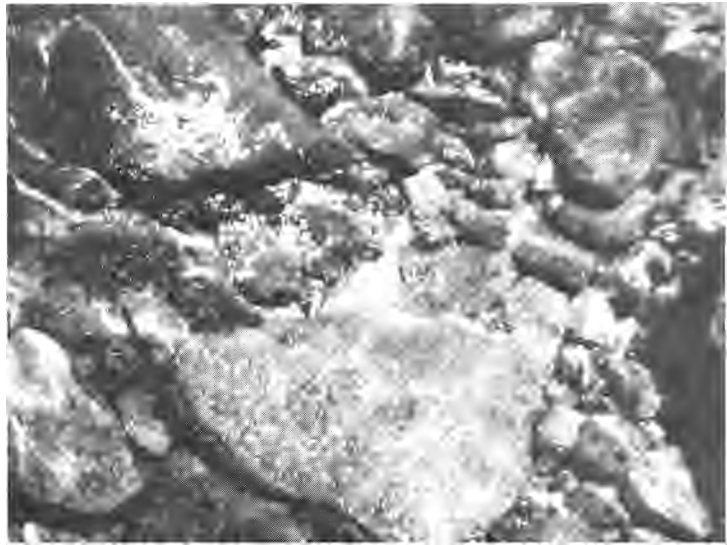


Fig. 1. — *Stizostedion vitreum* congregated on spawning grounds at Lake Gogebic, Michigan, 4 May 1948. From Eschmeyer (1950). (Photo provided by the Institute for Fisheries Research, Fisheries Division, Michigan Department of Natural Resources.)

Fig. 2. — Eggs of *Stizostedion vitreum* on spawning ground at Lake Gogebic, Michigan, 12 May 1948. From Eschmeyer (1950). (Photo provided by the Institute for Fisheries Research, Fisheries Division, Michigan Department of Natural Resources.)



ized, nesting broadcaster may be monogamous (Deedler & Willemsen 1964).

Broadcasters

Group A. Spawn over open substrate
Stizostedion vitreum (Eschmeyer 1950)
S. canadense (Nelson 1968)
S. marinum (Berg 1949)
Percarina demidoffi (Berg 1949)

Group B. Spawn over male-constructed pit
S. lucioperca (Kryzhanovshy et al. 1953)

Stranding

Stranders have the unique habit of encasing their eggs in long gelatinous strands. A ripe female is followed by several males through beds of vegetation (sometimes tree roots or debris) in slowly flowing or standing water. The males release sperm as she extrudes a convoluted egg strand (Worth 1892; Treasurer 1981). The strand is gelatinous, transparent, hollow, and arranged in bellowslike transverse folds. When first laid, the shape of the egg mass is similar to that of the ovarian cavity (Fig. 3), but eventually it stretches (Fig. 4) and may reach a length of 2.4 m and a width of 10 cm (Hardy 1978). Egg stranding is known to occur in *Perca flavescens* (Mitchill) (Worth 1892; Har-

rington 1947; Hergenrader 1969) and *P. fluviatilis* Linnaeus (Seeley 1886:27; Wheeler 1969:322; Treasurer 1981). It also may occur in *Gymnocephalus cernua* (Linnaeus), as described by Seeley (1886:36) and Wheeler (1969:321), although some authors (e.g., Nikol'skii 1961:369; Muss 1978:161) discuss spawning in *Gymnocephalus* without mentioning egg strands.

Stranders

Gymnocephalus cernua (Seeley 1886)
Perca flavescens (Worth 1892)
P. fluviatilis (Seeley 1886)

Stranding is probably a direct derivative of broadcasting. The eggs become encased in gelatin in the ovaries and when emitted remain part of a cohesive mass rather than becoming independently scattered. The derivation of stranding from percid spawning behaviors other than broadcasting is less likely, because each is specialized in a way that seems to preclude the evolution of stranding.

For a female to put all of her eggs in one highly visible basket, which stranding certainly does, and then abandon them would seem to be a strategy quickly selected against unless the eggs somehow are protected intrin-

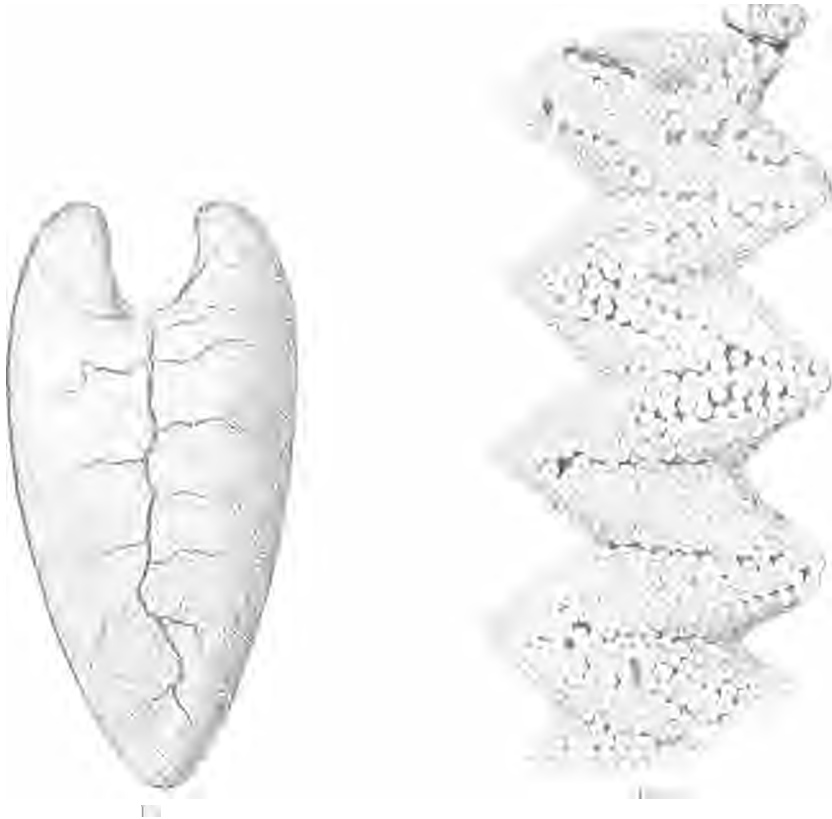


Fig. 3. — Eggs of *Perca flavescens* encased in ovaries (left) and in gelatinous strands after being spawned (right). From Worth (1892).

sically against predation and disease. Having toxic, or at least distasteful, eggs would be an obvious strategy, but observations by Seeley (1886:27) of predation by "birds and various fishes" on perch eggs put this method in doubt. Treasurer (1983) reported low mortality of perch eggs and attributed it to the improved ventilation and midwater position (thereby avoiding siltation) of the strand.

Burying

Egg-burying behavior is similar to broadcasting except for the important distinction that the release of eggs occurs just below, rather than above, the

surface of the substrate. In egg burying the female works her body partially below the surface of the substrate and, with her genital papilla buried and a male mounted on her back, expels eggs (Fig. 5). The substrates usually used are loose gravel, sand, or mixed gravel and sand. Egg burying is characteristic of many darters, including all species of *Percina* for which spawning observations have been published and many species of *Etheostoma*. Some egg buriers are thought to be territorial (Winn 1958), but other than the indirect protection associated with territoriality, eggs receive no parental care. Among darters, burying represents the primi-

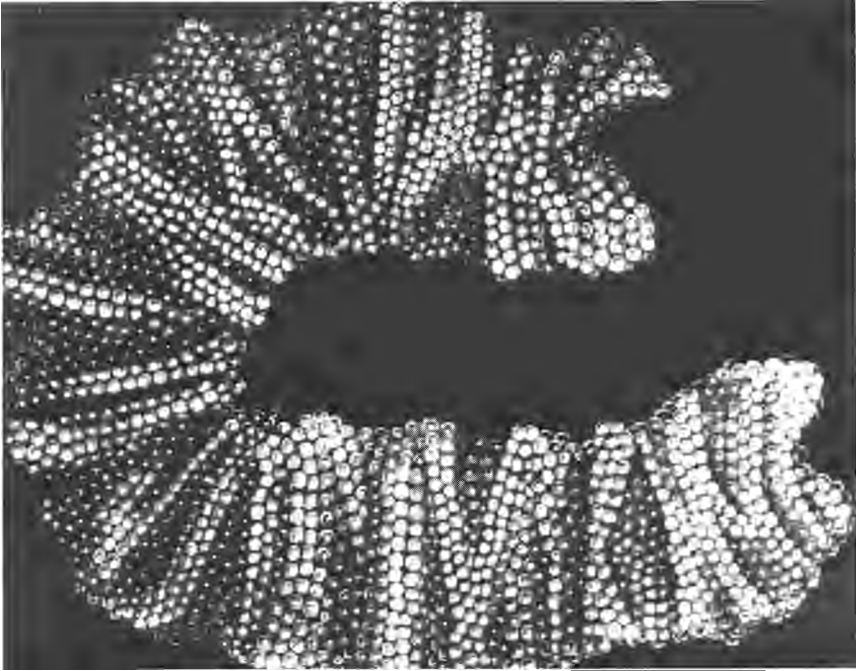


Fig. 4. — Egg strand of *Perca flavescens*. From Pearse & Achtenberg (1921).

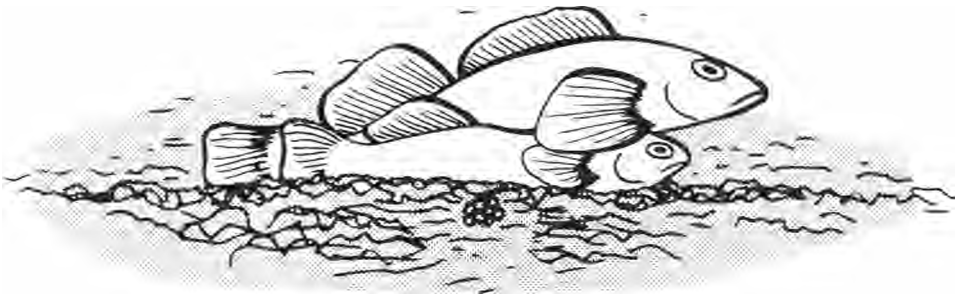
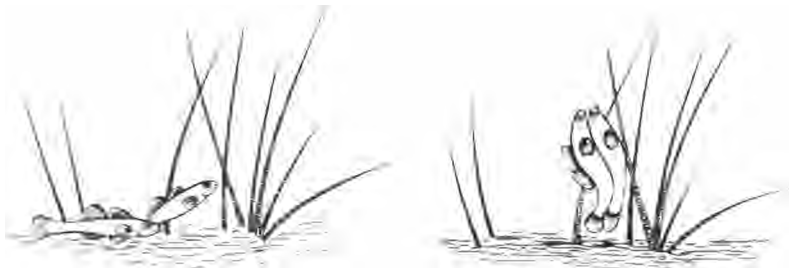


Fig. 5. — Egg-burying behavior. With a male mounted on her back, a partially buried female deposits *eggs* below the surface of the substrate. Eggs are fertilized as they are laid and then are abandoned by both parents.



A

Fig. 6. — Egg-attaching behavior. (A) The female selects the site of egg deposition. (B) The male mounts the female and releases sperm as eggs are attached to plants. The eggs subsequently are abandoned.

tive form of reproductive behavior; among percids, it represents an egg-hiding modification of broadcasting behavior.

Buriers

- Percina (Alvordius) maculata* (Petravicz 1938)
P. (A.) peltata (New 1966)
P. (A.) notogramma (Loos & Woolcott 1969)
P. (Ericosma) evides (Page et al. 1982)
P. (Hypohomus) aurantiaca (Howell 1971)
P. (Cottogaster) copelandi (Winn 1953)
P. (Percina) caprodes (Winn 1958)
Etheostoma (Litocara) nianguae (Pflieger 1978)
E. (Psychromaster) tuscumbia (Koch 1978)
E. (Etheostoma) tetrazonum (Pflieger 1978)
E. (E.) variatum (May 1969)
E. (Doration) stigmaeum (Winn 1958)
E. (Nothonotus) juliae (James 1983)
E. (N) rufilineatum (Stiles 1972)
E. (N) camurum (Mount 1959)
E. (N) bellum (W. D. Voiers personal communication)
E. (N) tippecanoe (Trautman 1981)
E. (Fuscatelum) parvipinne (B. M. Burr personal communication)
E. (Ozarka) cragini (Distler 1972)
E. (Oligocephalus) spectabile (Winn 1958)
E. (O.) caeruleum (Winn 1958)
E. (O.) radiosum (Scalet 1973)
E. (O.) swaini (Ruple et al. 1984)

Attaching

Attaching behavior is a derived behavior known among percids only in the genus *Etheostoma*. The female selects the site of egg deposition (presumably in some species within a male's territory), typically a plant or large rock, and with the male following her, elevates to the site. As she does so, the male follows and mounts, the two vibrate, and eggs and sperm are released (Fig. 6). Usually one to three adhesive eggs are released during each spawning act and are pushed by the female onto a plant, rock, or other object. At-

taching eggs to plants seems to involve behavior identical to that of attaching eggs to rocks; the substrate used is that which is readily available in the habitat. Eggs are abandoned and receive no direct parental care, although as in some burying species, territorial behavior may provide some protection.

Attachers

- Etheostoma (Etheostoma) blennioides* (Fahy 1954)
E. (Nanostoma) zonale (Winn 1958)
E. (N) coosae (O'Neil 1981)
E. (N) baileyi (Page personal observation)
E. (N) simoterum (Page & Mayden 1981)
E. (N) duryi (Page et al. 1982)
E. (N) barrenense (Winn 1958)
E. (N) rafinesquei (Winn 1958)
E. (N) sp. (Red Snubnose) (B. M. Burr personal communication)
E. (N) sp. (Lowland Snubnose) (B. M. Burr personal communication)
E. (Ioa) vitreum (Winn & Picciolo 1960)
E. (Vaillantia) chlorosomum (Page et al. 1982)
E. (Belophlox) okaloosae (Collette & Yerger 1962)
E. (Villora) edwini (Williams 1976)
E. (Ozarka) boschungii (Boschung 1979)
E. (O.) trisella (W. C. Starnes personal communication)
E. (Oligocephalus) lepidum (Strawn 1956)
E. (O.) asprigene (Page et al. 1982)
E. (O.) grahami (Strawn 1956)
E. (O.) ditrema (Seesock et al. 1978)
E. (Boleichthys) exile (Winn 1958)
E. (B.) fusiforme (Fletcher 1957)
E. (B.) gracile (Braasch & Smith 1967)
E. (B.) proeliare (Burr & Page 1978)
E. (B.) fonticola (Schenck & Whiteside 1977)
E. (B.) microperca (Burr & Page 1979)

The presence of both egg-burying and egg-attaching species within three subgenera of *Etheostoma* (*Etheostoma*, *Ozarka*, and *Oligocephalus*) suggests that egg attaching is derived directly from egg burying and has arisen independently in several unrelated groups

of darters. In fact, at least two species which usually attach their eggs have been observed to bury eggs under certain conditions (Petravicz 1936; Page & Mayden 1981). Egg attaching apparently also has arisen independently among species within subgenera; its distribution among species of Ozarka is inconsistent with the distribution of morphological synapomorphies (Fig. 7).

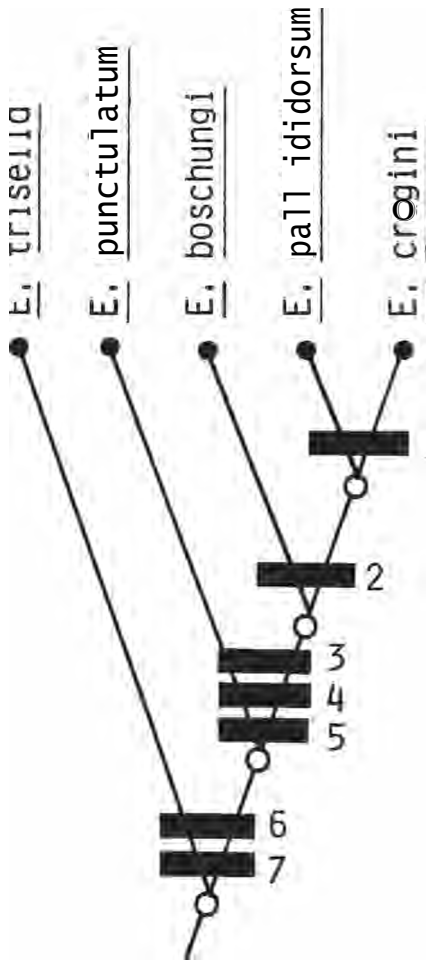


Fig. 7. — Hypothesized phylogenetic relationships among species of Ozarka. Synapomorphies (black rectangles) are (1) 25 or fewer pored lateral-line scales, (2) seven infraorbital pores, (3) interrupted supratemporal canal, (4) incomplete lateral line, (5) bright orange margin on the first dorsal fin, (6) bright orange venter on the breeding male, (7) heavily mottled body. Synapomorphous character states were identified by outgroup comparisons to *Etheostoma* (*Oligocephalus*) *whipplei* and *E. (Belophlox)* *fricksium*.

E. cragini Gilbert buries its eggs, but *E. boschungi* Wall and Williams and *E. trisella* Bailey and Richards attach their eggs to plants (Boschung 1979; W. C. Starnes personal communication). If the phylogeny based on morphology (Fig. 7) is accurate, *E. boschungi* and *E. trisella* must have evolved egg-attaching behavior independently of one another. The fact that *E. trisella* attaches its eggs to vegetation in headwaters (even seepages) (W. C. Starnes, personal communication) was a major factor in placing it in the subgenus Ozarka with *E. boschungi*, which has essentially the same spawning requirements and behavior (Boschung 1979; Williams & Robison 1980). Independent derivation of this behavior in the two species weakens the argument for their close relationship to one another.

The breeding behaviors of too few species of the subgenus *Etheostoma* are known to compare their distributions with a phylogeny based on morphology. However, it is interesting that the two known buriers [*E. variatum* Kirtland and *E. tetrazonum* (Hubbs and Black)] are in the *E. variatum* species group [including also *E. euzonum* (Hubbs and Black), *E. osburni* (Hubbs and Trautman), and *E. kanawhae* (Raney)], and the only known attacher, *E. blennioides* Rafinesque, is a member of the second major lineage [including *E. rupestre* Gilbert and Swain, *E. inscriptum* (Jordan and Brayton), *E. thalassinum* (Jordan and Brayton), *E. swannanoa* Jordan and Evermann, *E. blennius* Gilbert and Swain, and *E. histrio* Jordan and Gilbert], all of which eventually may be shown to be egg attachers. *E. sellare* (Radcliffe and Welsh), the sole member of the third major lineage in the subgenus, is a highly distinctive (Knapp 1976; Page 1981) species on the verge of extinction. It has a flattened genital papilla (Knapp 1976) similar to those of egg-clumping and egg-clustering species (Page & Swofford 1984). If *E. sellare* is found to belong to one of these latter behavioral groups, it could be of major significance in efforts to protect

the species from extinction. Suitable spawning sites may be a limiting factor for the only extant population of *E. sellare*.

Clumping

Egg clumping was first reported in 1939 for *E. maculatum* Kirtland (Raney & Lachner 1939) but was unreported for other darters until observed in 1981 in *E. aquali* Williams and Etnier and *E. microlepidum* Raney and Zorach (Page et al. 1982). In preparation for spawning, the male selects a cavity under a large rock as a territory and future nesting site. Ultimately, a female swims into the cavity being guarded by the male, wedges herself into the interface between the stone and the gravel substrate beneath the stone, and deposits eggs. As she does so, they are fertilized by the male. After spawning, the female leaves, and the male remains to guard the clump of eggs (Fig. 8). The adhesive eggs adhere to both the nest stone and the underlying substrate material; if a stone is lifted from the water, a clump of adhesive eggs remains attached to it (Fig. 9).

Egg clumping is known only among species of the subgenus *Nothonotus* of *Etheostoma*.

Clumpers

Etheostoma (Nothonotus) maculatum
(Raney & Lachner 1939)

E. (N) aquali (Page et al. 1982)

E. (N) microlepidum (Page et al. 1982)

Egg clumping is almost certainly a direct derivative of the egg-burying behavior (Page et al. 1982) characteristic of other species of *Nothonotus* [known in *E. juliae* Meek, *E. rufilineatum* (Cope), *E. camurum* (Cope), and *E. tippecanoe* Jordan and Evermann]. The transition from burying in some species of *Nothonotus* to clumping in others requires only that the male establish a territory beneath a stone and that a female deposit her eggs in the interface area between the stone and the underlying substrate.

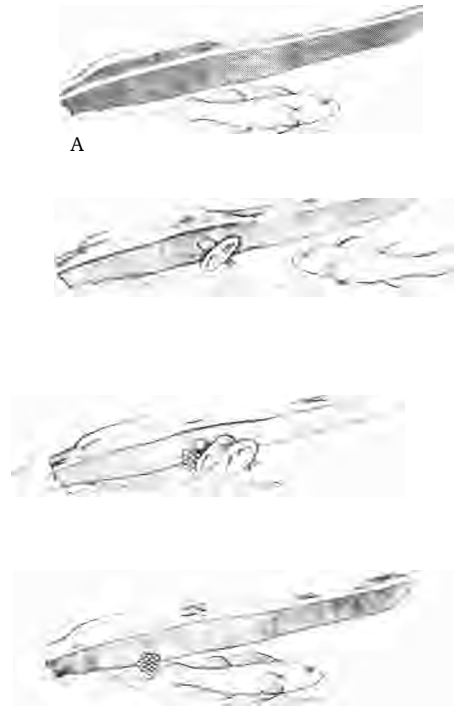


Fig. 8. — Egg-clumping behavior. (A) The male establishes a territory centered under a large stone. (B) The female enters the territory and wedges herself between the stone and the underlying substrate. (C) The male positions himself next to the female and fertilizes eggs as they are released by the female. (D) The male remains to guard the clump of eggs.

With 14 described and 1 undescribed species, the subgenus *Nothonotus* is one of the two largest subgenera of darters, and intrasubgeneric relationships are unclear. The egg-clumping species are members of the *E. maculatum* lineage within the subgenus (Fig. 10), but it is unknown at present at what point on the lineage egg clumping arose. *E. rufilineatum* has been observed to bury its eggs (Stiles 1972), and although spawning was not observed, Bryant (1979) felt confident that *E. acuticeps* Bailey also buries its eggs. Spawning behavior data on *E. rubrum* Raney and Suttkus and *E. moorei* Raney and Suttkus should pinpoint the origin of egg clumping in *Nothonotus*.

Although *Etheostoma sanguifluum* (Cope) has been considered a subspecies of *E. maculatum* Kirtland by some



Fig. 9. — A male *Etheostoma microlepidum* and his clump of eggs on the underside of a stone removed from East Fork Stones River, Rutherford County, Tennessee, on 6 May 1981. The male was guarding the eggs prior to their removal from the stream.

authors (Zorach & Raney 1967; Williams & Etnier 1978), the distinctive pigmentation of the first dorsal fin (especially the bright red spots at the front and rear of the fin) of the male of *E. sanguifluum* is shared with *E. aquali* Williams and Etnier but is absent in all other species of the subgenus *Nothonotus*. Recognition of a closer relationship between *E. sanguifluum* and *E. aquali*, than of either taxon to *E. maculatum* (Fig. 10), requires the elevation of *E. sanguifluum* to specific status. The form heretofore known as *E. maculatum vulneratum* (Cope) also possesses the distinctive dorsal fin pigmentation and should be named *E. sanguifluum vulneratum* (Cope).

Clustering

The first report of egg-clustering behavior in darters was by Seal in 1892 in a report on *E. olmstedii* Storer. Since then it has been documented in an

additional 15 species in the subgenera *Boleosoma* and *Catmotus* of *Etheostoma* listed below.

The male of an egg-clustering species establishes a territory centered about the cavity under a large (usually flat) stone. The cavity and the underside of the stone are cleared of silt and debris by fin-wagging activities of the male. A ripe female enters the cavity and, following courting by the male, rolls to one side and, once inverted, rises and lays eggs on the underside of the stone. The male inverts and fertilizes the eggs, which are arranged by the female in a single-layer cluster (i.e., eggs are rarely laid on top of one another) on the stone. The female leaves; other females sequentially may add eggs to the nest. The male remains and guards the eggs to hatching (Fig. 11). In species of *Boleosoma*, a log may be substituted for a stone.

Egg clustering is similar to egg clumping in that eggs are amassed under a stone and guarded by the male.

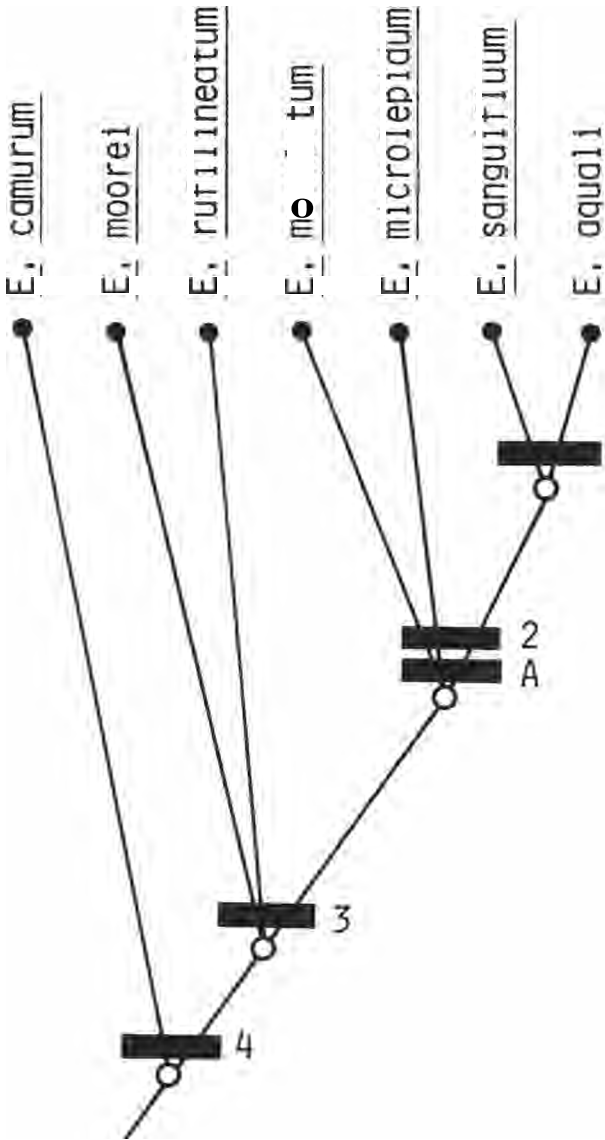


Fig. 10. - Hypothesized phylogenetic relationships among some of the species of *Nothonotus*. Synapomorphies (black rectangles) are (1) dorsal fin with two red spots at the front, one red spot at the rear, (2) haloed red spots on the side of the male, (A) egg-clumping behavior, (3) black spots on fins of the female, and (4) red spots on the side of the body. Synapomorphous Character states were identified by outgroup comparisons to *Etheostoma* (*Nothonotus*) *tippecano* E. (N.) *julia* and *E. (N.) acuticeps*.

It is dissimilar, and appears to be "perfected" in that every egg is exposed and can be tended to individually by the guarding male (Fig. 12).

The derivation of egg clustering from darters which attach their eggs to stones requires only that (1) eggs are laid on the underside rather than the tops and sides of rocks, (2) eggs are clustered in close proximity to one another rather than distributed over a broad area, and (3) the male remains and guards the eggs. Laying eggs on the underside rather than on more ex-

posed areas of rocks probably exposes them to fewer predators although some potential predators, e.g., crayfishes and caddisflies (Brigham et al. 1982:9.6), are common under rocks. Once the eggs under the stone are guarded by the male, the survival rate undoubtedly increases dramatically, and such a concentration of eggs is quickly selected for.

Variation in behavior divides egg-clustering species into three groups: (A) those in which both male and female invert only long enough to lay

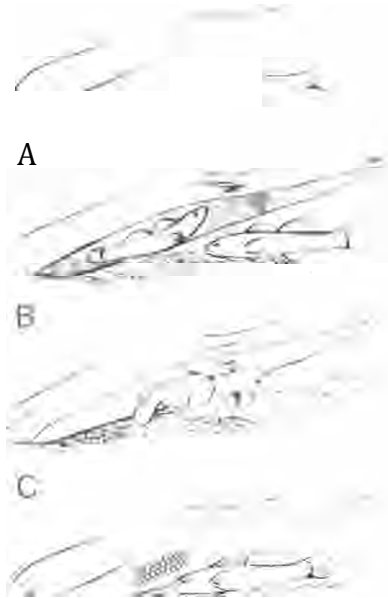


Fig. 11. — Egg-clustering behavior. (A) The male establishes a territory centered under a large stone. (B) The female enters the territory and selects a site for egg deposition on the underside of the stone. (C) The female inverts, rises, and deposits eggs on the stone; as she does so, the male follows and fertilizes the eggs. (D) The male remains to guard the cluster of eggs.

and fertilize each release of eggs (usually 1-5 eggs); (B) those in which the female, once inverted, remains inverted for a prolonged period of egg laying (several minutes to a few hours) but the male only briefly (a few seconds) and periodically inverts; and (C) those in which both male and female remain inverted for an extended period. Obviously, group B represents an advancement over group A, and group C represents an advancement over group B. Group A includes the primitive species of the subgenus *Catonotus*; B, the advanced species of *Catonotus* (Page 1975b); and group C, species of the subgenus *Boleosoma*. Winn (1958) distinguished between behavior types B and C.

Clusterers

Group A. Female and male briefly invert
E. (Catonotus) squamiceps (Page 1974)
E. (C.) olivaceum (Page 1980)
E. (C.) neopterum (Page & Mayden 1979)a

Group B. Female only has prolonged inversion

E. (C.) flabellare (Winn 1958)
E. (C.) sp. = Duskytail darter (Etnier personal communication)a
E. (C.) kennicotti (Page 1975a)
E. (C.) obeyense (Page et al. 1981)a
E. (C.) virgatum (Kornman 1980)a
E. (C.) smithi (Page & Burr 1976)
E. (C.) striatulum (Page 1980)a
E. (C.) barbouri (Page et al. 1982)a

Group C. Female and male have prolonged inversions

E. (Boleosoma) olmstedii (Atz 1940)
E. (B.) nigrum (Winn 1958)a
E. (B.) podostemone (Jenkins 1980)a
E. (B.) perlongum (Lindquist et al. 1981)
E. (B.) longimanum (Page et al 1981)a

^a Although known to be a clusterer, group assignment is predicted from the behavior of closest relatives and is not based on actual observations.

The phylogenetic sequence of breeding behaviors among *Catonotus* is concordant with a phylogeny of the subgenus based on morphology in that three synapomorphies unite the *E. flabellare* Rafinesque lineage as advanced and apart from the *E. squamiceps* Jordan species group (Fig. 13).

Both *Catonotus* and *Boleosoma* must have evolved from egg-attaching precursors. Although egg clustering itself could be considered a synapomorphy uniting these two subgenera, they differ markedly in their morphology and do not appear to be sister groups (Page 1981). *Boleosoma* shares derived characteristics with other groups of *Etheostoma* (Fig. 14) and almost certainly had an origin independent from that of *Catonotus*. It appears to be most closely related to K (*Loa*) *vitreum* (Cope), an

egg-attaching species. The sister-group of *Catonotus* should first be sought among egg-attaching species; however, if the attaching precursor now is extinct, an egg-burying group may be the closest extant relative.

EVOLUTION OF PERCID SPAWNING BEHAVIORS

Combining the evolutionary sequences discussed above produces the phyl-



Fig. 12. — Male *Etkeostoma neopteron* and his cluster of eggs on the underside of a stone removed from Birdsong Creek, Benton County, Tennessee, on 15 April 1978. The male was guarding the eggs prior to their removal from the stream.

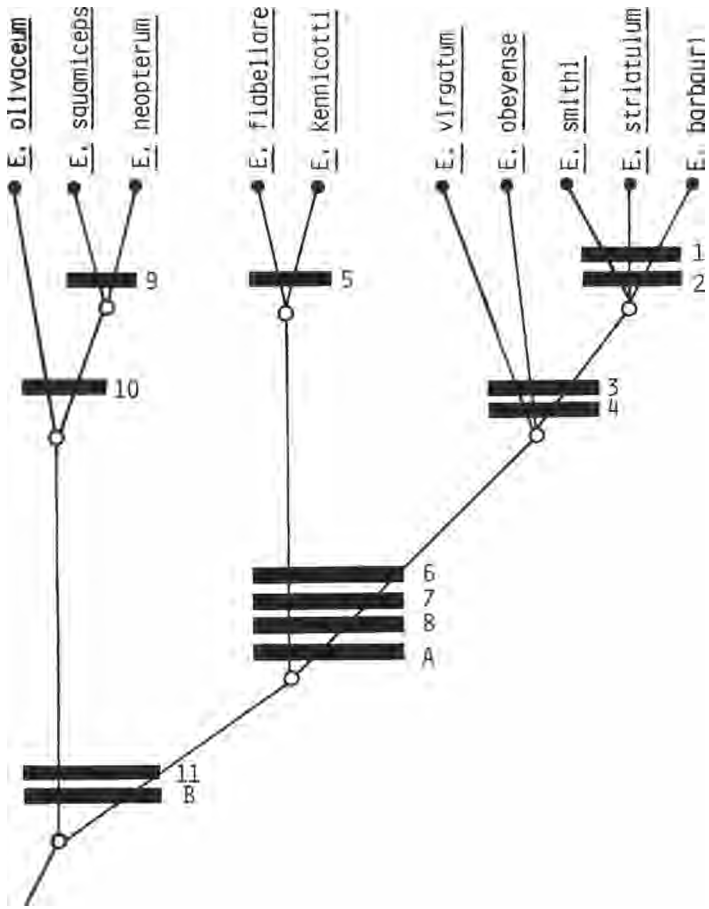


Fig. 13. — Hypothesized phylogenetic relationships among species of *Catonotus*. Synapomorphies (black rectangles) are (1) four infraorbital pores, (2) maximum standard length less than 50 mm, (3) bar pattern on the cheek, (4) blue-edged red fins on the breeding male, (5) large gold knobs on the first dorsal fin, (6) nape unscaled, (7) prepectoral area unscaled, (8) infraorbital canal widely interrupted, (A) type B clustering behavior (the female remains inverted during spawning), (9) infraorbital canal narrowly interrupted, (10) caudal peduncle with three black spots, (11) broad, flat nonbifurcate genital papilla on the female, (B) egg-clustering behavior. Synapomorphous character states were identified by outgroup comparisons to *Etheostoma* (*Psychromaster*) *tuscumbia* and *E. (Fuscateum)* *parvipinne*.

ogeny depicted in Fig. 15. There appear to be no reasonable alternatives to any of the transitions depicted. However, each type of behavior could have arisen, and in some instances almost certainly did arise, more than once. For example, although gamma clustering results from a modification of beta clustering, it does not mean that the only extant gamma-clustering group of darters (*Boleosoma*) arose from the only extant beta-clustering group (i.e., the *flabellare*

group of *Catonotus*); rather, all alpha and beta precursors of *Boleosoma* are extinct.

The phylogeny (Fig. 15) supports the contention that darters, the most primitive of which are buriers, are derivatives, and probably the sister group, of *Stizostedion*. This position disagrees with the conclusions of Collette (1963) based on osteology, but it agrees with those of Hubbs (1971) based on the survival of intergroup percid

hybrids. A classification necessitates the recognition of the subfamilies *E* (containing the tribes *L*, *E*, and *R*) and *P* (Table 1).

Each step in the evolution of spawning behaviors represents, for the species in which it evolved, a survival advantage over its precursor. Pit broadcasting concentrates the eggs in an area subsequently guarded by the male

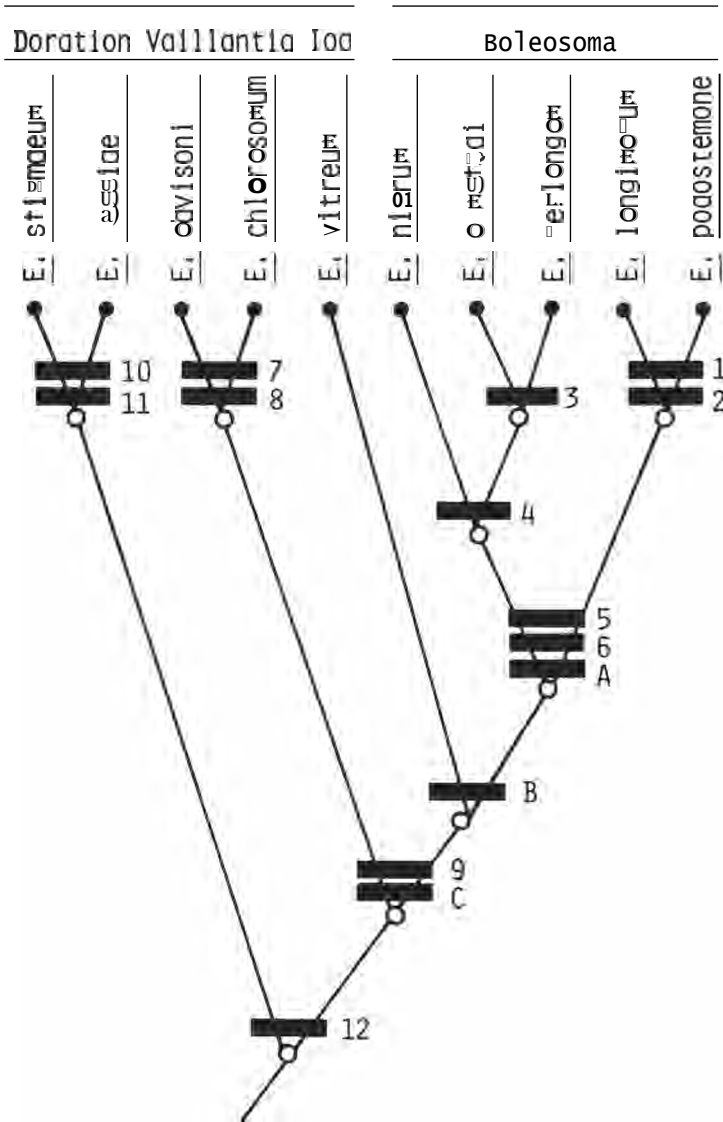


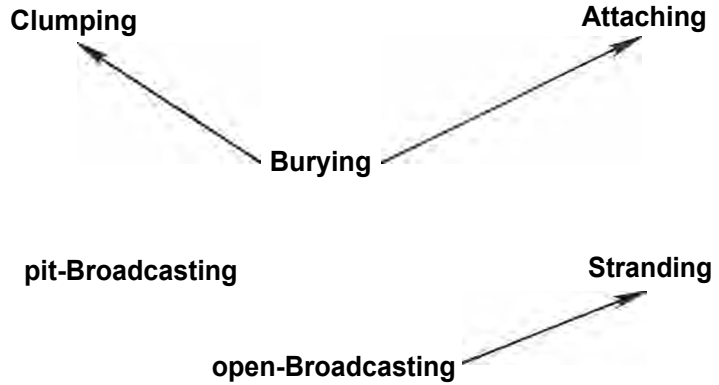
Fig. 14. — Hypothesized phylogenetic relationships among species of the subgenera Boleosoma, Ioa, Vaillantia, and Doration. Synapomorphies (black rectangles) are (1) broad branchiostegal membrane connection, (2) red-orange spots on the breeding male, (3) elongated second dorsal fin on the breeding male, (4) overall dusky breeding male, (5) bifurcate genital papilla on the female, (6) white knobs on paired fins, (A) egg-clustering behavior, (B) eggs attached to rocks, (7) black bridle around the snout, (8) extremely short second dorsal fin, (9) spatulate genital papilla on the female, (C) egg-attaching behavior, (10) blue bars on the adult male, (11) blue and red bands in the first dorsal fin of the adult male, (12) brown-black x/w marks on the body. Synapomorphous character states were identified by outgroup comparisons to *Etheostoma* (*Psychromaster*) *tuscumbia* and *E. (Litocara) nianguae*.

- Clustering

∩ - Clustering

a - Clustering

Fig. 15. — Hypothesized evolutionary relationships among percid breeding behaviors.



and thus increases the probability of their survival by reducing predation. Also, *S. lucioperca* males fan the eggs, presumably to prevent them from being covered by silt, and thereby reduce mortality due to anoxia.

Burying eggs reduces exposure to predators and probably to parasites, enhancing survivability. However, eggs can be buried only in flowing water habitats, usually in gravel but sometimes in sand, where burying does not subject the eggs to especially low oxygen levels such as would occur if eggs were buried in slow-flowing or standing water. Buriers are constrained behaviorally to flowing water and coarse substrates. Consequently, stream modifications, such as impoundments and channelization, prevent successful spawning by these species.

In the primitive state, species of *Nothonotus* bury their eggs in the sand-gravel mixture on the downstream side of a large stone in fast water. Clumping, as discussed above, evolved in a species of *Nothonotus* which buried its

eggs under a partially elevated stone, thereby enhancing crypticity. The advantage of male egg guarding followed.

The derivation of attaching from burying (or from any other behavior) is difficult to envision. However, the presence of both behaviors within several (at least three) subgenera of *Etheostoma* leaves no doubt that one is derived directly from the other. The strong positive correlation between primitive morphology and burying (e.g., all species of *Percina* are buriers) and between advanced morphology and attaching (e.g., in the subgenus *Boleichthys*) clearly indicates that the direction is from burying to attaching. For darters living in slow-flowing or standing water (e.g., *Boleichthys* species), the advantage of attaching is obvious; with demersal and adhesive eggs, the only alternatives to attaching are burying eggs in an oxygen-poor substrate (often rotting vegetation and mud) or migrating to suitable habitats for burying. Similarly, species living in bedrock pools [e.g., *E. simoterum* (Cope)] where

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