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PHYLOGENETIC PERSPECTIVES IN THE EVOLUTION OF PARENTAL CARE IN RAY-FINNED FISHES

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Abstract.—Among major vertebrate groups, ray-finned fishes (Actinopterygii) collectively display a nearly unrivaled diversity of parental care activities. This fact, coupled with a growing body of phylogenetic data for Actinopterygii, makes these fishes a logical model system for analyzing the evolutionary histories of alternative parental care modes and associated reproductive behaviors. From an extensive literature review, we constructed a supertree for ray-finned fishes and used its phylogenetic topology to investigate the evolution of several key reproductive states including type of parental care (maternal, paternal, or biparental), internal versus external fertilization, internal versus external gestation, nest construction behavior, and presence versus absence of sexual dichromatism (as an indicator of sexual selection). Using a comparative phylogenetic approach, we critically evaluate several hypotheses regarding evolutionary pathways toward parental care. Results from maximum parsimony reconstructions indicate that all forms of parental care, including paternal, biparental, and maternal (both external and internal to the female reproductive tract) have arisen repeatedly and independently during ray-finned fish evolution. The most common evolutionary transitions were from external fertilization directly to paternal care and from external fertilization to maternal care via the intermediate step of internal fertilization. We also used maximum likelihood phylogenetic methods to test for statistical correlations and contingencies in the evolution of pairs of reproductive traits. Sexual dichromatism and nest construction proved to be positively correlated with the evolution of male parental care in species with external fertilization. Sexual dichromatism was also positively correlated with female-internal fertilization and gestation. No clear indication emerged that female-only care or biparental care were evolutionary outgrowths of male-only care, or that biparental care has been a common evolutionary stepping stone between paternal and maternal care. Results are discussed in the context of prior thought about the evolution of alternative parental care modes in vertebrates.

Key words.—Comparative method, external fertilization, internal fertilization, nest construction, oviparity, phylogenetic character mapping, sexual dichromatism, viviparity.

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The males of certain fishes do all the work, and afterward take exclusive charge of the young.

Eggs being protected or unprotected by the parents has had little or no influence on the difference in color between the sexes. (Darwin 1871)

Among vertebrate animals, ray-finned fishes (Actinopterygii) show an unusually high diversity in reproductive features and behaviors. Approximately 20% of the 400+ extant families of actinopterygians include species that exhibit some form of extended parental care of offspring (Blumer 1979, 1982). Additionally, some actinopterygian lineages have evolved highly derived parental care traits such as placental viviparity (Reznick et al. 2002), male pregnancy (Berglund et al. 1986; Jones and Avise 1997), and mouthbrooding (Koblmuller et al. 2004). Such diversity makes the ray-finned fishes a natural model system for studying general patterns and processes of vertebrate parental care evolution (Amundsen 2003).

Studies on a few specific groups of fishes (Gross and Sargent 1985) and anuran frogs (Zimmerman and Zimmerman 1984, 1988; Weygoldt 1987) have suggested that for species with external fertilization, parental care evolves in stepping-stone fashion, first arising in males, then transitioning to biparental care, and terminating in female-only care upon male desertion. The stepping-stone model is elegantly simple and logically compelling, but it also has been contradicted by recent comparative work on some of the same organisms for which it was developed (Goodwin et al. 1998; Summers et al. 1999).

In addition, most previous work on the evolution of pa-

rental care in fishes has paid scant or no attention to the role of fertilization within a female's reproductive tract. Internal fertilization occurs in at least 21 teleost families and has led to viviparity (an extreme form of maternal care) in 14 of these (Gross and Shine 1981; Wourms 1981; Gross and Sargent 1985). Because gestation and internal fertilization presumably require elaborate suites of physiological, anatomical, and behavioral adaptations (Amoroso 1968; Schindler and Hamlett 1993), phylogenetic constraints and trade-offs may be particularly important in the evolution of this form of parental care. Such observations suggest that the evolutionary pathways toward parental care might differ between lineages with internal versus external syngamy.

Almost by definition, sexual selection is closely associated with the evolution of reproductive traits (Trivers 1972). It has been found, for example, to be positively associated with male parental care in some vertebrates, primarily birds (Price 1984; Heywood 1989; Hoelzer 1989; Grafen 1990), despite Darwin's (1871) pronouncement to the contrary (see opening quotation). Many ray-finned fishes also exhibit phenotypic manifestations of sexual selection, most often in the form of sexual dichromatism (Reimchen 1989; Houde and Endler 1990; Stott and Poulin 1996; Amundsen and Forgren 2001). This affords an opportunity to examine the possible role of sexual selection (via its observable surrogate, sexual dichromatism) in the evolution of various forms of parental care in ray-finned fishes.

Despite considerable interest in the diverse modes of parental care in fishes and the inherent utility of this group as a model for parental care evolution in animals, comparative

evolutionary analyses of these behaviors (Meyer and Lydeard 1993; Balshine-Earn and Earn 1998; Goodwin et al. 1998; Wilson et al. 2003) have been severely hampered by uncertainties about teleost phylogeny especially above the level of taxonomic families (Johnson 1993; Nelson 1994). This situation is gradually improving. In particular, recently published estimates of teleost phylogeny based on complete mitochondrial (mt) DNA genomic sequences from dozens of taxonomically diverse species (Ishiguro et al. 2003; Miya et al. 2003; Saitoh et al. 2003) have provisionally resolved many problematic fish clades, thereby making it possible to reconsider the evolution of a variety of reproductive traits across Actinopterygii (Mank et al. 2005).

Here we compile information from the literature on parental care and associated traits in more than 200 taxonomic families of fishes. Using a formal supertree (the first attempt to summarize phylogenetic data over such a large group of fishes), we address several long-standing questions. What were the likely precursor states and evolutionary pathways leading to various forms of parental care? How have alternative fertilization modes (internal versus external) affected the evolution of maternal care (both internal and external) and paternal care in fishes? And, was Darwin (1871) correct in his conjecture that sexual dichromatism bears no relationship to parental care of offspring?

MATERIALS AND METHODS

Database Construction

We searched the published literature on actinopterygian fishes, plus several sarcopterygian outgroup families, for accounts of the following: presence versus absence of sexual dichromatism and of nest construction and alternative modes of fertilization, embryo deposition, and postmating parental care.

Sexual dichromatism, defined as nuptial colorations that differ noticeably between the sexes, is the most common manifestation of sexual selection in fishes (Reimchen 1989; Houde and Endler 1990; Stott and Poulin 1996; Amundsen and Forsgren 2001). Sexual dichromatism can vary in degree among species, but due to difficulties of standardizing and quantifying this phenomenon across broad arrays of diverse taxa, we scored sexual dichromatism as being either pronounced (i.e., evident and obvious to the human eye) or absent in a given species. With regard to nest building, species that alter their habitat prior to egg deposition were deemed to construct nests (Breder and Rosen 1966).

For current purposes, internal fertilization was defined as syngamy occurring within a female's body (as opposed to within a male's body, as occurs in Syngnathidae within Gasterosteiformes). In addition, modes of embryo deposition were operationally defined as the retention versus lack of retention of fertilized eggs in the ovarian lumen or follicle. Thus, viviparity (which we consider to be a form of maternal care in the current study) was not distinguished here from ovoviviparity (also, these conditions are not differentiated in much of the available literature; see Wourms et al. 1988; Schindler and Hamlett 1993). Similarly, oviparity was operationally defined in the current study to encompass both ovuliparity (where ova are shed prior to external fertilization)

and zygoparity (where ova fertilized internally are then deposited outside a female's body prior to eclosion; Wourms and Lombardi 1992). Finally, we consider postmating parental care, which presumably increases mean survival rates of offspring (Gross and Shine 1981), to be any clear protection (internal or external) provided to postzygotic embryos or juveniles by older females, males, or both.

Supertree Construction

We used a formal matrix representation with parsimony approach (MRP) (Ragan 1992) to construct a supertree for actinopterygian fishes, with representatives of four Sarcopterygian families included only as outgroups for proper rooting. The underlying, or source, phylogenies for the supertree data matrix were based primarily on molecular data, although several morphological phylogenies were included as well. The supertree data matrix (consisting of cladogenetic information for all species in the source phylogenies) was coded according to Baum (1992) and Ragan (1992). We used the ordinal and superordinal classification described in Nelson (1994) as a higher level organizational framework for the data matrix (except when considering the Percomorpha, which has been shown in previous work to be polyphyletic at multiple taxonomic levels; Johnson 1993; Nelson 1994; Miya et al. 2003). Maximum parsimony reconstructions of large supertrees require vast amounts of computational time (Graham and Foulds 1982). To deal with this complexity in identifying most parsimonious trees using PAUP, we conducted multiple (> 100) heuristic searches with random-order additions of taxa (Sanderson et al. 1998). This effort produced a provisional best tree score, and we then searched all computer outputs to identify 25,000 parsimonious trees (the maximum that we could computationally handle) with that identical score. We then constructed a family-level 90% consensus tree from the 25,000 most parsimonious trees identified. The resulting supertree topology for 228 taxonomic families and a list of the underlying phylogenies that composed the data matrix are available in the supplemental materials (available online only at <http://dx.doi.org/10.1554/04-734.1.s1>). We also will make reference to an ordinal-level supertree that represents a condensed phylogeny for the 46 taxonomic orders of ray-finned fishes considered.

Comparative Analysis of Parental Care

We first used maximum parsimony as implemented by MacClade version 4 (Maddison and Maddison 2000) to estimate the minimum and maximum numbers of inferred independent evolutionary origins, losses, and transitions between various types of parental care and fertilization systems in the family-level actinopterygian supertree. We then used maximum likelihood as implemented by Discrete (Pagel 1994, 1997) to test for correlations in the evolution of particular pairs of reproductive traits, each coded as discrete binary characters (such as presence vs. absence of nest construction, or maternal vs. paternal care of offspring). We evaluated possible correlations by comparing likelihoods in a null model of evolution (i.e., with no correlation between traits) to the alternative correlated model. Each resultant likelihood ratio test has a χ^2 distribution with four degrees of

freedom, since there are four fewer parameters in the null model than the correlated model (Pagel 1994).

When a particular correlation was found to be statistically significant, we also used Discrete for contingency testing, which indicates if the evolution of one of the traits significantly tended to precede the other (thus suggesting but not proving causal directional evolutionary relationships between the two paired reproductive traits). Contingency testing does not identify where along the phylogeny one trait preceded another, but it does identify broad patterns in correlated trait evolution and provides theoretical frameworks for further analyses. Each contingency test was evaluated using a likelihood ratio statistic with a χ^2 distribution and one degree of freedom (Pagel 1994). Although Discrete can incorporate different branch lengths (ages of clades) into the analysis, the amalgamated nature of supertrees (in general, as well as in the current study) typically precludes accurate branch-length estimations. Therefore, as has been conventional in previous such analyses involving other traits and other organisms, we coded all branch lengths in Discrete as equal to one (e.g., Weiblen et al. 2000).

For the correlation and contingency tests, which involve multiple comparisons among traits, we computed a Bonferroni adjustment. We indicate associations that are significant under Bonferroni-corrected conditions and report associations that are significant under normal statistical rigor (i.e., without invoking this correction).

RESULTS

The supertree resolved 224 of the 400+ families of actinopterygian fishes, with four sarcopterygian families included as outgroups. In these cases, all nodes had greater than 90% consensus support, and the phylogenetic topology further substantiates the polyphyly previously reported for several percomorph orders including Perciformes, Gasterosteiformes, and Scorpaeniformes (Johnson 1993; Nelson 1994; Miya et al. 2003). Although we were able to resolve all gasterosteiform and scorpaeniform suborders, as well as many perciform suborders including Gobioidae, Blennioidei, Zoarcoidei, and Labroidei, the extreme polyphyly and a lack of higher-level phylogenies for the Percoidei prevented resolution of some percoideian families such as Aponogonidae.

We found sufficient information on reproductive characters for 206 of the 228 resolved families. Overall, parental care was present in 31% (62 of 174) of the families included in our analysis. This value is somewhat higher than a previous estimate of 20% by Blumer (1982), but that earlier study included many of the phylogenetically uncharacterized percoideian families.

Among the ovuliparous (externally fertilizing) fishes considered, parental care was present in 25% (49 of 193) of the taxonomic families. For these taxa, male-only parental care (41 families) was far more common in our study than either female-only care (five incidences) or biparental care (five incidences); the Cichlidae showed male-only, female-only, and biparental care. For internal fertilizers, the situation was dramatically different: parental care (either external or internal) was present in 90% (18 of 20) of the families examined.

Maximum Parsimony Inferences

Figure 1 shows the abbreviated (i.e., collapsed), ordinal-level supertree topology. As evidenced by the high number of polymorphic ordinal-level clades in Figure 1, shifts among alternative parental-care modes have occurred frequently in ray-finned fish evolution. Thus, parental care appears to have been evolutionarily quite labile in this group. However, at finer taxonomic scales, taxonomic orders that were polymorphic for parental-care modes usually resolved into families that were monomorphic for one or another mode of care (e.g., Fig. 2). In the 206-family tree (supplemental materials available online), parental care is mostly confined among modern families to approximately 35 terminal clades, and many large clades are entirely devoid or nearly so of species in which adults care for their young. For these reasons, and also from basic biological considerations (Baylis 1981), it seems highly likely that external fertilization devoid of parental care is the generalized basal condition for ray-finned fishes, from which more specialized modes of paternal or maternal care arose secondarily and recurrently in various actinopterygian lineages.

Based on maximum parsimony analyses of the family-level supertree, we estimate that parental care solely by the male emerged independently at least 22 times over the course of ray-finned fish evolution, probably always in lineages in which females release eggs that are fertilized away from their bodies (Fig. 3). Biparental care (i.e., by the two sexes either simultaneously or alternately within a species) arose independently on at least four occasions, but again almost certainly only in lineages in which syngamy is external. Parental care solely by the female (other than via internal gestation, which we will address later) evolved at least seven independent times in the ray-finned fishes, but in sharp contrast to the male-only care situation, in only three of these cases (43%) did such female care involve species with external fertilization. The type (male, female, or biparental) of parental differs significantly depending on the type (internal or external) of fertilization ($\chi^2 = 86.3$, $P < 0.0001$).

As judged by the maximum parsimony phylogenetic analyses, fertilization inside the female's body probably arose independently at least 13 times over the course of ray-finned fish evolution (Fig. 3). It apparently led to internal gestation (i.e., strict viviparity) in at least eight lineages, and to postpartum external care by females in four other lineages (Fig. 3). In no examined lineage did such internal fertilization coexist with paternal care, a trend also illustrated in Figure 2 (where all cases of internal fertilization occurred in species with either internal or external female care of offspring). A few reports do exist of the co-existence of paternal care and female-internal syngamy, but they concentrate on the Aponogonidae (Garnaud 1950, 1962), a perciform family omitted from our analysis due to lack of phylogenetic resolution. Although future phylogenetic work should permit inclusion of this family, its peculiar combination of reproductive traits will undoubtedly remain a rare exception due to the strong association of internal fertilization with female care (Gross and Sargeant 1985).

Internal gestation by females involves sheltering and often nourishing embryos within the body. From previous biolog-

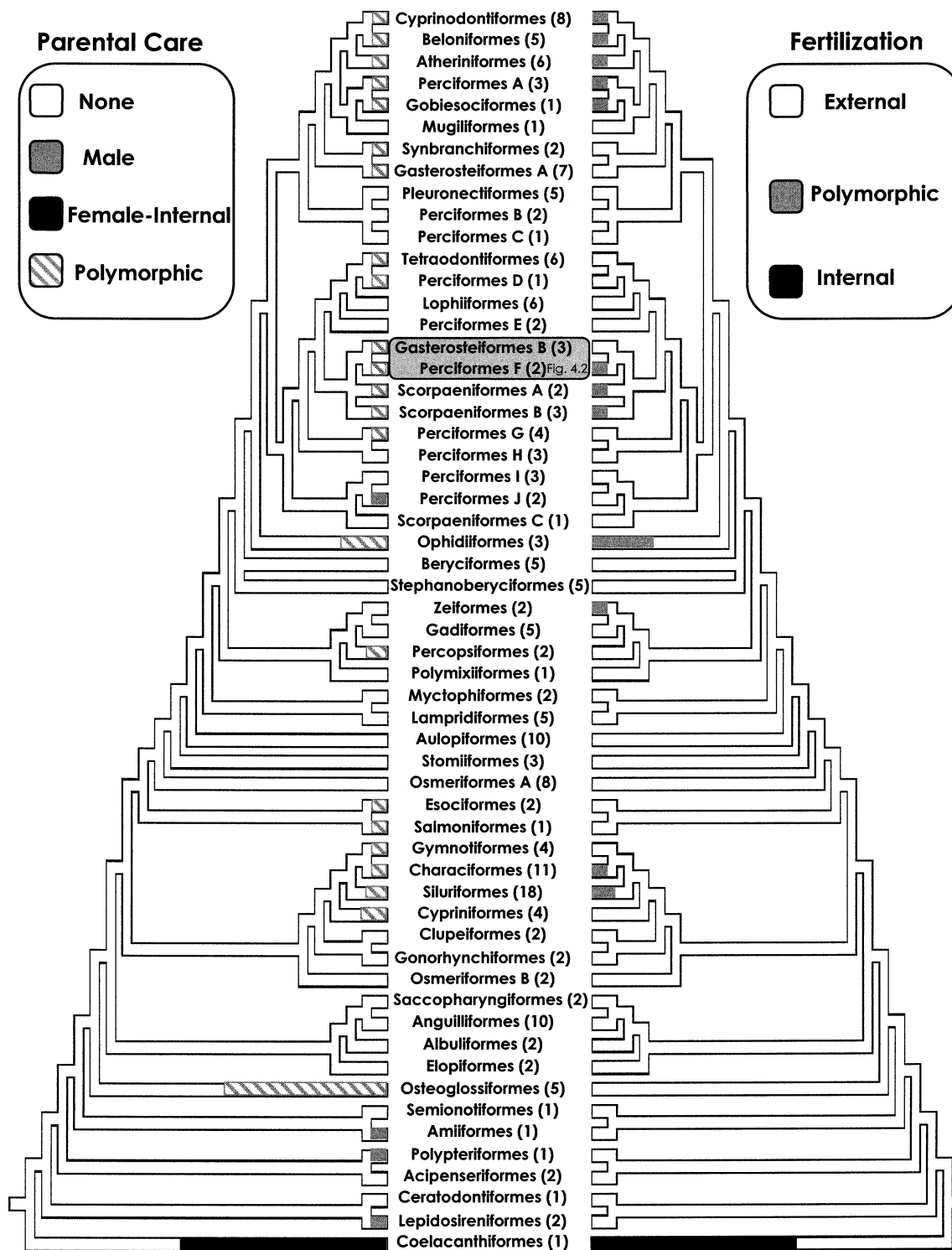


FIG. 1. Ordinal-level MRP supertree for the actinopterygian fishes. Plotted on the cladogram are character states for parental care (left) and mode of fertilization (right) as inferred by maximum parsimony reconstructions of finer level (interfamilial) molecular phylogenies. In parentheses are the numbers of surveyed families in each collapsed clade. For the polyphyletic orders, various monophyletic clades (each designated with an upper-case letter postscript) are composed of the following lower-level taxa: Perciformes A, Blennioidei; Perciformes B, Sphyraenidae, Polynemidae, Menidae; Perciformes C, Carangidae; Perciformes D, Gobioidi; Perciformes E, Emmeli-chthyidae, Lutjanidae; Perciformes F, Zoarcoidei; Perciformes G, Labroidei, Acanthuroidei; Perciformes H, Notothenoidei, Percidae; Perciformes I, Scombroidei, Stromateidae; Perciformes J, Gobioidi; Gasterosteiformes A, Syngnathoidei; Gasterosteiformes B, Gaster-osteioidei; Scorpaeniformes A, Cottoidei; Scorpaeniformes B, Scorpaenoidei; Scorpaeniformes C, Dactylopteroidei; Osmeriformes A, all omseriforms not in Osmeriformes B; Osmeriformes B, Alepocephalidae, Platytrocidae.

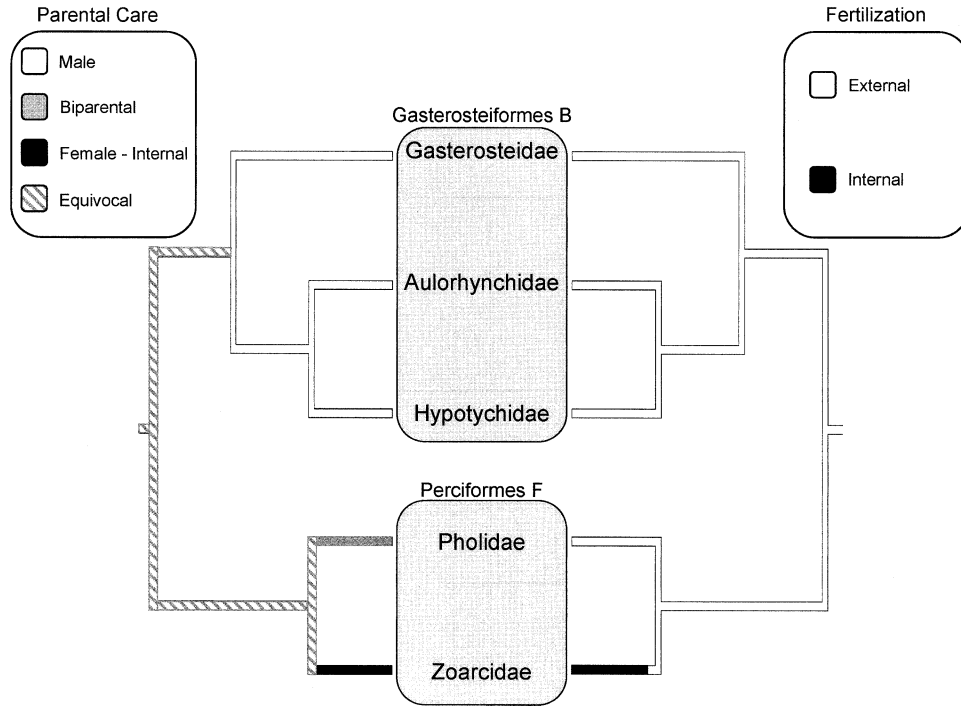


FIG. 2. Finer-scale phylogeny for the closely related clades Gasterosteiformes B and Perciformes F (see Fig. 1). Shown on this portion of the supertree are character states for parental care (left) and mode of syngamy (right), as deduced by maximum parsimony reconstructions.

ical considerations (Amoroso 1968; Thibault and Schultz 1978; Wourms 1981; Reznick et al. 2002), this extreme form of maternal care almost certainly is a derived condition in ray-finned fishes, supposedly always preceded by internal fertilization. Our parsimony reconstructions are entirely consistent with these notions (Figs. 1–3).

A summary of these and other historical pathways of evolutionary transition between reproductive states, as inferred from the parsimony analyses of MacClade, is presented in Figure 3.

TABLE 1. Results of tests for correlations and contingencies in the evolution of paired traits. For correlations that proved to be statistically significant vis-à-vis the null model, entries on the first line in each cell are the likelihood ratio and its associated *P*-value (χ^2 distribution, 4 df). For each of these significant correlations, entries on the second line of a cell indicate the deduced evolutionary directionality (trait X in all cases except one tended to precede the evolution of trait Y) and the associated *P*-value (χ^2 distribution, 1 df). Relationships shown in bold are significant even after the Bonferroni correction.

	X	
	Sexual dichromatism	Nest construction
Male care	10.2 (<i>P</i> = 0.038) X ↔ Y (ns)	82.6 (<i>P</i> < 0.001) X → Y (<i>P</i> < 0.001)
Internal fertilization	10.8 (<i>P</i> = 0.029) X → Y (<i>P</i> = 0.006)	ns
Y		
Viviparity	14.1 (<i>P</i> = 0.007) X → Y (<i>P</i> = 0.002)	ns
Nest construction	14.8 (<i>P</i> = 0.005) X → Y (<i>P</i> = 0.001)	—

Maximum Likelihood Inferences

For pairs of reproductive traits, Table 1 summarizes the results of the correlation and contingency tests via the maximum likelihood analyses. Several phylogenetic associations were statistically significant, before and sometimes also after Bonferroni corrections for multiple comparisons. The overall pattern is highly significant, as assessed by Fisher’s combined probability test (Sokal and Rohlf 1995) for correlation testing (*P* < 0.001) and even contingency testing (*P* < 0.001). Because it is unlikely that all significant putative relationships between pairs of traits are attributable to Type I errors alone, we will briefly describe each phylogenetic association that proved to be significant under standard statistical rigor.

According to the correlation tests, both sexual dichromatism and nest construction were positively correlated with the evolution of male-only parental care. Furthermore, in the case of nest construction (but not of sexual dichromatism), contingency tests revealed a significant evolutionary directionality to the association, with nest construction tending to having preceded (and thus, perhaps, having contributed to the evolution of) male parental care. Unfortunately, similar statistical tests of biparental and female-only external care were not possible due to the rarity of these states in species that shed eggs prior to fertilization.

Sexual dichromatism and internal fertilization were positively correlated (*P* = 0.029), with contingency tests suggesting that the former may precede the latter (*P* = 0.006). Finally, sexual dichromatism was also positively correlated with (*P* < 0.007) and contingently preceded (*P* < 0.002) both internal gestation and viviparity.

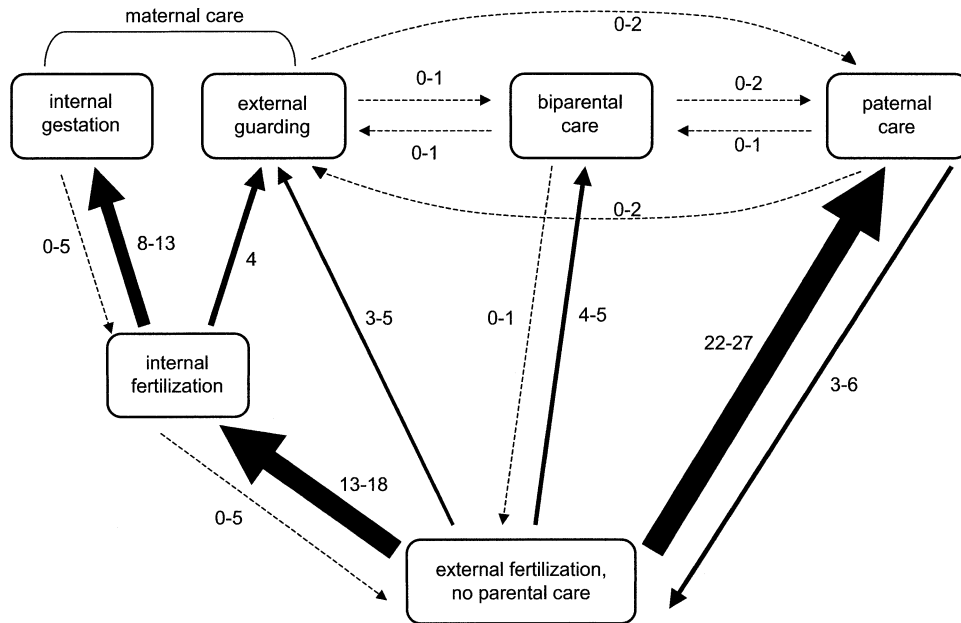


FIG. 3. Maximum parsimony inferences regarding independent evolutionary transitions among parental care modes in the surveyed actinopterygian fishes. Arrow sizes reflect relative numbers of evolutionary transitions; numerals adjacent to the arrows register minimum and maximum estimated numbers of evolutionary transitions. Broken arrows indicate transitions that might or might not have occurred (i.e., those whose estimated minimum number was zero and whose maximum number was ≥ 1).

DISCUSSION

Inevitably, results from our phylogenetic analysis remain provisional, in part because the actinopterygian tree is far from fully resolved. As additional phylogenetic information becomes available, especially for families in the Percoidei, the supertree topology should become denser and better resolved at internal nodes.

Supertrees (Ragan 1992), which offer a method for merging phylogenies from diverse and otherwise incompatible data matrices, are becoming increasingly important for phylogenetic analyses across large time spans (tens and hundreds of millions of years), in part because no sequence from a single gene or a set of genes can reasonably be expected to resolve relationships over such a vast span of genetic distances under a single model of molecular evolution (Bininda-Emonds et al. 2002). In a data matrix underlying supertree construction, only tree topologies are employed, with each column in the data matrix corresponding to a monophyletic clade from the various source trees to be amalgamated. Despite the resulting complexity problems, supertree methods extend the upper-limit for the number of taxa that can be surveyed in a single phylogeny. They have made possible the construction of cohesive phylogenies for such groups as Angiosperms (Davies et al. 2004) and Chiroptera (Jones et al. 2002), and even prompted preliminary attempts at the complete tree of life (Maddison and Schultz 2004).

The provisional actinopterygian supertree presented here is based on numerous source phylogenies, many of which came from molecular data, others were based on relatively robust morphological datasets, and other from multiple kinds of information. Their heterogeneous nature means that these data subsets clearly cannot be treated uniformly or homogeneously, so only the amalgamating algorithms of supertree

construction can hope to combine these divergent datasets into a cohesive phylogenetic structure.

While the supertree is not a complete survey of all actinopterygian families, the data from future source phylogenies can be added to the matrix, increasing both taxon sampling and probably the robustness of the cladogram. Despite these current limits to our understanding of actinopterygian phylogeny, several broad patterns have emerged from our comparative phylogenetic analyses of parental care and associated reproductive traits in ray-finned fishes.

Sexual Dichromatism, Mode of Fertilization, and Parental Care

In our analysis, sexual dichromatism proved to be significantly correlated with the evolution of each of the following: internal fertilization, viviparity (the most common form of maternal care), male parental care, and nest construction. Furthermore, the evolution of internal fertilization, viviparity, and nest construction were significantly contingent upon the presence of sexual dichromatism. This suggests that Darwin's (1871) postulate that dichromatism and parental care are unrelated characters in fishes is incorrect. Sexual dichromatism (especially nuptial coloration) is a manifestation of sexual competition in many fish species (Endler 1980; Warner and Schultz 1992; Wedekind et al. 2001; Okuda et al. 2003). Thus, perhaps the same competition for mates that drives sexual selection also drives the evolution of parental care (both internal and external; see below).

Evolutionary transitions from external fertilization and oviparity to internal fertilization and viviparity are presumably far from trivial mechanistically. Internal fertilization normally requires an intromittant male organ such as a gonopodium, which has a complex physiology and musculature

(Rosen and Gordon 1953; Zauner et al. 2003). The female reproductive tract must be physiologically conducive to internal fertilization. With regard to viviparity some, if not all, of the following changes must normally occur along the evolutionary path from egg-laying to live-bearing: the retention of developing embryos in the female reproductive tract to advanced states of development; a reduction in the egg envelop; an increase in egg size with a concomitant decrease in egg number; the emergence of endocrine adaptations; and the development of mechanisms for nutrient and gas exchange between zygote and mother (Amoroso 1968; Wourms 1981; Wourms et al. 1988; Guillette 1989; Schindler and Hamlett 1993; Reznick et al. 2002).

Despite the difficulties presumably associated with the evolution of such suites of complex characters, we estimate that viviparity has evolved on at least eight separate occasions in the Actinopterygii, and this is almost certainly a considerable underestimate due to the necessary omission of several perciform families. Thus, the hurdles have been overcome multiple times, suggesting that selection pressures for viviparity may sometimes be strong. Viviparity does indeed offer several potential advantages including increased protection of embryos, larger propagule size, and higher trophic level of offspring at the time that progeny become independent (Wourms and Lombardi 1992). Viviparity also appears to be an irreversible condition in the ray-finned fishes, as no significant (i.e., where the minimum estimate was greater than zero) transitions back toward oviparity were inferred from our phylogenetic analyses. Because of this evolutionary ratchet and because viviparity places the entire energetic postmating burden on the female, internal fertilization and viviparity should be considered a distinct pathway from external fertilization in the evolution of parental care in Actinopterygii (see below).

The Evolution of Parental Care

Our findings support earlier reports of correlations between external fertilization and male-only care and between internal fertilization and female-only care (Trivers 1972; Dawkins and Carlisle 1976; Ridley 1978; Gross and Shine 1981; Gross and Sargent 1985). However, evidence also emerged that female-only care occasionally evolves independently of male-only care in the presence of external fertilization. Despite such exceptions, it is clear that male-only care generally evolves in lineages with external syngamy, and female-only care evolves primarily in lineages with internal fertilization (Fig. 3). Because of this dichotomy, the evolution of parental care should be thought of as two separate pathways with the mode of fertilization being the fundamental point of divergence (Fig. 3), and with sexual selection acting on both pathways to foster evolutionary change. Considering these two evolutionary pathways, the one leading toward maternal-only care is the somewhat less traveled route in ray-finned fishes, probably because complex suites of anatomical and physiological adaptations must be required for internal fertilization and viviparity.

For species with external syngamy, there is little or no evidence from our analyses that biparental care is an intermediate state between paternal and maternal care. Thus, our

analyses do not add support for the conventional stepping-stone model in the evolution of parental care (Gittleman 1981; Zimmerman and Zimmermann 1984, 1988; Gross and Sargent 1985; Weygoldt 1987). Rather, our work is more consistent with some recent evidence from anuran frogs (Summers et al. 1999) that female-only and biparental care are independent evolutionary transitions from the basal state of no care. An important qualification, however, is that because biparental care is rare and female-only care with external fertilization is even rarer, our analyses may simply lack the requisite sensitivity to detect the intermediacy of the biparental care state, because few evolutionary transitions would be expected to occur from one-parent care to two-parent care.

The relationship between sexual selection and parental care is likely related to competition for limiting resources, which itself might be due in various species to any or a combination of several genetic and ecological factors: for example, anisogamy (pronounced differences in size between male and female gametes), restrictions on suitable spawning habitats, energetic food constraints, highly unequal sex ratios, or consistent differences between the sexes in mate availabilities. Such limitations foster reproductive competition, usually among males, and this competition can lead to a high variance in male reproductive success that often results in the evolution of sexual dichromatism via sexual selection (Darwin 1871). This process may manifest differently, however, in species with external versus internal syngamy, due to unique phylogenetic constraints and peculiarities of each fertilization system.

For species with external fertilization, this competition is suggested by positive correlations between nest construction and paternal care, as well as between sexual dichromatism and male parental care. The first of these correlations (i.e., between nest construction and male parental care) is a likely outgrowth of territorial defense of spawning sites by males. In other words, nest construction and the protection of progeny therein would merely require a prolongation and elaboration of typical defense behavior, and thus would be especially adaptive when, for example, eggs and fry face heavy predation (Loiselle 1978). Nest construction in this sense may be a pre-adaptation for male parental care.

The relationship between sexual dichromatism and male parental care is less straightforward, and it may be that this positive correlation is not causative but rather that both traits are the result of sexual selection. There are many accounts of the role of sexual selection in the evolution of dichromatism in fish (Reimchen 1989; Houde and Endler 1990; Stott and Poulin 1996; Amundsen and Forsgren 2001). Our results may suggest that male parental care is also influenced by sexual selection, a relationship that has been proposed both theoretically and empirically for several types of animals (Hoelzer 1989; Iwasa and Pomiankowski 1999; Tallamy 2000), including fish (Östlund and Ahnesjö 1998; Pampoulie et al. 2004). In some fishes, males are known to take better care of the offspring when in the presence of breeding females (Pampoulie et al. 2004), and females have been shown to choose mates based on the quality of their parental care (Östlund and Ahnesjö 1998; Östlund-Nilsson 2000), suggesting that male-care behavior is affected by sexual selection. These

effects have also been shown in birds (Møller and Thornhill 1998; Valendo et al. 2001; Siefferman and Hill 2003). It is therefore possible that the same forces of intrasexual (and/or intersexual) reproductive competition that foster the evolution of sexual dichromatism also promote the evolution of male parental care.

For species with female-internal fertilization, sexual dichromatism may simply be an evolutionary by-product of enhanced competition among males for mating success. This would likely occur because, in such situations, maternal investment in reproduction becomes higher (almost necessarily), paternal investment in progeny is likely lower, and female fecundity (especially in species with internal gestation) becomes an even more limiting factor in reproduction. Empirically, internal syngamy almost never co-exists with male parental care, so reproductive involvement by males in these situations must be limited to premating and gametic components, thus creating the classical anisogamy-related limitation on female reproduction that often results in sexual selection (Trivers 1972). But internal fertilization also creates a ready opportunity for male desertion, thus leaving the female with all of the parental care responsibilities. In this way, internal fertilization is not only a pre-adaptation to internal gestation, but also should normally promote competition among males for mates, resulting in sexual dichromatism via sexual selection.

Synopsis

This study represents the first attempt to scrutinize the evolution of parental care in actinopterygian fishes in a formal phylogenetic context. Our comparative analyses indicate the existence of two principal evolutionary routes to extended parental care in fishes: (1) to female-only care (either internal or external) via female-internal fertilization; and (2) to male-only care directly from external fertilization. Other evolutionary pathways exist as well but appear to be much less frequently traveled. Finally, our phylogenetic results taken at face value (there are caveats) add no support for the conventional notion that biparental care is an evolutionary stepping stone between male-only care and female-only care. These results should provide a useful backdrop and model for further studies of parental care evolution in other groups of animals.

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