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REVIEW PAPER

The evolution of reproductive and genomic diversity in ray-finned fishes: insights from phylogeny and comparative analysis

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Collectively, ray-finned fishes (Actinopterygii) display far more diversity in many reproductive and genomic features than any other major vertebrate group. Recent large-scale comparative phylogenetic analyses have begun to reveal the evolutionary patterns and putative causes for much of this diversity. Several such recent studies have offered clues to how different reproductive syndromes evolved in these fishes, as well as possible physiological and genomic triggers. In many cases, repeated independent origins of complex reproductive strategies have been uncovered, probably reflecting convergent selection operating on common suites of underlying genes and hormonal controls. For example, phylogenetic analyses have uncovered multiple origins and predominant transitional pathways in the evolution of alternative male reproductive tactics, modes of parental care and mechanisms of sex determination. They have also shown that sexual selection in these fishes is repeatedly associated with particular reproductive strategies. Collectively, studies on reproductive and genomic diversity across the Actinopterygii illustrate both the strengths and the limitations of comparative phylogenetic approaches on large taxonomic scales.

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Key words: comparative method; genome evolution; mating behaviour; sexual selection; supertree; taxonomic diversification.

INTRODUCTION

With more than 20 000 living species representing more than 400 taxonomic families, ray-finned fishes (Actinopterygii) are ideal subjects for comparative analyses of reproductive evolution because they display a remarkable diversity of morphologies and behaviours related to procreation (Amundsen, 2003). This variety manifests at multiple levels of reproductive biology, *e.g.* sex-determining mechanisms, including male heterogamety (XY), female heterogamety (ZW) and autosomal genetic triggers (Devlin & Nagahama, 2002), pre-mating

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reproductive behaviours of many kinds (Gross, 1996; Henson & Warner, 1997) and post-mating parental tactics ranging from no offspring care to extended internal gestation of embryos by females and sometimes even by males (Blumer, 1979, 1982). Accompanying this reproductive diversity is striking morphological and behavioural manifestations of sexual selection, as well as an interesting heterogeneity in genomic features such as DNA content (Gregory, 2005). Furthermore, various reproductive traits have probably evolved independently on many occasions across the Actinopterygii, thus creating a wealth of opportunities for comparative phylogenetic approaches in which cladogenetic structure provides historical backdrop for the study of evolutionary patterns and processes (Felsenstein, 1985; Harvey & Pagel, 1991; Martins, 1996; Avise, 2006).

Most exercises of comparative phylogenetics in fishes have been conducted on single traits in relatively small clades, often with great success. Platyfishes and swordtails (*Xiphophorus*) provide an example germane to the evolution of decorative features under sexual selection. Swordtails are named for the long and pointed extension of the male's caudal fin. This sword is present in some *Xiphophorus* lineages but absent in others. Comparative analyses (see Fig. 1) helped reveal that swords evolved several times independently (Meyer *et al.*,

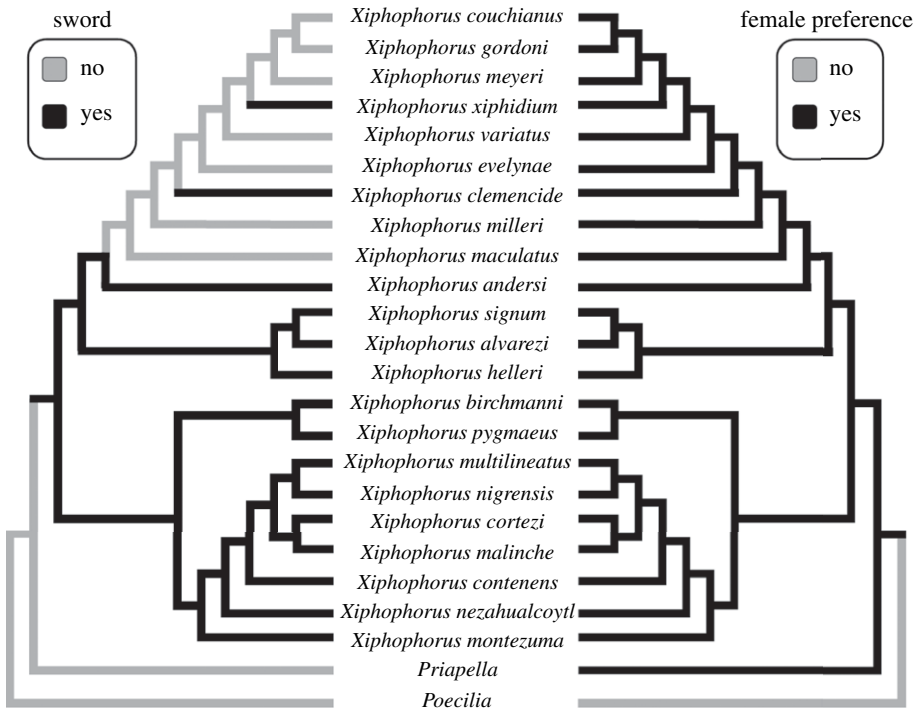


Fig. 1. Comparative phylogenetic analysis of sexual selection in *Xiphophorus* and related genera. The topology is from a maximum parsimony reconstruction of mitochondrial and nuclear loci (Meyer *et al.*, 1994; Lockhart *et al.*, 1995). The left panel plots presence versus absence of a sworded tail, which evolved independently at least three times in this clade (Meyer, 1997). The right panel likewise plots the females' preference for the trait in males, which predates the actual evolutionary appearance of swords (Basolo, 1995).

1994, Meyer, 1997) and that female mating biases for males displaying this feature predated evolution of the sword itself (Basolo, 1990, 1995, 1996). Apparently, sexual selection based on female choice promoted repeated evolution of this flamboyant male feature despite its hindrance to an individual's mobility (a problem for males especially in predator-rich environments). Recent molecular analyses have further suggested that convergent sexual selection for male swords has acted on the same underlying genetic mechanisms (Zauner *et al.*, 2003).

Similar analyses have been conducted on various other reproductive traits in fishes, such as male brood-pouch designs in syngnathids (Wilson *et al.*, 2001, 2003), and livebearing and placental structures in poeciliids (Meyer & Lydeard, 1993, Reznick *et al.*, 2002). Although such studies on specific features in particular small clades can offer many evolutionary insights, the study of multiple categories of traits in much larger clades offers novel challenges as well as opportunities. The general goals in such analyses are to uncover pervasive evolutionary patterns and processes that occur over long timescales.

The stage for extending the scope of comparative phylogenetics to the full actinopterygian clade was set by the availability of extensive catalogues of reproductive behaviours in thousands of these species (Breder & Rosen, 1966; Blumer, 1979, 1982; Taborsky, 1994; Devlin & Nagahama, 2002) coupled with recent advances in knowledge about actinopterygian phylogeny (Elmerot *et al.*, 2002; Ishiguro *et al.*, 2003; Miya *et al.*, 2003; Saitoh *et al.*, 2003; Inoue *et al.*, 2004). In addition, a recent expansion of genomic information for these fishes (Volf, 2005) has allowed researchers to investigate possible mechanistic underpinnings of reproductive diversity. Here, we will illustrate the comparative phylogenetic approach as applied to large taxonomic assemblages by reviewing recent work on ray-finned fishes and placing results in the context of current thought about the evolutionary sources of reproductive and genomic diversity in this huge vertebrate clade.

BACKGROUND

COMPARATIVE METHODOLOGIES

The basic notion of comparative phylogenetics has been a part of evolutionary biology for more than a century, but in the past few decades (Felsenstein, 1985), quantitative and statistical frameworks for comparative methods have been formally developed. Several methods now exist to 'correct' for phylogenetic non-independence of lineages, *i.e.* to accommodate the possibility that a given trait is possessed by two or more lineages by virtue of shared ancestry rather than separate origins. Cladograms are the usual starting points for such analyses (Felsenstein, 1985; Harvey & Pagel, 1991). Although debate continues on the appropriateness and need for phylogenetic corrections (Ricklefs, 1996; Price, 1997; Harvey & Rambaut, 1998), comparative phylogenetic approaches have gained popularity for at least two basic reasons: ancestral states themselves are often of inherent interest and spurious correlations can be a problem in comparative data sets when phylogeny is neglected.

Of course, it is possible to assess trait correlations without phylogenetic corrections, using standard statistical association tests such as correlation analyses

or chi-square tests. Because standard statistical approaches, however, entail an assumption that extant taxa provide independent data points, they lack the historical perspective that is the hallmark of comparative phylogenetics.

For comparative analyses at lower taxonomic levels (as exemplified in Fig. 1), it is customary to estimate molecular phylogenies from DNA sequences at one or a few loci. This expedience disappears as the number of taxa in the data set increases. For analyses of very large clades or higher taxonomic levels, building a custom molecular phylogeny may require incorporating information from multiple loci in many hundreds of taxa, a task that may be prohibitive in cost and time and is also likely to be computationally intractable. On the other hand, large phylogenies are attractive for comparative analyses because they permit views of broad patterns in the evolutionary forest that would not necessarily be discernable from close inspections of individual trees.

This conundrum has been partially alleviated by supertree construction (Baum, 1992), the basic methodology of which is outlined in Fig. 2. Supertrees are amalgamated representations of smaller inter-leaved cladograms, including those based on entirely different data sets (molecular or otherwise). Supertrees have become such an important tool for evolutionary analyses (Jones *et al.*, 2002; Pisani *et al.*, 2002; Ruta *et al.*, 2003; Cardillo *et al.*, 2004; Davies *et al.*, 2004; Grotkopp *et al.*, 2004; Fernandez & Vrba, 2005) that they themselves have merited thorough reviews (Bininda-Emonds *et al.*, 2002, Bininda-Emonds, 2004).

After a cladogram or a supertree has been developed, several potential types of comparative analysis are available depending on the questions to be investigated. All of these methods can be performed by hand, but as the analysis of large clades can become quite tedious, various computer programs allow for a certain degree of automation. The primary methods

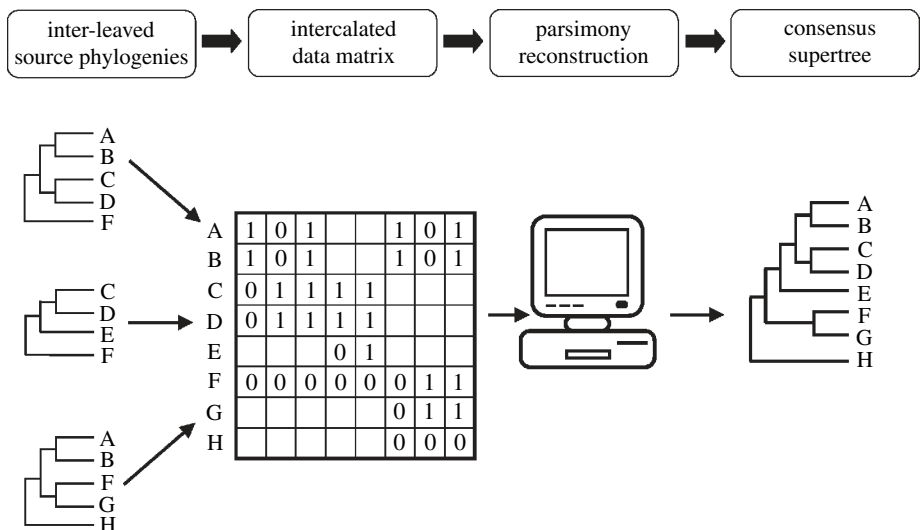


FIG. 2. Flow chart outlining the basic steps of supertree construction (see text). Each column in the matrix represents a monophyletic clade from a source phylogeny, dichotomously coded for presence (1) or absence (0) of a taxon in a given clade.

and examples of commonly used computer programs are summarized in Table I.

The most basic type of comparative phylogenetic analysis examines how a single trait has evolved in terms of number of independent origins, direction of evolutionary transitions and likelihood of reversion to the ancestral state. MacClade (Maddison & Maddison, 2000) and MULTISTATE (Pagel, 1994, 1997) are popular software programs for these purposes. MacClade attempts to optimize ancestral states (at internal nodes) to accommodate the fewest required evolutionary transitions (according to maximum parsimony), whereas MULTISTATE (a maximum likelihood, or ML, approach) calculates the probability of observing the data under a set of evolutionary models specified by the investigator. For ML analyses, the likelihood of different models of evolutionary transitions can be compared with a likelihood ratio test (Pagel, 1994). MacClade and MULTISTATE usually are implemented on discrete data, although they can also handle continuous data if the researcher can assign the data to categories.

More complex analyses can test for correlated evolution or the statistical propensity for associations between two or more traits across lineages. Suites of correlated characters could have resulted from the same evolutionary forces or they could be present if one of the correlated traits (an independent variable) has causally influenced the evolution of another (a dependent variable). Independent contrast (IC) methods (Felsenstein, 1985) search for possible associations by computing the numerical relationship between pairs of traits at each node in a phylogeny, after which the data points can be regressed and analysed for overarching patterns. The most commonly used IC software is Comparative

TABLE I. Common comparative approaches and associated computer programs for that correct for shared ancestry among traits

Questions	Program (Platform)	Algorithm	Applications	Citation
Single trait evolution	MacClade (MacIntosh)	Maximum parsimony	Transitions among states	Maddison & Maddison (2000)
	MULTISTATE (PC)	Maximum likelihood	Directional evolution of discrete traits	Pagel (1994, 1997)
Correlated evolution	CAIC (MacIntosh)	Independent contrasts	Correlation testing between continuous traits	Purvis & Rambaut (1995)
	CONTINUOUS (PC)	Maximum likelihood	Correlation testing between continuous traits	Pagel (1994, 1997)
	DISCRETE (PC)	Maximum likelihood	Correlated evolution between binary traits	Pagel (1994, 1997)
Species richness	MacroCAIC (MacIntosh)	Independent contrasts	Testing continuously distributed traits as possible causes of diversification	Agapow & Isaac (2002)

Analysis by Independent Contrasts (CAIC). CAIC is intended for continuously distributed traits and operates essentially by computing, at each internal node, an ancestral state that is a trait average of the respective daughter lineages (Purvis & Rambaut, 1995). ML methods also exist to examine correlated evolution *via* ICs. The program DISCRETE is applicable to pairs of binary traits, whereas CONTINUOUS can be used on pairs of continuously distributed characters (Pagel, 1994, 1997).

To examine the possible roles of particular traits in cladogenesis, MacroCAIC (Agapow & Isaac, 2002) uses ICs (in a fashion similar to CAIC) to test whether or not lineages with a given character state are more prone to diversification.

Sister clade comparisons can be implemented when some (but not all) of a clade's phylogeny is known or when the nature of the data set violates underlying assumptions of other IC methods. These are similar to IC except that sister clades diverged from a single node (by definition) and thus can be assumed to be of the same age (Cracraft, 1981). Thus, sister clade comparisons automatically correct for divergence time. In favourable cases (when knowledge about a cladogram's structure is strong and a trait in question originated multiple times independently), it is possible to conduct many sister clade comparisons and search for overall statistical signal using a sign test, a randomization test for matched pairs, or some other appropriate statistical method (Nee *et al.*, 1996, Vamossi & Vamossi, 2005). Sister clade comparisons are advantageous in that the researcher need not know the structure of the entire cladogram, but they can suffer from serious reductions in statistical power because attention is confined to less than all internal nodes.

ACTINOPTERYGIIAN PHYLOGENY

Large-scale comparative phylogenetics requires cohesive cladograms involving perhaps hundreds or thousands of taxa. Although such phylogenies exist (at least in provisional form) for several major eukaryotic groups (Sibley & Ahlquist, 1990; Jones *et al.*, 2002; Davies *et al.*, 2004), until recently the paucity of useful phylogenetic data and confusion surrounding several key taxonomic assemblages (Johnson, 1993) had hindered even preliminary attempts to phylogenetically resolve the entire Actinopterygii. This situation is changing, thanks in large part to the publication of full mitochondrial genomic sequences from numerous fish species (Ishiguro *et al.*, 2003; Miya *et al.*, 2003; Saitoh *et al.*, 2003, Inoue *et al.*, 2004). These recent molecular studies have sampled broadly across the entire Actinopterygii, and when combined with numerous lower level phylogenies (both morphological and molecular) have created the first opportunities to assemble higher level supertrees for the entire actinopterygian clade.

In this review, reference will often be made to a family-level actinopterygian supertree that was generated by Mank *et al.* (2005) based on the published cladogenetic structures in 38 source phylogenies for various partially overlapping actinopterygian groups. The source phylogenies themselves had been based on diverse types of molecular and phenotypic data. More than 500 binary-coded bits of intercalated cladogenetic data (as illustrated methodologically in Fig. 2) went into construction of the supertree, which actually is a 90% consensus phylogeny of 25 000 equally parsimonious trees based on

extensive heuristic computer searches. That consensus supertree resolved 228 of the 421 recognized actinopterygian families representing all of the 42 recognized orders and their approximately 10 000 extant species. Most of the unresolved families were in the traditional order Perciformes, which has proved to be highly polyphyletic (Johnson, 1993, Miya *et al.*, 2003). Other findings summarized in this review came from taxonomically more focused supertrees, such as the 1544-species atherinomorph supertree (Mank & Avise, 2006b), or from more specific lower taxa phylogenies referenced hereafter.

New phylogenetic information can be incorporated into existing supertree data matrices with relative ease (although subsequent maximum parsimony searches of these large matrices can be computationally intensive and time consuming). This relative ease of revision is advantageous because all supertrees are inherently provisional, always pending improvement as additional phylogenetic information becomes available.

MALE REPRODUCTIVE TACTICS

Ray-finned fishes probably display more diversity in male reproductive tactics than any other vertebrate clade. Many fishes spawn in mass conspecific aggregations where scramble competition and sperm competition are likely to be primary reproductive determinants of male fitness. At the other end of the spectrum, in many fish species, a territorial male (which often exhibits costly sexually selected traits) pairs with just one or a few females. In effect, these 'bourgeois' males attempt to monopolize the reproductive output of associated females to the fitness detriment of other males (Emlen & Oring, 1977; Gross, 1996; Taborsky, 2001). In response to this reproductive challenge, various alternative reproductive tactics have evolved by which other males seek to break the monopoly that bourgeois males otherwise hold on fitness enhancing resources.

These male alternative reproductive tactics (MARTs) have been catalogued (Taborsky, 1994, 1998, 2001; Gross, 1996) and can generally be divided into parasitic and cooperative behaviours. Sneaking, the most common parasitic tactic, involves sneaker males that lack sexually selected body ornaments and by virtue of speed or stealth attempt to steal fertilizations by releasing sperm onto the nests of bourgeois males during spawning episodes. Female mimicry, another form of parasitic behaviour, involves males which look or behave like females and thereby dupe territorial males to gain access to spawning sites where they deposit sperm. Piracy is the least common parasitic MART, usually employed only by large males that display sexually selected traits. A pirate can fertilize eggs after evicting a territorial male from a spawning site, but he may also depart after one or a few spawns, leaving the bourgeois male to guard what could be a mixed-parentage brood. Finally, cooperative MARTs may be employed by satellite males (which often lack sexually selected phenotypic traits). Satellite males are tolerated by bourgeois males, and their presence near a nest may help attract females. Satellite males may also help bourgeois males defend territories and care for offspring in exchange for fertilization opportunities.

THE ORIGIN AND EVOLUTION OF MARTS

Various MARTs described above have proved to be scattered throughout the actinopterygian supertree (Mank & Avise, in press-*b*). Comparative endocrinological analyses, however, suggest that similar parental behaviours observed in distantly related species are proximally mediated by similar hormone profiles (Fig. 3). Thus, selection appears likely to have shaped the expression of reproductive hormones (or their receptor proteins) to produce convergent MARTs repeatedly across the ray-finned fishes (Knapp, 2004; Fitzpatrick *et al.*, 2005). Hormones under potential convergent selection include arginine vasotocin, which results in secondary sexual characteristics and spawning behaviour both in females and in female mimics (Foran & Bass, 1998, 1999; Carneiro *et al.*, 2003), and 11-keto-testosterone that controls sexually selected traits and spawning behaviour both in bourgeois and in pirate males (Brantley *et al.*, 1993; Borg, 1994; Ros *et al.*, 2004).

In addition to implicating evolutionary convergence for the hormonal controls of MARTs, comparative phylogenetic analyses have identified evolutionary pathways of increasing MART complexity (Fig. 4). Namely, the first and numerically predominant evolutionary response to attempted mate monopolization often appears to involve sneaker tactics. This makes biological sense because, being the simplest of the MARTs, sneaking is often a conditional strategy based on body size, with small males acting as sneakers early in life and later transitioning to bourgeois tactics (Gross & Charnov, 1980; Mazzoldi & Rasotto, 2002; Aubin-Horth & Dodson, 2004; Leiser & Itzkowitz, 2004). On some occasions, this adaptation may subsequently become genetically embedded in lineages when a heritable mechanism evolves such that sneaker fathers tend to sire sneaker sons (Heath *et al.*, 2002).

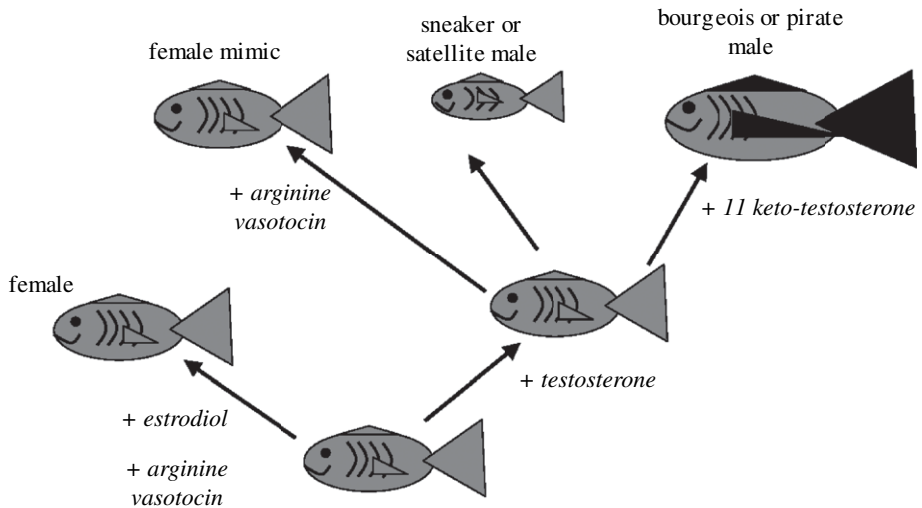


FIG. 3. A generalized model for endocrine hormone profiles underlying various MARTs in actinopterygian fishes. The multiple origins of various male reproductive tactics across the actinopterygian phylogeny may rest in part on convergent evolution in underlying hormones and hormone receptor functions (see text).

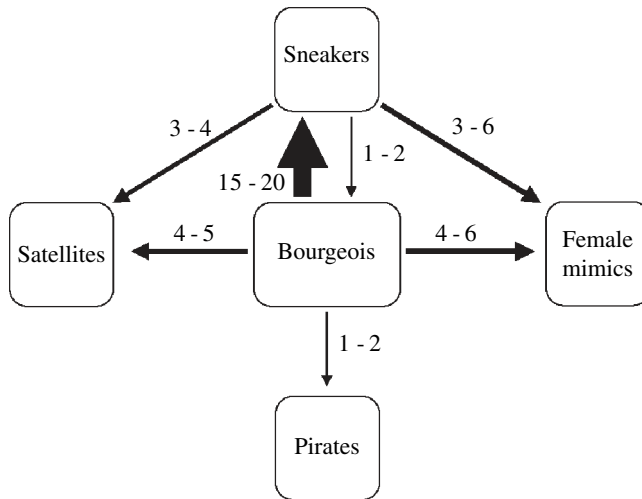


FIG. 4. Results from comparative phylogenetic analyses of MARTs in actinopterygian fishes (after Mank & Avise, in press-b). Alternative mating tactics evolve in response to mate monopolization; therefore, distinct pairing is the inferred ancestral state to bourgeois and MART strategies. Arrow sizes correspond to mean estimated numbers of parsimony-inferred evolutionary transitions between different MARTs, and numbers beside arrows indicate minimum and maximum estimates under maximum parsimony reconstruction criteria.

Furthermore, according to the phylogenetic analysis, in some lineages, sneaking has transitioned to one or the other of two presumably more complex MARTs: female mimicry and satellite behaviour (Fig. 4). This too seems biologically plausible. Female mimicry requires the addition of ‘female’ reproductive behaviour and morphology to sperm production, so it would seem to represent a level of complexity beyond simple sneaking, and satellite tactics would seem to require the addition of elaborate cooperative behaviours to mere sneaking per se (Stiver *et al.*, 2005). The phylogenetic reconstructions, however, have also implied more direct routes to female mimicry and satellite behaviour from bourgeois tactics, suggesting that sneaking may not always be a necessary intermediate step.

Finally, phylogenetic analyses gave no indication that piracy is consistently integrated as a component of these evolutionary pathways (Mank & Avise, in press-b). Perhaps the phenomenon is under-reported in the literature, or perhaps selective forces acting upon this late-in-life type of adaptation are rather weak, reducing the likelihood that this tactic could be incorporated into a generalized evolutionary pathway.

PARENTAL CARE

Parental strategies influence fecundity and other life-history traits and have also been shown to affect cladogenetic patterns in fishes (Lydeard, 1993). Extensive catalogues of parental behaviours in ray-finned fishes (Breder & Rosen, 1966; Blumer, 1979, 1982) indicate that approximately 20% of actinopterygian taxonomic families contain at least some species in which adults provide post-zygotic care of one sort or another, ranging from internal gestation

by females (or by males in the case of syngnathid pipefishes and seahorses), to external brooding by either or both parents. The evolution of parental care can be conceptually divided into two pathways: one for species with external fertilization and the other for species in which syngamy occurs inside the female reproductive tract.

SPECIES WITH EXTERNAL FERTILIZATION

Although maternal or bi-parental care of offspring is displayed by a few actinopterygian fishes with external fertilization, parental care (when present) is normally provided primarily or exclusively by males (Blumer, 1979, 1982). Typically, a male maintains and defends a spawning territory (often including a nest) where he may mate with several females successively during a spawning cycle. Thus, males tend to be in close physical proximity to their progeny from earlier spawns, probably accounting in part for a common evolutionary progression from defence of a mating territory to paternal care for developing embryos and fry. Indeed, a phylogenetic reconstruction of care-giving behaviours on the current actinopterygian supertree has indicated that paternal care tends to evolve repeatedly in lineages in which males build and defend spawning sites (Mank *et al.*, 2005).

Results from parsimony reconstructions have further indicated that maternal and bi-parental care have also arisen on multiple occasions in the Actinopterygii, thus making it possible to evaluate competing models of parental care evolution (Fig. 5). Under the stepping-stone hypothesis originally developed for labroid fishes (Gittleman, 1962; Barlow, 1974; Gross & Sargent, 1985), bi-parental care is an intermediate transitional state between paternal and maternal care. Under a competing independent-origins model developed for anuran frogs (Summers *et al.*, 1999), the three categories of parental care (maternal, paternal and bi-parental) arise separately from care absence and

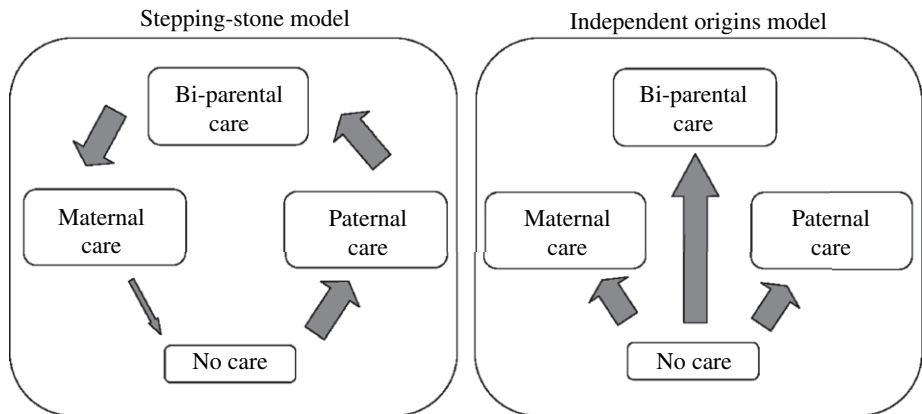


Fig. 5. Competing hypotheses regarding the evolution of parental care evolution in species with external fertilization (see text). Recent comparative phylogenetic analyses tend to favour the independent origins model for actinopterygian fishes.

are not linked in any evolutionary progression. For actinopterygian fishes, comparative phylogenetic analyses indicate that the evolution of parental care conforms better to the independent origins model (Mank *et al.*, 2005).

SPECIES WITH INTERNAL FERTILIZATION

Internal fertilization obviously affects proximity relationships between parents and embryos. For species with female-internal syngamy (both in zygoparity where fertilized eggs are laid shortly after mating and in viviparity where embryos are delivered live-born after a lengthy internal gestation), the mother is closely associated with her developing offspring, whereas males typically have long departed. Given this spatio-temporal situation, males tend to be freed from obligate offspring care, undoubtedly explaining why female-internal fertilization and maternal-only care (*via* pregnancy and/or external brooding) are closely linked phylogenetically (Gross & Shine, 1981; Mank *et al.*, 2005).

Internal gestation requires complex suites of behavioural, morphological and physiological adaptations (Amoroso, 1968; Schindler & Hamlett, 1993) related to the requirements for copulations (as opposed to gamete release) as well as subsequent offspring nurturing. Despite these seemingly major biological hurdles, live-bearing has evolved multiple times in the ray-finned fish clade (Breder & Rosen, 1966; Lydeard, 1993; Reznick *et al.*, 2002; Mank & Avise, 2006*b*). Preliminary evidence further suggests that live-bearing may sometimes have involved evolutionary convergence at particular loci such as the gene encoding an insulin-like factor that controls foetal growth and development (Lawton *et al.*, 2005).

Phylogenetic analyses also add strength to the notion that live-bearing is highly adaptive because most lineages with internal fertilization have proceeded to internal gestation, whereas relatively few lineages exhibit external brooding (Mank *et al.*, 2005). Furthermore, livebearing lineages in the Actinopterygii appear to exhibit significantly higher rates of cladogenesis than externally brooding sister clades (Lydeard, 1993; Mank & Avise, 2006*b*).

GENOMIC PERSPECTIVES

A growing understanding of extant actinopterygian genomes, although not yet as sophisticated as genetic knowledge for mammals and birds, is also providing new opportunities for comparative phylogenetic evaluations of evolutionary patterns and processes.

MODES OF SEX DETERMINATION

The mechanism by which sex is determined can greatly influence the sex ratio in a population. Under sex chromosome systems, *e.g.* Mendelian segregation and syngamy tend to produce 1:1 sex ratios in the absence of confounding factors, whereas environment-conditioned sex determination can in some cases produce highly unequal numbers of males and females. Sex ratio in turn is an important component in such evolutionary considerations as effective population size and mating systems (Hartl & Clark, 1997), and it can play an enormous

role in the evolution of sexually selected traits (Kvarnemo & Ahnesjö, 1996; Wade & Shuster, 2004).

In some large vertebrate clades, particular modes of sex determination have been conserved over vast stretches of evolutionary time. For example, birds have maintained a single sex chromosome system (female ZW heterogamety) across their 150-million-year existence (Fridolfsson *et al.*, 1998, Handley *et al.*, 2004), and mammals have retained another sole mechanism of sex determination (male XY heterogamety) since their origin approximately 250 million years ago (Foster & Graves, 1994; Lahn & Page, 1999). Such evolutionary conservatism can aid in analyses of how a single category of sex determination may change through time (Ellegren & Carmichael, 2001; Iwase *et al.*, 2003), but this lack of diversity also precludes studies of how categorically different sex-determination systems originate and interconvert.

The situation in actinopterygian fishes is remarkably different, with many distinct types of sex-determining systems having evolved over the past 230 million years. These include both XY and ZW systems, constitutive autosomal sex determination, hermaphroditism, unisexuality and various environmentally mediated mechanisms of sex determination (Devlin & Nagahama, 2002). Indeed, sex-determining mechanisms in actinopterygian fishes are so variable that the primordial ancestral state remains unresolved (Mank *et al.*, 2006b), and even the basic molecular mechanisms of sex determination are poorly characterized for the vast majority of this clade (Nanda *et al.*, 2002, Kondo *et al.*, 2003; Volff *et al.*, 2003).

Phylogenetic investigations have made clear that the major categories of sex determination have each arisen on multiple independent occasions throughout the evolutionary history of actinopterygians. Few, if any other vertebrate clades match this level of diversity nor do they generally show such high rates of evolutionary change in this seemingly complex trait.

Closer phylogenetic examination has revealed more. First, despite its fairly common occurrence and multiple origins, unisexuality (gynogenesis and hybridogenesis) clearly is a derived and evolutionarily short-lived condition in fish lineages (Avise *et al.*, 1992). Second, much the same can be said for hermaphroditism (Smith, 1975; Mank *et al.*, 2006b), an adaptation often associated with reef species, possibly due to their pelagic dispersal syndrome (Ghiselin, 1969). Third, although it was previously understood that convergent evolution must have resulted in multiple independent origins of both male heterogametic and female heterogametic sex chromosomes (Solari, 1994; Ota *et al.*, 2000; Woram *et al.*, 2003), supertree analyses have further revealed just how remarkably labile heteromorphic sex chromosomes systems in fishes can be (Mank *et al.*, 2006b). In some cases, single genera and even individual species simultaneously display both XY and ZW modes of sex determination (Devlin & Nagahama, 2002).

Much remains to be learned at the DNA sequence level about sex chromosome evolution in fishes. The genomes of only two species (both pufferfishes) have been fully sequenced to date (Aparicio *et al.*, 2002; Jaillon *et al.*, 2004), but they both lack discernible sex chromosomes; and only limited regions of sex chromosomes have been sequenced in a handful of other fish species (Harvey *et al.*, 2003; Felip *et al.*, 2004; Peichel *et al.*, 2004).

COMPARATIVE GENOMICS

Several rounds of large-scale or even genome-wide gene duplications have been provisionally documented within the Actinopterygii, both near the evolutionary root of teleostean fishes (Wittbrodt *et al.*, 1998; Meyer & Schartl, 1999; Robinson-Rechavi *et al.*, 2001; Christoffels *et al.*, 2004) and near the base of several major clades nested therein (Uyeno & Smith, 1972; Allendorf & Thorgaard, 1984; Ferris, 1984; Larhammar & Risinger, 1994; Vasil'ev, 1999). These duplications, together with the proliferation of several families of repetitive elements (Voff *et al.*, 2001*a, b*; Nogare *et al.*, 2002), rapid changes in insertion/deletion ratios (Neafsey & Palumbi, 2003), repeated origin and dissolution of heteromorphic sex chromosomes (Mank *et al.*, 2006*b*) and smaller scale chromosomal re-patterning (*e.g. via* illicit recombination of non-homologous chromosome segments), indicate that genomic architecture in the Actinopterygii is evolutionarily dynamic. These genomic alterations have also resulted in reduced levels of genetic synteny compared to some otherwise comparable vertebrate clades (Thomas *et al.*, 2003). It thus seems utterly remarkable that chromosome counts show a strongly leptokurtic or peaked frequency distribution (centred at $2N = 48$ and $2N = 50$) across teleostean species and higher taxa (Mank & Avise, in press-*a*). Thus, for reasons that remain completely unknown, the extreme evolutionary dynamism displayed by many internal structural features of fish genomes have all occurred within the context of an extreme evolutionary conservatism in chromosome numbers.

GENOMIC CATALYSTS OF DIVERSITY

The genomic enlargements and rearrangements mentioned above have been suggested as engines that may have helped drive the diversification of the teleost fishes (Meyer & Malaga-Trillo, 1999; Meyer & Schartl, 1999; Taylor *et al.*, 2003; Hoegg, 2004). These ideas are based on empirical findings coupled with conceptual models of how evolutionary radiations might relate to these kinds of genomic alterations (Stephens, 1951; Ohno, 1970; Lynch & Force, 2000; Lynch, 2002; Navarro & Barton, 2003*a, b*). Comparative phylogenetic analyses of extant actinopterygian genera are consistent with these notions: substantial increases in genome size appear to be significantly correlated with increased bursts of cladogenesis (Mank & Avise, 2006*a*). Whether these changes in genome size arose through proliferations of transposable elements, regional gene duplications, or whole-genome polyploidizations generally remain unknown, however.

Unusually high rates of genomic change may also partially explain the diversity of sex-determining mechanisms in actinopterygian fishes (Devlin & Nagahama, 2002; Mank *et al.*, 2006*b*). Illicit recombination, where crossing-over occurs between non-homologous regions of the genome, is perhaps an important factor behind the repeated origin of particular sex chromosome modes and the frequent and rapid evolutionary inter-conversions among them. This process could, *e.g.* move sex-determining genes from constitutive to inducible promoters (and *vice versa*), fostering changes to and from ecological (or other condition dependent) controls of sex.

Non-homologous recombination of chromosomes or chromosomal segments is often promoted when repetitive elements proliferate in a genome (McDonald, 1990, 1995, 1998; Capy, 1997; Brosius, 1999), a phenomenon that has been documented in several fish lineages (Kawakami *et al.*, 2000; Nogare *et al.*, 2002). Cytogenetic rearrangements can also be fostered *via* recombination among translocated gene duplicates, perhaps further contributing to the rapid evolution of sex-determining mechanisms in fishes. Particular gene duplications might also play a role. Gene duplicates often assume new but related functions (Dulai *et al.*, 1999; Manzanares *et al.*, 2000) that can alter the flow of existing molecular pathways. This phenomenon has been linked to changes in the sex-determination pathway for at least one fish species, *Oryzias latipes* (Nanda *et al.*, 2002), and future comparative genomic analyses may well reveal examples in other species as well. All of this genomic action would be evolutionarily ineffective if it were not also the case that fishes in general show strong developmental flexibility (*e.g.* compared to mammals and birds) with regard to gonadal and sexual differentiation.

THE MULTIFARIOUS ROLE OF SEXUAL SELECTION

Sexual selection derives from inequities in reproductive potentials between males and females, an imbalance that results in mate-choice and mate-access competition among individuals of either sex (Gould & Gould, 1997). In fishes, sexual selection has been shown to be a cause of the following: sexual dichromatism wherein one sex is brighter or more ornately patterned than the other (Endler, 1980; Houde & Endler, 1990; Amundsen & Forgren, 2001), elongated fins (Harrington, 1997; Marcus & McCune, 1999; Kuwamura *et al.*, 2000), presence of breeding tubercles (Kortet *et al.*, 2003, 2004) and presence of electrical mating calls (Curtis & Stoddard, 2003).

Many of the reproductive syndromes described in previous sections of this article alter the reproductive efforts required for males or females. Theoretically, any exacerbation or alleviation of sexual selection could result in a gain or loss, respectively, of sexually selected traits. Recent comparative work has uncovered many of the ways in which sexual selection is linked to the evolution of phenotypic diversity in the ray-finned fishes. Additionally, the widespread occurrence of sexually selected traits in conjunction with other forms of phenotypic diversity makes Actinopterygii an ideal clade for testing numerous theoretical predictions about the causes and consequences of sexual selection.

MARTS AND SEXUAL SELECTION

MARTs can be interpreted as a response to mate monopolization (Taborsky, 1994, 1998, 2001), and some theoretical relationships between mate acquisition tactics and sexual selection seem relatively clear. Mate monopolization often promotes differential reproductive output among males, a classic contributor to sexual selection (Emlen & Oring, 1977). From this perspective, MARTs and sexually selected traits might be phylogenetically associated with one another by virtue of having arisen from the same sets of evolutionary pressures. In support of this hypothesis, phylogenetic correlation analysis across the

ray-finned fishes (Mank & Avise, in press-*b*) has shown that lineages exhibiting MARTs also tend to be those in which sexually selected ornaments are present in bourgeois males. Furthermore, MARTs were not phylogenetically associated with male brood care, thus suggesting that they often have arisen from selection on males to circumvent mate monopolization rather than brood care avoidance.

SEXUAL SELECTION AND PARENTAL CARE

Investments in parental care can alter the skew between the sexes in terms of reproductive energy burdens, theoretically resulting in an evolutionary link between sexual selection and parental behaviours. Indeed, like other physical manifestations of sexual selection in male fishes, such as bright colours, elongated fins and other bodily features, sexual selection has been implicated as a contributing factor in the evolution of paternal care. For example, nest-tending male sticklebacks and gobies have been shown to act as better parents when in the presence of potential mates (Ostlund & Ahnesjo, 1998; Pampoulie *et al.*, 2004). Comparative phylogenetic analysis of the actinopterygian super-tree is consistent with the notion that sexual selection and paternal care are intertwined because lineages with male parental care also significantly tend to exhibit sexually selected traits (Mank *et al.*, 2005). Further analyses will be needed to clarify whether sexual selection causally influences or simply is correlated with male parental investment.

In the ray-finned fishes, sexual selection on males is also significantly associated with live-bearing, according to comparative phylogenetic analyses (Mank *et al.*, 2005). Internal gestation, which entails protection and nourishment of embryos, in effect merely amplifies an inherent asymmetry already present between males and females with respect to energetic investment in individual gametes (by virtue of anisogamy—the pronounced difference in size between egg cells and sperm cells). By increasing the differential reproductive potential between the sexes, internal gestation can theoretically exacerbate the forces of sexual selection on males.

SEX CHROMOSOMES AND SEXUAL SELECTION

The evolutionary lability of sex chromosomes in fishes makes these animals uniquely well suited for phylogenetic tests of several models predicting that sexually selected male ornaments (such as showy fins) should arise more often under female heterogamety than under male heterogamety (Fisher, 1952; Lande, 1981; Kirkpatrick & Ryan, 1991; Reeve & Pfennig, 2003; Kirkpatrick & Hall, 2004; Albert & Otto, 2005). This theoretical prediction is based on the special inheritance pattern of heterogametic sex chromosomes, combined with the assumption that genes controlling expression of a sexually selected male ornament and genes that control female preference for that trait are tightly linked on a sex chromosome. More specifically, only under female heterogamety would a showy male bequeath his Z chromosome (containing this linkage group) to his sons (who would be showy) as well as to his daughters (who would prefer showy males). No analogous outcome arises under male

heterogamety because a showy male would either bequeath his Y chromosome to his sons only or his X chromosome to his daughters only. Thus, the combined sex linkage of genes for both male ornament and female preference should increase the likelihood that a male ornament would sweep through a female heterogametic population and thereby facilitate the spread of sexually selected traits in species with ZW sex chromosome systems.

Empirical support for this theory has come from studies on a few isolated species (Prowell, 1998; Iyengar *et al.*, 2002), and the association between female heterogamety and male ornaments has been anecdotally invoked to explain the profusion of male ornaments in birds (which are all ZW) compared to mammals (which are XY). A critical comparative phylogenetic evaluation of this theory across the Actinopterygii, however, found no such expected association (Mank *et al.*, 2006a). This indicates either that the theoretical models do not apply to fishes (for any of several possible reasons, such as autosomal control of sexually selected traits) or that the relationship between the chromosome mode of sex determination and male adornments is too small to be detected.

This 'negative' result does not mean that sex-determination mode plays no role in the evolution of sexually selected characters. For example, any autosomal (Sola *et al.*, 1981; Chourrout, 1986; Solari, 1994) or environmental (Devlin & Nagahama, 2002) factors that might act to bias sex ratios could thereby also affect both the form and the intensity of sexual selection.

SEXUAL SELECTION AND TAXONOMIC DIVERSIFICATION

Sexual selection can lead to increased taxonomic diversification when mating preferences result in assortative mating and reproductive (prezygotic) isolation (Darwin, 1871; Lande, 1981, 1982; West-Eberhard, 1983). Increased prezygotic isolation would be expected to accelerate taxonomic diversification compared to post-zygotic barriers to gene flow, which can require long periods of time to accumulate. This theory linking sexual selection and cladogenesis has been anecdotally invoked to explain observed patterns of diversity in some clades of ray-finned (actinopterygian) fishes (McMillan *et al.*, 1999; Mendelson, 2003), especially for the cichlids (Dominey, 1980; Knight *et al.*, 1998; Maan *et al.*, 2004). These theoretical predictions and anecdotal invocations were recently substantiated by a comparative appraisal throughout the Actinopterygii that found a link between manifestations of sexual selection and increased rates of taxonomic diversification (Mank, in review).

LIMITATIONS OF THE COMPARATIVE METHOD

Although comparative phylogenetic analyses can add insights into evolutionary processes, they also suffer from several inherent limitations that stem either from the underlying biological phenomena addressed or from technical aspects of the analyses themselves. First, the comparative method is necessarily limited by data available from extant lineages (or, in the case of palaeontological approaches, secure fossil evidence). This means that brief transitional states that leave little or no trace in extant species, or traits that increase extinction risks and thereby remove lineages from available modern samples, are difficult to

identify and study with the comparative method. An example germane to the current review involves MARTs. Phylogenetic analyses suggest that these alternative reproductive tactics by males often evolve along pathways of increasing complexity, with sneaking arising first and subsequently transitioning in some cases to female mimicry or satellite behaviours (Mank & Avise, in press-*b*). At face value, the phylogenetic analyses also indicate that these latter behaviours sometimes arose directly from the bourgeois tactic (Fig. 4). The available analyses, however, cannot eliminate the possibility that sneaking typically existed as a transient intermediate that simply has gone undetected in the phylogenetic reconstructions.

More generally, the incidence of short-lived adaptations can be underestimated by comparative phylogenetic methods. The phenomenon of unisexuality provides another example. Supertree reconstructions identified three separate origins for unisexuality in the actinopterygian clade (Mank *et al.*, 2006*b*), but finer-scale examinations and more direct evidence (Avise *et al.*, 1992) prove that this is a gross underestimate. Unisexual lineages suffer from reduced adaptive ability, which greatly increases their extinction risk (Stanley, 1975; Vrijenhoek *et al.*, 1977, 1985). Without extant modern descendents, even common ancient states can be overlooked in comparative phylogenetic appraisals alone.

A second category of difficulties arises when evolutionary transitions among character states (including those that survive to the present) have been frequent in the clade under consideration. In such cases, maximum parsimony and other reconstruction methods usually cannot specify with any precision the actual numbers or exact cladogenetic placements of particular transitions. In such cases, researchers may have to be content in concluding merely that the trait in question is evolutionarily labile.

Another limitation is that a truly thorough comparative phylogenetic analysis would often require corrections for tree branch lengths (or times since shared ancestry). In the usual absence of a complete and accurate fossil record, researchers are forced to rely on molecular clocks to date internal nodes in a phylogeny, but these can be rather erratic and inaccurate (Langley & Fitch, 1974; Rodriguez-Trelles *et al.*, 2001; Kolaczkowski & Thornton, 2004). Divergence dates can be especially difficult to determine for many supertrees due to the amalgamated and often heterogeneous nature of their underlying data matrices. Because time-dated phylogenies are normally far more difficult to estimate reliably than are cladograms, this general problem of temporal estimation afflicts nearly all current phylogenetic research (comparative or otherwise), at least to some extent.

Finally, it is wise to remember that any findings from comparative phylogenetics are inherently descriptive (rather than experimental) and correlational (rather than causal). Although comparative phylogenetics offers some powerful and relatively novel tools for biological inquiry, its findings should normally be interpreted mostly as helpful starting points for further evolutionary investigations.

FUTURE DIRECTIONS

Further comparative work on the actinopterygians should proceed on several fronts. With respect to phylogeny estimation *per se*, much work remains.

Great strides have recently been made in clarifying historical relationships among many of the 400+ taxonomic families of ray-finned fishes, both through traditional phylogenetic sequence analysis (as exemplified by Ishiguro *et al.* 2003; Miya *et al.* 2003; Inoue *et al.* 2004) and through the Bar Code of Life initiative for fish (www.fishbol.org). Despite these steps, the phylogenetic information available to date (as published in the first actinopterygian supertrees) is sufficient to resolve only about 50% of extant families. Most lower level phylogenies are no more complete.

With respect to genomic features, the molecular era has barely dawned on the Actinopterygii, and researchers studying this clade lack the extensive comparative genomic tools available for higher vertebrate clades. Furthermore, the only two genera (*Fugu* and *Tetraodon*) with completed draft sequences (Aparicio *et al.*, 2002; Jaillon *et al.*, 2004) were chosen precisely because they contain unusually compact genomes that were relatively straightforward to sequence. But this fact could also make these species poor or misrepresentative models for evolutionary genomics in fishes. Additional genomic resources are in development for many fish species (Volf, 2005), but the great diversity of actinopterygian fishes means that researchers will need many reference points for meaningful comparative analyses.

Another promising front involves new developments linking reproductive evolution to its underlying molecular mechanisms. For a handful of well-studied species, researchers have worked out key molecular details of sex determination (Nanda *et al.*, 2002; Volf *et al.*, 2003), viviparity (Lawton *et al.*, 2005), internal fertilization (Zauner *et al.*, 2003) and spawning strategies (Ros *et al.*, 2004), but much work remains to be accomplished before we can know whether particular molecular mechanisms are shared across the Actinopterygii.

CONCLUSIONS

Despite their spectacular diversity of morphologies, life histories, behaviours and genomic features related to reproduction, ray-finned fishes historically have been underutilized in comparative evolutionary studies. This situation is gradually changing with recent developments in actinopterygian genomics and the elaboration of analytical methods for generating and analysing large cladograms in a comparative phylogenetic context. As we have tried to illustrate here, these scientific advances are creating many exciting opportunities for capitalizing upon the exuberant biological diversity of the world's largest vertebrate clade.

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