

# Evolutionary Origins of Viviparity in Fishes

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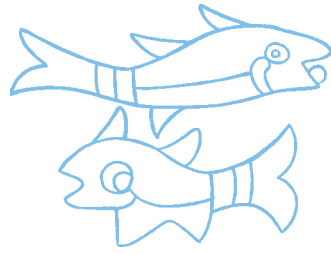
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## Abstract

Phylogenetic analyses have proven to be valuable in the characterization of evolutionary transformations, including the evolution of reproductive patterns. Application of such methods to fishes reveals that viviparity has originated on at least 29 separate occasions, distributed as follows: teleosts, 11 origins; basal actinopterygians, 1 origin; actinistians (coelacanth), 1 origin; elasmobranchs, 15 origins; and holocephalans, 1 origin. Five of the origins of viviparity in elasmobranchs are based on the assumption that oviparity in skates is primitive, not secondarily derived. The origins of viviparity are spread widely over geological time; some can be traced to the Paleozoic and Mesozoic, whereas others appear to be much more recent. Data derived from a phylogenetic approach can be used to test hypotheses about selective pressures, evolutionary sequences, protoadaptations and constraints affecting the evolution of viviparity.

## Resumen

Se ha demostrado que los análisis filogenéticos son muy valiosos en la caracterización y cuantificación de transformaciones evolutivas, incluyendo la evolución de patrones reproductivos. La aplicación de estos métodos en los peces revela que la viviparidad se ha originado en, al menos, 29 ocasiones separadas, distribuidas de la siguiente manera: teleósteos, 11 orígenes; actinopterygios, 1 origen; actinostios (celacantos), 1 origen; elasmobranquios, 15 orígenes, y holocéfalos, 1 origen. Cinco de los orígenes de la viviparidad en elasmobranquios se basan en la hipótesis de que la oviparidad en rayas es primitiva, no derivada secundariamente. El origen de la viviparidad está ampliamente disperso a lo largo de los tiempos geológicos; algunos se remontan al Paleozoico y al Mesozoico, mientras que el origen de otros parece ser mucho más reciente. Datos derivados de un acercamiento filogenético pueden utilizarse para probar hipótesis sobre presiones de selección, secuencias evolutivas, protoadaptaciones y restricciones que han afectado la evolución de la viviparidad.



## Introduction

The existence of viviparity in fishes raises difficult but fascinating questions about the evolution of this reproductive pattern. For more than a century, biologists have considered how live-bearing reproduction has evolved in fishes and other vertebrates, and have speculated about selective pressures, constraints, and historical sequences. Such speculation has produced a variety of hypotheses, but has offered little way to distinguish between true explanations and those that are merely plausible. For example, several factors are postulated to have affected the evolution of viviparity among fishes, including habitat, climate, egg size, and maternal defense ability (for reviews, see Wourms, 1977; Compagno, 1990; Wourms and Lombardi, 1992). Likewise, researchers have disagreed on whether viviparity evolved once or multiple times in particular groups, such as cyprinodontiform fishes (*e.g.*, Hubbs, 1924; Breder and Rosen, 1966). Conflicting evolutionary scenarios also are available for evolution of reproductive features in sharks (Smedley, 1927; Wourms *et al.*, 1988) and matrotrophy in atherinomorphs (Turner, 1947; Miller, 1979; Wourms *et al.*, 1988).

The methods of phylogenetic analysis offer a powerful means of testing hypotheses about the evolution of viviparity and other biological features. Phylogenetic analyses draw on the principles of cladistics to reconstruct evolutionary transformations in quantitative and qualitative terms. As applied to squamate reptiles, this approach has allowed us to distinguish and define

the numerous independent origins of viviparity, and to test hypotheses about factors that have affected the evolution of this reproductive pattern (Blackburn, 1982, 1985a, 1999a, 2000a; Shine, 1985; Méndez de la Cruz *et al.*, 1998). This approach also has facilitated reconstructions of the evolution of placentation in mammals (Luckett, 1977) and squamates (Blackburn, 1995, 1998; Stewart and Thompson, 1996), as well as the historical relationship between viviparity and matrotrophy in amniotes (Blackburn, 1992).

The present analysis uses a phylogenetic approach to identify the independent origins of viviparity that have occurred in fishes. That viviparity has evolved convergently a number of times among fishes is apparent from even a casual acquaintance with their systematics and reproduction. Indeed, the idea that piscine viviparity has originated on multiple occasions has been raised by workers for many decades (*e.g.*, Hubbs, 1924; Turner, 1938a, 1942; Kent, 1965; Breder and Rosen, 1966), and has figured into various reviews and analyses (*e.g.*, Hogarth, 1976; Wourms, 1977, 1981; Parenti, 1981; Wourms *et al.*, 1988; Compagno, 1990). This paper draws on and updates a general analysis of vertebrate viviparity (Blackburn, 1985b); most of that analysis has been published, but the piscine portion has appeared only in summary form (Blackburn, 1992, 1999b). A recent study focusing on elasmobranchs (Dulvy and Reynolds, 1997) offers an opportunity to compare independent analyses of these fishes,

and implications of the different assumptions on which they are based. Findings from the present paper are available for the testing of hypotheses about how viviparity and matrotrophy have evolved among fishes.

### Piscine Reproductive Patterns

Comparisons of diverse species warrant a standard terminology for reproductive patterns. Inconsistent terminologies have caused considerable confusion, particularly between researchers working on different vertebrate groups. For example, some researchers have extended the concept of “viviparity” to all species with internal fertilization, a usage that would include all chondrichthyans and reptiles, as well as birds and monotremes. Most other researchers apply the term to species that give birth to their young, while still others confine it to those that provide nutrients for development by placental means. These and related inconsistencies have been discussed elsewhere (Wourms, 1981; Blackburn, 1994, 2000b).

The bipartite classification developed for fishes by Prof. John Wourms (1981) has provided a simple but effective means of classifying vertebrate reproductive diversity, and has been adopted by most researchers working on fishes as well as amniotes. Accordingly, species are classified as oviparous or viviparous, depending on whether they lay eggs or give birth to their young. As applied to vertebrates in general, species that lay developing eggs that only hatch some time after existing the mother are classified on the oviparous side of the dichotomy (Blackburn, 2000b). The classification of otherwise diverse taxa as viviparous emphasizes important similarities between species in which young develop to term inside the maternal reproductive tract, and emerge as autonomous, free living offspring. A separate distinction is based on whether nutrients for development come from the yolk (lecithotrophy) or an alternative maternal source (matrotrophy) (Wourms, 1981; Wourms *et al.*, 1988; Blackburn, 1999c). For complementary characterizations of piscine reproductive patterns, see Balon (1975, 1981) and Compagno (1990).

### Methods of Analysis

To analyze piscine reproductive patterns phylogenetically, reproductive data for all available taxa were collected from the literature. Major

reviews (Bertin, 1958; Budker, 1958, 1971; Amoroso, 1960; Breder and Rosen, 1966; Hoar, 1969; Wourms, 1977, 1981; Dodd, 1983; Compagno, 1988; Wourms *et al.*, 1988; Hamlett, 1989; Wourms and Lombardi, 1992; Hamlett *et al.*, 1993; Hamlett and Hysell, 1998) offered valuable guides to the primary literature on reproduction. Unknown taxa were assumed to share the same reproductive mode as their closest relatives (*i.e.*, members of the same family, subfamily, or order). Reproductive data were superimposed over established phylogenies, cladograms, and phylogenetically-based classification systems, and the most parsimonious interpretations of reproductive evolution were adopted throughout. To avoid circularity, phylogenies and classifications that relied heavily on reproductive characters generally were avoided; one case where that was not possible is considered below. Based on outgroup analysis and the taxonomic distribution of oviparity, this pattern was assumed to be ancestral for each of several major piscine clades: Chondrichthyes, Euselachii (elasmobranchs), Sarcopterygii, Actinopterygii, and Teleostei (Wourms, 1977, 1981; Wourms and Lombardi, 1992). Each of these groups is deemed monophyletic (see the contributed chapters in Stiassny *et al.*, 1996). The analysis provisionally was based on the assumption that viviparity evolves irreversibly from oviparity. As discussed below, relaxing the latter assumption notably affected the interpretation of only a single clade.

### Origins of Viviparity

Among bony fishes, at least 13 evolutionary origins of viviparity can be recognized, as listed in Table 1. Each of the origins represents a separate viviparous clade derived from a more inclusive group that also contains oviparous species. Therefore, under the assumptions that oviparity is plesiomorphic and that viviparity evolves irreversibly, each taxon listed must represent a separate origin of the live-bearing reproductive mode. All but two of these origins are found among the Teleostei. Most of the latter (8 out of the 11) have occurred at subfamilial levels; however, two have occurred at familial levels (Embiotocidae, Comephoridae), and one, at a supra-familial level (Bythitoidei). The two nonteleost origins (Actinistia and a basal actinopterygian, *Saurichthys*) are based at least in part on evidence from the fossil record. Inferences of reproductive mode from fossils can be risky, but in these cases,

**Table 1.**

Evolutionary origins of viviparity among bony fishes. For most clades, the reproductive references are representative of those available. Phylogenetic references are restricted to those documenting relationships between viviparous clades and their oviparous relatives. Possible additional origins are indicated in the text.

	<b>Reproductive data</b>	<b>Phylogenetic data</b>
Actinistia <sup>a</sup>	Watson, 1927; Smith <i>et al.</i> , 1975; Wourms <i>et al.</i> , 1980	Cloutier and Ahlberg, 1996; Panchen and Smithson, 1987; Schultze, 1987
<i>Saurichthyes</i>	Bürgin, 1990	Grande and Bemis, 1996; Bemis <i>et al.</i> , 1997
Zoarcidae <sup>a</sup>	Andriashev, 1954, 1986; Breder and Rosen, 1966; Mead <i>et al.</i> , 1964; Korsgaard and Petersen, 1979	Andriashev, 1954, 1986; Anderson, 1994; Nelson, 1994
Bythitoidei <sup>b</sup>	Mead <i>et al.</i> , 1964; Nielsen, 1969; Wourms and Cohen, 1975; Cohen and Nielsen, 1978; Nielsen <i>et al.</i> , 1999	Nielsen, 1969; Cohen and Nielsen, 1978; Nelson, 1994
Hemirhamphidae <sup>a</sup>	Weed, 1933; Breder and Rosen, 1966; Soong, 1968; Wourms, 1981; Meisner and Burns, 1997	Rosen and Parenti, 1981; Anderson and Collette, 1991; Lauder and Liem, 1993; Meisner, 2001
Poeciliinae <sup>a</sup>	Turner, 1937a, 1940a; Gordon, 1955; Rosen and Bailey, 1963; Thibault and Schultz, 1978; Grove and Wourms, 1991	Parenti, 1981; Meyer and Lydeard, 1993; ( <i>cf.</i> Ghedotti, 2000)
Goodeinae	Turner, 1933, 1937b; Mendoza, 1938; Lombardi and Wourms, 1985a,b; Schindler <i>et al.</i> , 1988	Meyer and Lydeard, 1993; Parenti, 1981; Webb, 1998
Anablepinae	Turner, 1938a, 1940b,c, 1957; Miller, 1979; Knight <i>et al.</i> , 1985; Schindler and de Vries 1988; Ghedotti <i>et al.</i> , 2001	Parenti, 1981; Meyer and Lydeard, 1993; Ghedotti, 2000
Sebastinae (Scorpaenidae)	Graham, 1956; Krefft, 1961; Moser, 1967; Takemura <i>et al.</i> , 1987; Takahashi <i>et al.</i> , 1991; Wourms, 1991	Eschmeyer, 1969; Nelson, 1994
Comephoridae	Chernyayev, 1971, 1974	Gosline, 1973; Nelson, 1994; Hunt <i>et al.</i> , 1997
Embiotocidae	Eigenmann, 1894; Hubbs, 1921; Turner, 1938b; Wiebe, 1968; Webb and Brett, 1972; Gardiner, 1978	Greenwood <i>et al.</i> , 1966; Nelson, 1994
Clinidae <sup>a</sup>	Springer, 1970; Veith, 1979; George and Springer, 1980; Gunn and Thresher, 1991	Penrith, 1969; Springer, 1970; George and Springer, 1980; Nelson, 1994
Labrisomidae <sup>a</sup>	Rosenblatt and Taylor, 1971	Springer, 1970; Rosenblatt and Taylor, 1971; George and Springer, 1980; Nielsen <i>et al.</i> , 1999

<sup>a</sup> In part; <sup>b</sup> Aphyonidae, Bythitidae

the evidence is definitive. *Saurichthyes* is a Triassic genus, and fossils of pregnant females (representing two species) have been found to contain several developing embryos (Bürgin, 1990). The other case is represented in the fossil record by a specimen of the early Mesozoic form *Holophagus* (= *Undina*) (Watson, 1927; *contra* Schultz, 1972). Subsequent discovery of viviparity in extant *Latimeria* (Smith *et al.*, 1975 and more recent papers) corroborated this early inference.

Among chondrichthyans, 16 potential origins of viviparity were identified (Table 2). All but one are represented by extant elasmobranchs, the exception being that of the holocephalan *Delphyodontos dacriformes* of the Lower Carboniferous (Lund, 1980). Of the 15 origins found among elasmobranchs, three have occurred at sub-generic levels (*Halaelurus*, *Galeus*, *Apristurus*), and the remainder at ordinal or other supra-familial levels. Recognition of multiple origins of viviparity among batoids and their allies is based on the assumption that oviparity in rajids is plesiomorphic. Five of these origins are eliminated if one assumes that oviparity in Rajidae has evolved secondarily, as discussed below.

## Discussion

This analysis has distinguished a total of 29 separate evolutionary origins of viviparity among fishes. Previously, a minimum of 105 origins have been defined among reptiles (Blackburn, 1999a, 2000a) and 5-6 origins among amphibians (Blackburn, 1985b; also see Wake, 1993; Wake and Dickie, 1998). Thus, the piscine origins represent approximately 20% of the origins now recognizable within the subphylum Vertebrata.

### Osteichthyan Origins of Viviparity

The 13 origins defined among bony fishes (Table 2) are firmly established, and few if any are likely to be eliminated as further information accumulates. The origins are widely scattered taxonomically, being found in 6-7 separate orders, each of which consists chiefly of oviparous species. In one large teleost order with multiple origins of viviparity (Cyprinodontiformes), cladistic relationships among the viviparous lineages are well established (Parenti, 1981; Meyer and Lydeard, 1993; Webb, 1998); alternative interpretations (Ghedotti, 2000) do not challenge recognition of the three origins as indepen-

dent. Likewise, within two other large orders with multiple origins of viviparity (Scorpaeniformes and Perciformes), the viviparous clades are not closely related to one another. Rather, they tend to belong to separate sub-ordinal taxa (*e.g.*, subfamilies) in which oviparous species predominate (classification of Nelson, 1994). Thus, the viviparous clades defined herein clearly represent independent lineages whose viviparity has originated convergently. With one exception based on new information (that in *Saurichthyes*), these origins are essentially those recognized in an unpublished analysis from several years ago (Blackburn, 1985b). Phylogenetic data that have accumulated since that time chiefly have served to corroborate and redefine the origins recognized. Likewise, the defined origins largely are congruent with the list of families with viviparous species tabulated by Wourms (1981; also see Wourms *et al.*, 1988) –a reflection of the fact that viviparity in bony fishes generally has evolved at familial and sub-familial levels. In contrast, in squamate reptiles, viviparity often has evolved at sub-generic levels (Blackburn, 1999a), requiring detailed information on intergeneric relationships for phylogenetic analysis.

Because this analysis has adopted conservative interpretations of reproductive evolution, additional, undetected origins of viviparity are very likely among teleosts. For example, multiple origins are quite possible in the large ophidiiform group Bythitoidei (*sensu* Nelson, 1994). Given that reproductive mode has been used in this group to define and unite the families Bythitidae and Aphyonidae (Cohen and Nielsen, 1978; also see Mead *et al.*, 1964), to recognize these fishes as a single origin of viviparity involves circular reasoning. However, our current understanding of phylogenetic relationships hinders further definition. Another origin may be represented by the Parabrotulidae, a small family in which viviparity has long been known (Parr, 1933; Turner, 1936; Nielsen, 1968). Although parabrotulids were previously thought to be closely related to zoarcids (Nielsen, 1968), they appear to be allied with the viviparous Bythitoidei (Mead *et al.*, 1964; Nelson, 1994). Pending a better understanding of their phylogenetic relationships, the parabrotulids conservatively are not treated here as a separate origin of viviparity; however, alternative interpretations are plausible. Another potential case of viviparity, not counted in the present analysis, involves interpretation of a fos-

**Table 2.**

Evolutionary origins of viviparity among chondrichthyans. Reproductive references are representative of those available. Phylogenetic sources justify recognition of the viviparous clades and their relationships with oviparous groups. Use of alternative phylogenetic interpretations only modestly affects the analysis (see Table 3).

	<b>Phylogenetic data</b>	<b>Reproductive data</b>
<i>Delphyodontos</i>	Lund, 1980	Compagno, 1973; Nelson, 1994; Didier, 1995; de Carvalho, 1996
Hexanchiformes	Dean, 1903; Gudger, 1940; Breder and Rosen, 1966; Budker, 1971	Compagno, 1973, 1977; de Carvalho, 1996 (cf. Shirai, 1996)
Brachaeluridae, Orectolobidae	Waite, 1901; Last and Stevens, 1994	Dingerkus and DeFino, 1983; Dingerkus, 1984, 1986; Shirai, 1996
Ginglymostomatidae Rhincodontidae	Smedley, 1927; Gudger, 1940; Breder and Rosen, 1966; Joung <i>et al.</i> , 1996	Dingerkus, 1984, 1986; Dingerkus and DeFino, 1983; Shirai, 1996
Lamniformes	Springer, 1948; Balon, 1975; Compagno, 1984; Gilmore, 1993; Last and Stevens, 1994; Cox and Francis, 1997	de Carvalho, 1996; Shirai, 1996
<i>Apristurus saldanha</i> (Scyliorhinidae)	Wourms <i>et al.</i> , 1988; Compagno <i>et al.</i> , 1989	Compagno, 1984, 1988
<i>Galeus polli</i> (Scyliorhinidae)	Breder and Rosen, 1966; Compagno, 1984; Compagno <i>et al.</i> , 1989	Compagno, 1984, 1988
<i>Halaelurus lutarius</i> (Scyliorhinidae)	Bass <i>et al.</i> , 1975; Compagno, 1988; Wourms <i>et al.</i> , 1988	Compagno, 1984, 1988
<i>Eridacnis</i> , <i>Gollum</i> (Proscylliidae), Pseudotriakidae	Compagno, 1984; Compagno <i>et al.</i> , 1989	Compagno, 1988, 1990
Carcharinidae and its allies <sup>a</sup>	Breder and Rosen, 1966; Balon, 1975; Compagno, 1984, 1988; Randall, 1992; Last and Stevens, 1994; Cox and Francis, 1997	Compagno, 1988, 1990
Squaliformes	Breder and Rosen 1966; Compagno, de Carvalho, 1996; Shirai, 1996, 1984; Compagno <i>et al.</i> , 1989; Last and Stevens, 1994; Cox and Francis, 1997	
<i>Squatina</i> + Pristiophoridae	Whitley, 1940; Gudger, 1951; Breder McEachern <i>et al.</i> , 1996 (cf. de Breder and Rosen, 1966; Compagno, Carvalho, 1996; Shirai, 1996) 1984; Last and Stevens, 1994	
Torpediniformes	Compagno <i>et al.</i> 1989; Michael, McEachern <i>et al.</i> , 1996; Shirai, 1993; Last and Stevens, 1994; Cox 1996 and Francis, 1997	
Pristidae	Setna and Sarangdhar, 1949; McEachern <i>et al.</i> , 1996; Shirai, Bigelow and Schroeder, 1953; 1996; Compagno <i>et al.</i> , 1989; Michael, 1993; Last and Stevens 1994	
Rhiniformes Rhynchobatiformes	Whitley, 1940; Setna and Shirai, 1996; (also see McEachern, Sarangdhar, 1949; Bigelow <i>et al.</i> , 1996) Schroeder, 1953; Compagno, 1984; Michael, 1993	
Myliobatiformes	Bigelow and Schroeder, 1953; McEachern <i>et al.</i> , 1996; Shirai, 1996; Daiber and Booth, 1960; Breder and Rosen 1966; Compagno <i>et al.</i> 1989; Last and Stevens, 1994; Cox and Francis, 1997	

<sup>a</sup> Triakidae, Leptochariidae, Hemigaleidae, and Sphyrnidae.

sil of the Triassic form *Birgeria nielsenii* as being that of a pregnant female (Beltan, 1977). As a sister group to the (entirely oviparous) Acipenseriformes (Grande and Bemis, 1996), *Birgeria* would represent an independent origin of viviparity. However, because the inference of live-bearing habits in this species has been challenged on several grounds (Bürgin, 1990), this putative origin is in need of corroboration.

### Chondrichthyan Origins of Viviparity

Unlike the situation in osteichthyans, the viviparous chondrichthyan clades are not isolated phylogenetically among oviparous groups; furthermore, they commonly are represented at high (*e.g.*, ordinal) taxonomic levels. The situation reflects the fact that most sharks are viviparous (Wourms, 1981; Wourms *et al.*, 1988), with many of the oviparous species of chondrichthyans being confined to two speciose groups (Rajidae and Scyliorhinidae). As a consequence, to define the independent origins of viviparity requires an understanding of higher-order phylogenetic relationships. For this reason, to attempt to define the chondrichthyan origins of viviparity prior to the 1970s would have been difficult or impossible.

At present, despite some unresolved phylogenetic questions, multiple origins of viviparity can be defined with confidence (Table 2). For example, three of the origins have occurred at or near the level of individual species, in genera that also contain oviparous members (*Apristurus*, *Halaaelurus*, *Galeus*). The family Proscylliidae also contains both oviparous and viviparous species. Assuming that these four taxa are phylogenetically valid, they must represent at least four separate origins of viviparity. A fifth origin of viviparity in the extinct holocephalan *Delphyodontos* is incontrovertible, if Lund's (1980) inference of live-bearing habits is correct. Likewise, recognition of independent origins of viviparity in lamniforms and in carcharinids and their allies appears to be well-established (Dulvy and Reynolds, 1997; Table 2), being based on detailed cladistic reconstructions (Compagno, 1988; de Carvalho, 1996; Shirai, 1996).

Reproductive evolution in certain other groups may be less certain. In Orectolobiformes, the question of whether viviparity has evolved once (Blackburn, 1985b) or twice (Dulvy and Reynolds, 1997; this analysis) is based on phylogenetic interpretations that have not been firmly corroborated. Likewise, whether viviparity is

viewed as having evolved separately in Hexanchiformes (*sensu* Shirai, 1996) and Chlamydoselachiformes depends on the particular phylogenetic interpretation adopted (Blackburn, 1985b). Here, the more parsimonious interpretation of a single origin is assumed (Table 2). However, given that the groups may have been separated since the early Mesozoic (Shirai, 1996), convergent origins are quite plausible.

The conclusions reached in this analysis are similar to those of a previous, unpublished analysis (Blackburn, 1985b) (see Table 3). The latter was based in part on earlier phylogenetic interpretations that were not explicitly cladistic (*e.g.*, Compagno, 1973, 1977; Dingerkus and DeFino, 1983; Dingerkus, 1984). Differences between the two analyses of reproductive evolution are minor, and largely reflect a better understanding of phylogenetic relationships (*e.g.*, addition of one origin each in Lamniformes and Orectolobiformes) and accumulation of reproductive data (*e.g.*, addition of the origins in *Halaaelurus* and *Apristurus*). Conclusions reached in a third independent analysis (Dulvy and Reynolds, 1997) are also very similar (Table 3), the one notable difference having to do with reproductive evolution in the Squalea (including batoids). This difference reflects alternative assumptions about the likelihood of a reversal from viviparity to oviparity in Rajidae; allowing for a reversal eliminates the discrepancy (Table 3, footnote c). The fact that three independent analyses have reached such similar conclusions offers strong evidence that those conclusions are objective and relatively robust. While accumulation of more data will permit further refinement, there can be no question that viviparity in chondrichthyans has originated on multiple occasions. At least 16 origins can now be recognized, few of which are controversial under the assumptions governing this analysis.

### Reversibility of Reproductive Evolution

An underlying assumption of this analysis is that the transformation from oviparity to viviparity is irreversible. This assumption is commonly accepted in analyses of reproductive evolution, for both theoretical and empirical reasons. Although a recent paper suggested that viviparity frequently has reverted to oviparity in squamates (de Fraipont *et al.*, 1996), subsequent analyses have shown that the claim is unwarranted, and found no evidence that such a reversion has ever occurred (Blackburn, 1999a;

**Table 3.**

Alternative interpretations of the evolution of viviparity in chondrichthyans. Although based on somewhat different phylogenetic sources, conclusions of the analyses are similar. Differences mainly reflect different assumptions about the reversibility of viviparity in batoids.

	This study	Blackburn, 1985	Dulvy and Reynolds, 1997
<i>Delphyodontos</i>	1	1	0 <sup>d</sup>
<i>Chlamydoselachii</i>	0 <sup>a</sup>	1	0 <sup>b</sup>
Hexanchea	1	1	0 <sup>b</sup>
Orectolobiformes	2	1 (??)	2
Lamniformes	1	0 <sup>b</sup>	1
Scyliorhinidae			
<i>Apristurus</i>	1	0	0
<i>Galeus</i>	1	1	1
<i>Halaelurus</i>	1	0	1
Proscylliidae			
<i>Gollum, Pseudotriakis</i>	1	0 <sup>b</sup>	1
<i>Eridacnis</i>	0 <sup>b</sup>	0 <sup>b</sup>	1
Carcharinidae and allies	1	1	1 <sup>e</sup>
Squaliformes	1	1	1 <sup>f</sup>
<i>Squatina, Pristiophoridae</i>	1 <sup>c</sup>	2 <sup>c</sup>	0
Torpediniformes	1 <sup>c</sup>	1 <sup>c</sup>	0
Pristidae	1 <sup>c</sup>	1 <sup>c</sup>	0
Rhynchobatiformes and allies	1 <sup>c</sup>	1 <sup>c</sup>	0
Myliobatiformes	1 <sup>c</sup>	1 <sup>c</sup>	0
<b>Total</b>	<b>16</b>	<b>13</b>	<b>9-10</b>

<sup>a</sup> Viviparity in *Chlamydoselachii* may have evolved in common with other Hexanchiformes.

<sup>b</sup> Conservatively combined with another origin.

<sup>c</sup> These origins are based on the assumption that oviparity in Rajidae is plesiomorphic.

<sup>d</sup> An origin in holocephalans was mentioned but not included quantitatively.

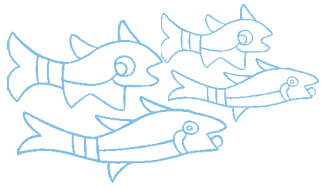
<sup>e</sup> The analysis mentions 5 to 6 origins in Carchariniformes, but defines 5.

<sup>f</sup> Combined with the subsequent taxa listed.

Shine and Lee, 1999; also see Lee and Shine, 1998). Furthermore, if re-evolution of oviparity from viviparity had occurred frequently, such would be apparent from the taxonomic distribution of reproductive modes. However, in reptiles and mammals, as well as in teleosts, viviparous species tend to be fairly derived representatives of their respective lineages in terms of non-reproductive characters.

Relaxation of the assumption that viviparity evolves irreversibly has little effect on the analysis of reproductive evolution in osteichthyans. None

of the defined origins of viviparity is eliminated, in part because the viviparous clades are so widely distributed phylogenetically. However, the interpretation of reproductive evolution in the Poeciliinae may require modification. A recent cladistic analysis of this subfamily found that the sole oviparous species (*Tomeurus gracilis*) does not occupy a basal position, and suggested that its oviparity is secondarily derived (Ghedotti, 2000). Assuming the phylogenetic conclusions to be valid, an alternative explanation is that viviparity has had multiple origins in the subfamily.



Among chondrichthyans, allowing for the possibility that viviparity can revert to oviparity does eliminate multiple origins of viviparity in the Squalia (Table 3; also see Compagno, 1977; Dulvy and Reynolds, 1997). The main reason is that the oviparous rajids are so deeply nested within the batoids and their squalan allies. In this analysis, a reversion to oviparity in rajids requires five fewer reproductive transformations (one origin of viviparity and one reversal to oviparity *vs.* six origins of viviparity). Strictly speaking, therefore, allowing for a reversion to oviparity offers the most parsimonious interpretation of reproductive evolution. However, since parsimony analysis is a principled methodological approach, not a guarantor of truth, the plausibility of this interpretation depends on the likelihood that oviparity has re-evolved from viviparity.

For oviparity in rajids to be secondarily derived would have required 1) a re-evolution of the eggshell (or at least a re-expression of the relevant genes); 2) deposition of the egg at a much earlier stage of development; 3) loss of specializations for matrotrophy; and 4) re-establishment of lecithotrophy. While not impossible, such modifications appear to be unprecedented in vertebrate history (Blackburn, 1985b; 1999a). On the other hand, viviparity is known to have evolved on at least 23 other occasions among fishes, and more than 100 times among squamate reptiles. Therefore, multiple origins of viviparity among batoids and their allies arguably is quite plausible. Furthermore, all elasmobranchs have internal fertilization, a major protoadaptation for viviparity (Blackburn, 1985b). In view of the strong evidence that vertebrate viviparity evolves from oviparity as a micro-evolutionary event, and given the paucity of evidence that the reverse transformation has ever occurred, a strong argument can be made for viewing rajid oviparity as plesiomorphic rather than secondarily derived. For the present, questions about the possible reversion to oviparity in rajids can be considered as unresolved, and in need of further study.

### Piscine Viviparity in Historical Perspective

The origins of viviparity in fishes are widely scattered over geological time. The earliest known origin among chondrichthyans for which evidence is available is that of the extinct holoccephalan *Delphyodontos*, from the Carboniferous (Lund, 1980). In osteichthyans, the earliest

known origins of viviparity are represented by fossils of the coelacanth *Holophagus* (Watson, 1927) and the actinopterygian *Saurichthyes* (Bürgin, 1990), both from the upper Triassic. Given that Orectolobiformes and Carchariformes both diversified in the Cretaceous (Carroll, 1988; Shirai, 1996), their origins of viviparity may also date to the Mesozoic. Thus, viviparity in both sarcopterygians and actinopterygians appears to date back as far as 240 million years ago, and in chondrichthyans, to about 380 million years ago.

Viviparity has evolved much more recently in other cases. For example, molecular data suggest that the viviparous Goodeinae began diversifying during the Miocene, about 14.5 million years ago (Webb, 1998). The species flock containing *Comephorus* dates to 4.9 million years ago (Hunt *et al.*, 1997), indicating a more recent origin of viviparity in this genus. Another recent origin has been suggested for *Chlamydoselachus*, on the grounds that a well developed egg capsule surrounds the egg throughout gestation (Dean, 1903). However, the genus is part of a viviparous clade that may date to the early Mesozoic (Shirai, 1996), and inferences about the timing of its reproductive evolution are tenuous, especially given its potential relationship to the hexanchids sharks. In any case, viviparity in fishes clearly has a long evolutionary history. Inferences that viviparity and internal fertilization first arose among fishes (Wourms, 1981) are well founded.

### Conclusions

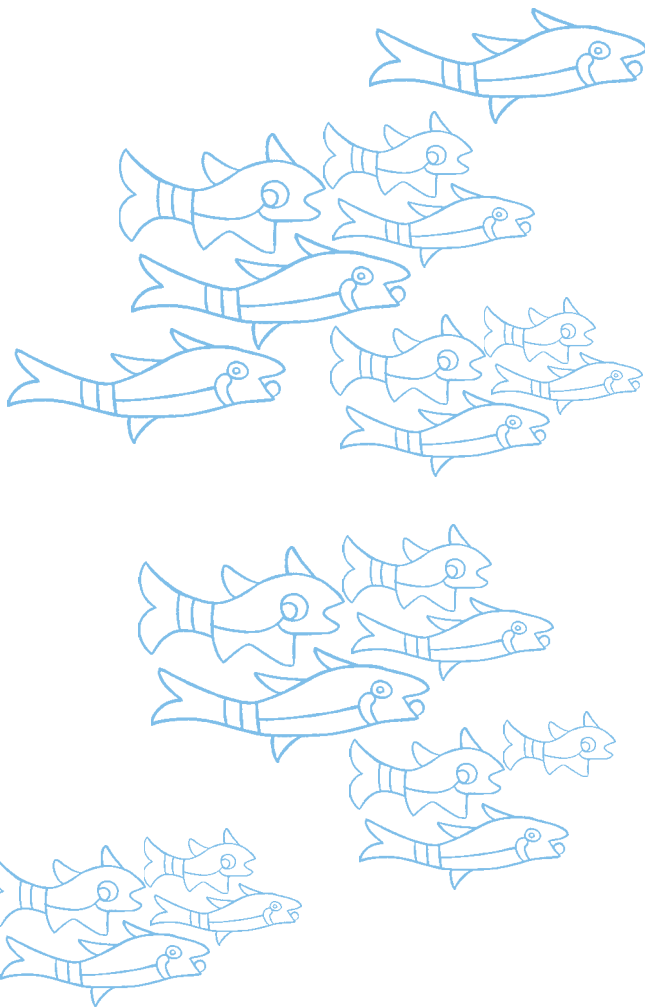
The evolution of viviparity may represent the most striking example of convergent evolution found among vertebrates (Blackburn, 1992). Over 140 independent evolutionary origins have now been distinguished, 29 of which have occurred among fishes. The definition of these origins of viviparity provides a basis for testing hypotheses about how and why this pattern has evolved, as well as for distinguishing the evolution of specializations for fetal nutrition. Given the vast ecological and reproductive diversity of viviparous fishes (Wourms, 1981; Wourms and Lombardi, 1992), whether meaningful evolutionary generalizations can be made and extended to viviparous amniotes remains to be determined. Phylogenetic approaches are particularly promising as tools for helping us understand the evolution of viviparity and associated reproductive specializations.

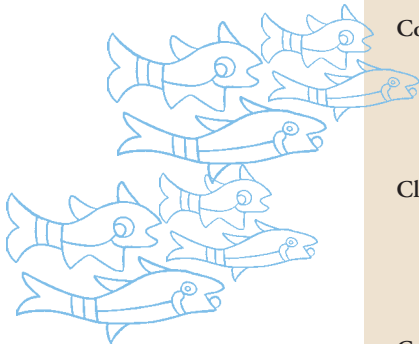
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