Evolutionary transitions among egg-laying, live-bearing and maternal inputs in sharks and rays

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SUMMARY

Sharks and rays are thought to have a large number of independent origins of live-bearing. We examined evolutionary transitions to live-bearing and maternal input to embryos in this subclass by optimizing reproductive characters onto a composite phylogeny. Egg-laying (40% of all species) is the likely ancestral reproductive mode for this clade, and there is evidence that live-bearing has evolved independently 9–10 times and maternal input 4–5 times. Most transitions (12–15) have been toward live-bearing with provisioning limited to yolk. These have occurred from egg-laying ancestors or live-bearing taxa that provide maternal input to embryos. Only 2–3 transitions have occurred in the other direction, i.e. away from yolk-only live-bearing. Egg-laying has evolved from live-bearing ancestors in skates, Rajidae (25% of all species) and possibly in the zebra shark, *Stegostoma fasciata*. Thus, although there has been an overall trend toward the evolution of live-bearing in elasmobranchs, the evolution of additional maternal input has been extremely labile.

1. INTRODUCTION

Vertebrate reproduction is typically characterized according to two key features: parity (live-bearing versus egg-laying), and mode of maternal input (transfer of nutrients to the embryo via a placenta or other means) (Wourms 1981; Blackburn 1992). Live-bearing and maternal inputs are thought to be selectively advantageous when benefits of increased offspring survival outweigh costs to the parent due to lower fecundity or mobility (Shine 1989; Clutton-Brock 1991; Roff 1992).

Live-bearing (viviparity) is much less common than egg-laying (oviparity) in the vertebrates, with a patchy phylogenetic distribution restricted to mammals, many reptiles, some amphibians and fishes (Shine 1989; Clutton-Brock 1991). It is thought to have arisen independently over 100 times in vertebrates (table 1). By contrast, the evolution of prepartum maternal input (matrotrophy) has been more conservative, with estimates of only 23–24 independent origins, with half of these transitions occurring in teleost (bony) fishes (table 1). The phylogenetic patchiness of live-bearing has hampered efforts to understand both the evolution of live-bearing from egg-laying, and the diversity of nutrient transfer modes from mother to embryo (Shine 1989; Clutton-Brock 1991).

Sharks and rays (Elasmobranchii: *ca.* 815 species) (Nelson 1994) are well suited for studying parity and maternal input because they are thought to have large numbers of independent origins of these traits (table 1). They exhibit all major vertebrate reproductive modes including two forms of egg-laying and at least five forms of live-bearing: yolk, uterine milk, oophagy, adelphophagy (intra-uterine cannibalism) and placental nutrition, as well as combinations of these (Nakaya 1975; Gilmore 1993; Wourms 1994).

This study reconstructs the evolution of elasmobranch live-bearing and maternal input and compares these trends with other vertebrate taxa. A phylogenetic analysis of these traits was used to distinguish between alternative possibilities for the ancestral character state in this clade, namely egg-laying (Wourms 1977) or live-bearing (Lund 1980). We provide an estimate for the number of transitions to live-bearing which is considerably lower than previously thought. We also show at least one direct reversal from live-bearing to egg-laying, and that overall, most transitions have been toward live-bearing with yolk-only nutrition (leicithotrophy).

2. MATERIAL AND METHODS

(*a*) *Phylogenetic tree reconstruction*

A composite phylogeny (figure 1) was assembled based on the assumption that elasmobranchs are monophyletic (Compagno 1973, 1977; Nelson 1994). Relationships between the distant outgroups (Teleostomi and Placodermi) of the elasmobranchs were treated conservatively as unresolved because their relationships are unclear (summarized by Nelson

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Table 1. *Proportion of live-bearers, number of independent origins of live-bearing and maternal input estimated in major vertebrate groups*

(Maternal input refers to the period between fertilization and birth. Based on Wourms (1981), Wourms & Lombardi (1992), Shine (1985, 1989), Wake (1989), Clutton-Brock (1991), Blackburn (1992) and this study.)

group	incidence of live-bearing (%)	transitions to live-bearing	transitions to maternal input (matrotrophy)
mammals	99	1–2	1
birds	0	0	0
reptiles	<15	98	3
amphibians	<10	5	3
teleost fishes	2–3	10–13	12
sharks and rays			
previous estimates	55	15–18	5
this study	40	9–10	4–5
totals (this study)		123–128	23–24

(1994)). The Chimaeriformes (ratfish or chimaeras) are a sister group of sharks and rays, which together comprise the Chondrichthyes (Compagno 1973; Nelson 1994; B. Mould, unpublished data). Ratfish relationships were resolved using Dingerkus (unpublished data) and Nelson (1994).

The phylogeny of de Carvalho (1996) was used for this study. This is a revision of Shirai (1992) and broadly concurs with Shirai (1996). The rajiform phylogeny of McEachran *et al*. (1996) was inserted at the location presented by de Carvalho (1996). This phylogeny is consistent with earlier evidence demonstrating that torpedo rays are the sister group of other rays, skates and allies (Muñoz-Chápuli *et al*. 1994; Chang *et al*. 1995). The ordinal arrangement of the galeomorphs by de Carvalho (1996) is well supported (Shirai 1992, 1996).

The cladistic phylogeny of the monophyletic Lamniformes (mackerel sharks) (Compagno 1990) is consistent with the molecular phylogenies of Martin *et al*. (1992) and Naylor *et al*. (1997), and was added at the location presented by Shirai (1992). The phylogenies of Carcharhiniformes (ground sharks) (Compagno 1988), and Orectolobiformes (carpet sharks) (Dingerkus 1983, 1986), were added at the locations presented by de Carvalho (1996). None of the phylogenies included reproductive characters in their reconstruction; therefore, any errors will be random with respect to estimates of transitions among reproductive modes.

(*b*) *Reproductive data*

Reproductive data were extracted from major texts and species catalogues published by the Food and Agriculture Organization of the United Nations (Breder & Rosen 1966; Compagno 1984*a*,*b*; 1988), and were supplemented by more detailed recent literature and correspondence with other researchers. This information was used to categorize taxa into modes of parity and nutrition, with terminology adapted from Wourms (1981), Compagno (1988, 1990), Blackburn (1992) and Yano (1992, 1993) (table 2). Since there are few data on mode 2, we have assumed these species to be live-bearing and combined these data with mode 3 for analysis. Reproduction in the tiger shark, *Galeocerdo cuvier*, is unclear, but maternal input is believed to occur (J. P. Wourms, personal communication). Therefore, this species has been classed as matrotrophic. Explicit reproductive data were available for all nine orders: 41 out of 42 families (including all 30 shark families), 116 out of 164 genera (sharks, 95 out of 102) and 350 out of 815 species (257 out of 359 sharks and 93 out of 456 rays) (Nelson 1994). Presentation of our phylogeny and estimates of the number of transitions therefore represent a wide range of taxa, but are necessarily conservative. Egg-laying is assumed to be ancestral in teleosts (Wourms 1981).

(*c*) *Analysis of character evolution*

The composite phylogeny was assembled using MacClade 3.0 (Maddison & Maddison 1992). All taxa were included for which we had information on reproduction and phylogenetic position. We used unordered character states, allowing any reproductive mode (table 2) to transform to any other using the Fitch parsimony option (Maddison & Maddison 1992). The minimum and maximum numbers of transitions between character states were calculated by hand because the tree included equivocal branches. Multiple nodes were treated as 'soft polytomies' because they were assumed to be unresolved rather than multiple speciation events.

The validity of transition counts based on figure 1 was assessed by comparing the number of transitions derived from alternative phylogenies: (1) Galeomorphii ordinal arrangement (Compagno 1988, p. 384 and fig. 21. 4a); (2) Squalea (Shirai 1996); (3) requiem sharks and allies, and mackerel sharks (Naylor 1992, Naylor *et al*. 1997); (4) *Mustelus–Triakis–Scylliogaleus* (Compagno 1988, p. 395 and fig. 21. 8a) and (5) *Gollum* and *Pseudotriakis* (Compagno 1988, p. 392 and fig. 21. 6c).

3. RESULTS

(*a*) *Transitions between egg-laying and live-bearing*

The most parsimonious reconstruction of reproductive modes had 20 steps (figure 1). This phylogeny suggests that egg-laying is ancestral in chondrichthyans. In the Squalea, live-bearing has evolved once and egg-laying has been derived from live-bearing once. Live-bearing has evolved twice in the carpet sharks (Orectolobiformes), once in the mackerel sharks (Lamniformes) and 5–6 times in the ground sharks (Carcharhiniformes) (figure 1). Overall, live-bearing is the commonest form of parity, occurring in 60% of species (figure 2) and has evolved 9–10 times from egg-laying (figure 3*a*). Conversely, egg-laying has been derived from live-bearing twice, once at the base of the skate family (Rajidae) and in a carpet shark, *Stegostoma fasciata*. The derived form of egg-laying is found in 25% of species (figure 2). This is supported by the sequence of appearance of contemporary squalean taxa in the fossil record (table 3). This shows that, within the same lineage, egg-laying skates appeared later than live-bearing ancestors.

(*b*) *Maternal provisioning of embryos*

Within live-bearers the commonest form of maternal input is yolk supplemented with uterine analogues of milk (matrotrophy), which is found in 31% of species (figure 2). Yolk-only live-bearing (leicithotrophy) is the second commonest mode (18% of species). Placental structures are found in only 9% of species (figure 2).

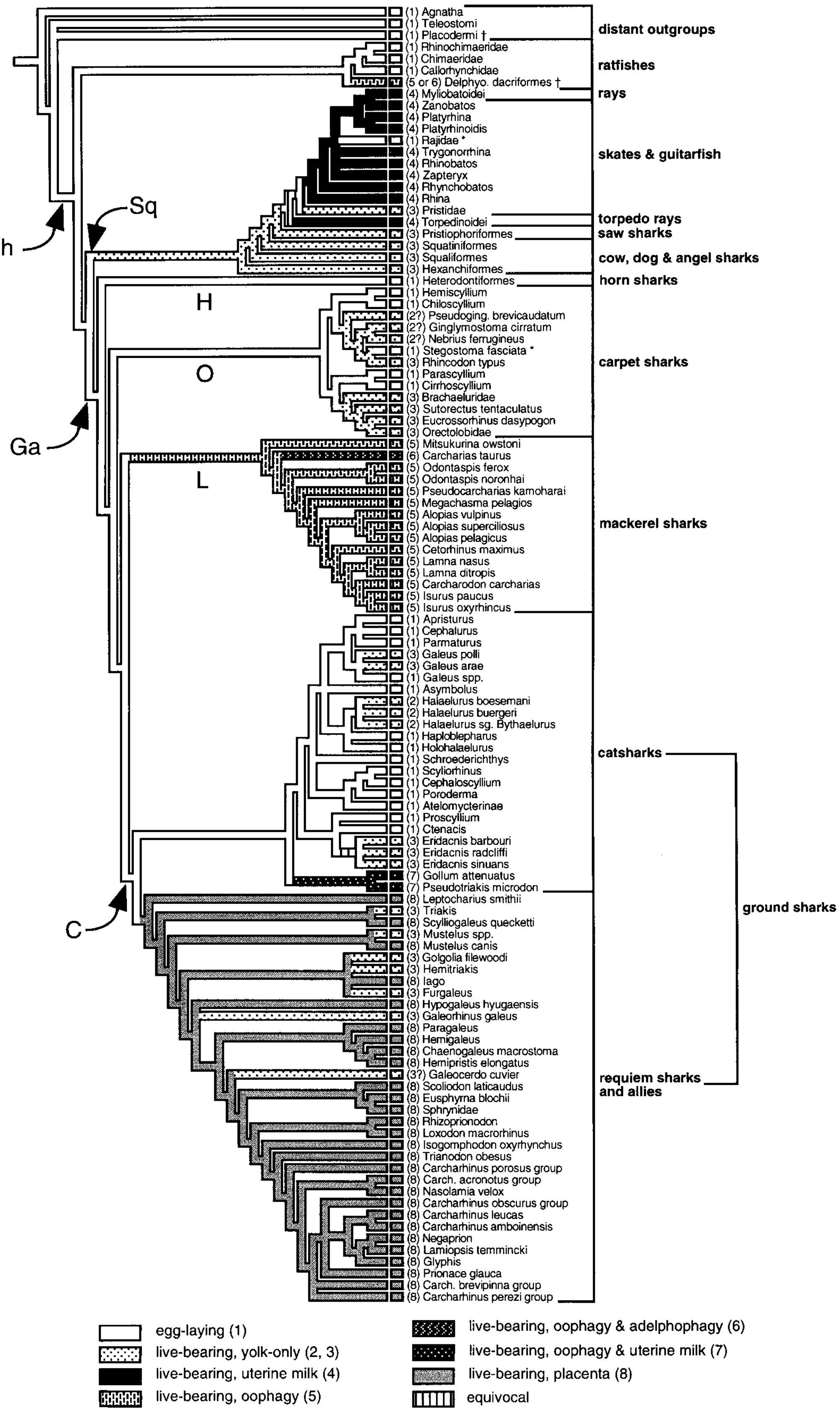

Figure 1. Phylogenetic distribution of reproductive modes in elasmobranchs and their outgroups. Character states assigned to each taxon are shown in parentheses in front of each taxon name and refer to the reproductive modes shown in table 2. Asterisks indicate taxa exhibiting a reversal to egg-laying. † indicates extinct taxa. **Ch** indicates the chondrichthyan clade (sharks, rays and ratfish). **Sq** and **Ga** indicate the suborders Squalea and Galeomorphii, respectively. Within the Galeomorphii, each order is denoted by letters at the base of each clade; **H** = Heterodontiformes, **O** = Orectolobiformes, **L** = Laminformes and **C** = Carcharhiniformes. The remaining five orders are within the Squalea. The *Carcharhinus* complex is as described by Compagno (1988).

Table 2. *Reproductive modes and definitions used in the character reconstruction*

(Based on Wourms (1981), Campagno (1988, 1990), Blackburn (1992) and Yano (1992, 1993).)

code	parity mode	nutrition mode	technical term	description
1	egg-laying	yolk	oviparity, single or extended oviparity	paired eggs laid, embryos derive nourishment solely from the yolk. Egg membrane sclerotinized to form a case. Most development outside mother, e.g. Rajidae, Heterodontiformes and Scyliorhinidae
2	egg-laying	yolk	multiple or retained oviparity	several egg-cases accumulate in each oviduct and are retained, unhatched, for up to several months before being laid, resulting in embryos at slightly different stages of development. Note: in some species eggs may be retained until development is complete, whereupon hatching and parturition coincide, e.g. some Orectolobiformes and *Halaelurus* spp. (see methods)
3	live-bearing	yolk	leicithotrophic viviparity or ovoviparity	embryo retained until birth, when development is complete. Embryos feed solely on yolk, e.g. Hexanchiformes, Squaliformes, Squatiniformes, Pristiophoriformes and some *Galeus* spp.
4	live-bearing	yolk plus maternal contribution	matrotrophy; uterine milk	embryo feeds initially on yolk, supplemented by indirect absorption of uterine fluid enriched with mucus, fat or protein through specialized structures, e.g. Torpedinoidei, Rhinidae, Rhinobatidae and Myliobatidae
5	live-bearing	yolk plus maternal contribution	matrotrophy; oophagy	mother continues to ovulate; embryos feed solely on the ova produced after the yolk sac is absorbed, e.g. all Lamniformes apart from *Carcharias taurus*
6	live-bearing	yolk plus maternal contribution	matrotrophy; adelphophagy	embryos feed initially on yolk, then ova, and then cannibalize siblings, e.g. *Carcharias taurus*
7	live-bearing	yolk plus maternal contribution	matrotrophy; oophagy and uterine milk	mother continues to ovulate; these ova are consumed by embryos and replenish the external yolk sac. Villified embryonic surfaces indicate absorption of uterine milk, e.g. *Gollum attenuatus* and *Pseudotriakis microdon*
8	live-bearing	placental	matrotrophy	nutrition supplied by the mother via a direct placental blood vessel link to embryo. Some species may also supplement placental nutrition with uterine milk. Villified surfaces on the embryo allow absorption of nutrients in addition to those transferred via the placental link, e.g. mainly Triakidae, Hemigaleidae, Carcharhinidae and Sphyrinidae, with some exceptions

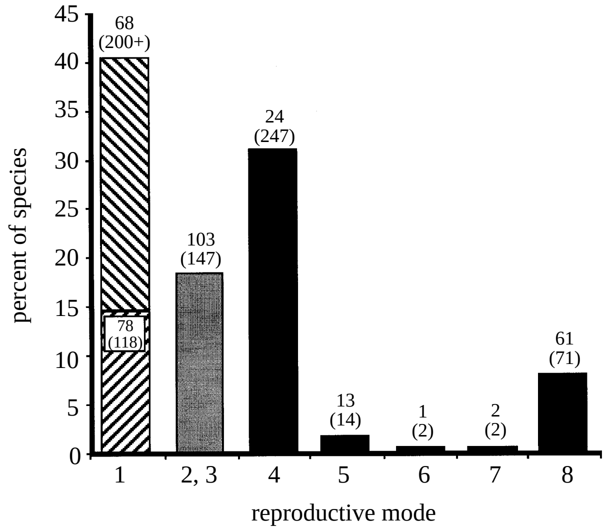

Figure 2. Approximate frequencies of reproductive modes by percent of elasmobranch species. This is based on an assumption that all taxa within a clade have the same reproductive mode as for those which we have data (species with data = 350). The number above each bar shows the actual number of species for which data were available, and the number in parentheses indicates the number of species to which these data were extrapolated. Egg-laying (diagonal shading), live-bearing with yolk-only (grey shading) and live-bearing with maternal input (black) are as coded in table 2. The upper portion of the egg-laying bar represents egg-laying derived from live-bearing ancestors.

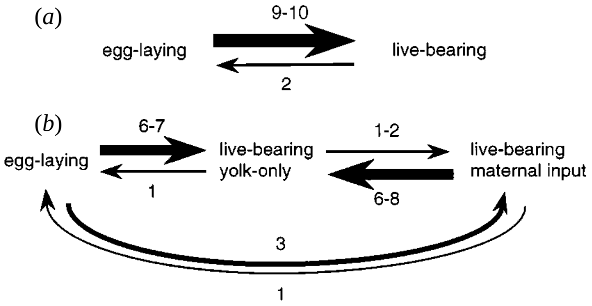

Figure 3. (*a*) Transitions between egg-laying and live-bearing. (*b*) Transitions among egg-laying, live-bearing yolk-only (no maternal input), and live-bearing with maternal input. Arrow width is proportional to the number of transitions.

Maternal input beyond providing yolk (matrotrophy) is inferred to have evolved 4–5 times (figure 3*b*). There have been numerous reversals, to either egg-laying (one) or yolk-only live-bearing from live-bearing with maternal input (6–8) (figure 3*b*). Yolk-only live-bearing appears to be the most stable state with a total of 12–15 transitions toward this mode, yet only 2–3 transitions away from this mode. There appear to have been three transitions directly from egg-laying to maternal input (figure 3*b*).

Several distinct modes of maternal input have evolved independently. Oophagy has evolved twice, once in the catsharks (*Gollum* and *Pseudotriakis*) and once in mackerel sharks. Placentation is found only in the Carcharhiniformes (ground sharks) and appears to have evolved 1–2 times with 4–7 reversals (figure 1).

Table 3. *Date of appearance of a ratfish outgroup and selected squalean families in the fossil record and their mode of reproduction*

(Summarized from Cappetta *et al.* (1993).)

order: family	date of appearance (millions of years before present)	mode of reproduction
Chimaeriformes: Chimaeridae	311.3	ancestral egg-laying
Hexanchiformes: Hexanchidae	203.3	live-bearing yolk only
Squatiniformes: Squatinidae	157.1	live-bearing, yolk only
Rajiformes: Rajidae	97	derived egg-laying
Rajiformes: Dasyatidae	97	live-bearing uterine milk

(*c*) *Comparison with other possible trees*

Comparison of transition counts across alternative phylogenetic hypotheses do not alter the major patterns illustrated by our results: (1) galeomorph ordinal arrangement does not change the transition counts; (2) an alternative Squalea arrangement is less equivocal, with one less reversal from live-bearing (maternal input) to live-bearing (yolk-only); (3) alternative requiem sharks and allies and mackerel shark arrangements do not change transition counts; (4) an alternative *Mustelus–Triakis–Scylliogaleus* arrangement does not change transition counts; and (5) an alternative *Gollum* and *Pseudotriakis* arrangement results in one less transition from egg-laying to live-bearing (maternal input).

4. DISCUSSION

(*a*) *Ancestral reproductive mode*

These results support earlier suggestions that egg-laying is ancestral in sharks, rays and ratfishes (Wourms 1977; Wourms & Lombardi 1992), contrary to the possibility that live-bearing with intra-uterine feeding is ancestral (Lund 1980). The ancestral nature of egg-laying is supported by the presence of egg-laying in the outgroups Agnatha, Placodermi and Teleostomi, and in more closely related Chimaeriformes, despite live-bearing in the extinct ratfish, *Delphyodontus dacriformes* (Lund 1980). The absence of claspers in the cladoselachians (ancestral fossil elasmobranchs) may also support the ancestral nature of egg-laying (J. P. Wourms, personal communication).

(*b*) *Evolutionary transitions to live-bearing*

The available data suggest that live-bearing has evolved from egg-laying between nine and ten times, considerably lower than the 18 transitions estimated by Wourms & Lombardi (1992) and Wourms (1994). The latter estimate was based on character reconstruction restricted to the galeomorph phylogenies of Compagno (1988). Nonetheless, our results still support Wourms's general view of elasmobranchs as having a high degree of evolutionary flexibility in the reproductive mode. This estimate now ranks elasmobranchs below reptiles and teleost fishes in terms of the number of transitions to live-bearing.

(*c*) *Reversal to egg-laying*

We have identified two reversals from live-bearing to egg-laying (Rajidae and the zebra shark, *S. fasciata*). The interpretation of derived egg-laying in Rajidae is much more parsimonious than an alternative possibility, that egg-laying has been retained throughout the clade with live-bearing having evolved independently between 12 and 13 times (see phylogenies in figure 1 and Shirai (1996), respectively). The reversal in *S. fasciata* must be treated with caution because it is nested within a clade exhibiting a facultative reproductive mode (multiple oviparity). Also, it may be an artefact of poor knowledge of reproduction in this order. The sequence of squalean taxa in the fossil record also supports a reversal to egg-laying from live-bearing in Rajidae (table 3). Macroevolutionary conclusions based on the fossil record are robust and stable (Benton 1994) and the elasmobranch fossil record shows good congruence with phylogenetic data (Naylor *et al*. 1997; N. K. Dulvy and J. D. Reynolds, unpublished data).

The only other clear case that we know of for a reversal from live-bearing to egg-laying involves the cordylid lizards, *Platysaurus* (van Wyk & Mouton 1996). Other squamate taxa that might also qualify are the Viperidae, Angidae and Iguanidae (de Fraipont *et al*. 1996). Eight reversals from live-bearing to egg-laying have been proposed for squamates (de Fraipont *et al*. 1996). However, this study only considered the maximum possible number of transitions, providing an extremely unconservative estimate for a poorly resolved clade. Reproductive reversals between planktonic and non-planktonic larvae have been identified in marine invertebrates (Strathmann 1993). Such reversals could result from a shift in trade-offs between juvenile survivorship and maternal interbrood survivorship (Clutton-Brock 1991; Roff 1992).

(*d*) *The evolution of increased maternal input in live-bearers*

Researchers have classified live-bearing according to the level of maternal contribution: yolk-only (leicithotrophy, e.g. teleosts and elasmobranchs), incipient matrotrophy (low levels of maternal input, e.g. monotremes, squamates, teleosts and elasmobranchs), and matrotrophy (significant maternal input, e.g. therians, squamates, elasmobranchs and some teleosts) (Wourms 1977, 1981; Wourms *et al*. 1988; Blackburn 1992). This results in an evolutionary sequence of increasing maternal contribution from egg-laying to yolk-only nutrition to full maternal input via intermediate combinations.

Our data do not support a linear, irreversible progression toward a 'pinnacle' of maximum maternal input. We find two reversals to egg-laying and numerous reversals from live-bearing with maternal input to live-bearing with yolk-only nutrition. This suggests that maternal inputs in live-bearing elasmobranchs have been highly labile. Future studies of better resolved phylogenies should permit tests of transition probabilities against null models that include branch lengths and the distribution of alternative states.

The evolution of parental care in shorebirds (Charadriides) also appears to have been labile with reversals to the ancestral state (biparental care), and numerous reductions in the level of care at low taxonomic levels (Székely & Reynolds 1995). Our data support suggestions that the evolution of maternal input is convergent (Wourms *et al*. 1988; Blackburn 1992; Wake 1992), with oophagy and uterine milk each evolving twice, independently. Other non-placental vertebrates have evolved alternative forms of maternal input, such as egg-laying monotremes that suckle their young after hatching (Blackburn 1992). Birds are similarly constrained to egg-laying, but have evolved parental care behaviours, resulting in low brood size and well-developed young similar to sharks and rays.

Our results are therefore consistent with the hypothesis that there has been a trend toward the evolution of live-bearing in sharks and rays, with at least one reversal to egg-laying. However, the evolution of maternal input appears to be evolutionarily labile, with a tendency to reverse to yolk-only live-bearing.

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