

# Reproductive Evolution of Chondrichthyans

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## 3.1 INTRODUCTION

### 3.1.1 Chondrichthyan Reproduction

The living Chondrichthyes are comprised of about 1100 species of neoselachian elasmobranchs (sharks and rays) and more than 30 species of holocephalans (chimaeras) (Compagno 1990, 2002). Although the number of living chondrichthyans is small relative to some other vertebrate groups, a diversity of reproductive modes has evolved (Wourms 1977). Wourms (1981) pointed out that these modes could be divided into two major categories based on fetal nutrition: lecithotrophy, where the entire development of the embryo is supported solely by the yolk; and matrotrophy, where at least part of the fetal development is augmented by additional maternal input of nutrients. In addition, chondrichthyan reproductive modes may be further divided by whether embryonic development is external to the mother's body (oviparity), or internal (viviparity).

### 3.1.2 Oviparity

Oviparity is obviously a lecithotrophic mode of reproduction. All chondrichthyan eggs deposited externally have leathery, structurally complex and remarkably durable shells (Hamlett and Koob 1999). Oviparity may be divided into two types: single (= external) oviparity and multiple (= retained) oviparity (Nakaya 1975; Compagno 1990). The former is the only type of reproduction in the Heterodontiformes and the batoid family Rajidae and occurs along with various forms of viviparity in the Orectolobiformes and the carcharhiniform family Scylorhinidae. In this type of oviparity one egg is

deposited at a time from each oviduct, usually in pairs; tens of eggs (but perhaps hundreds for a few species) may be deposited over the course of a spawning season. Multiple oviparity occurs only in a small number of scylorhinid species (and perhaps an orectolobiform) and entails the retention of a small number of eggs (usually = 10) in the oviduct during most of development before deposition and hatching on the seabed.

### 3.1.3 Yolk-sac Viviparity

Viviparity includes both lecithotrophic and a variety of matrotrophic modes of reproduction (Table 3.1) (Wourms 1977, 1981; Compagno 1990; Wourms and Lombardi 1992). Yolk-sac viviparity involves retention of fertilized eggs throughout development within the uterus with no additional maternal nutritional input beyond the yolk. This form of lecithotrophic reproduction is the most widespread among elasmobranchs and occurs in all living orders except the Heterodontiformes (which is oviparous) and the Lamniformes which has more advanced forms of viviparity (Compagno 1990). Yolk-sac viviparity was formerly called "ovoviviparity", a term widely used, understood, and accepted in the biological community. The term has been abandoned by most recent authors (Wourms 1977, 1981; Compagno 1990; Hamlett 1999) as suggested by Budker (1958) and Hoar (1969). Ranzi (1932, 1934) showed that although some "ovoviviparous" elasmobranchs, including some Torpediniformes and Squaliformes, lost 23-46 percent organic weight during gestation, another "ovoviviparous" squalid actually gained 1 percent and three triakids gained 11-369 percent. In true yolk-sac viviparity, substantial (= 20-25%) weight loss is expected because the organic material in the egg must provide not only material for structural development of the embryo but also for energetic costs of development (Chapter 13 of this volume). Thus, weight loss less than about 20% or weight gain during development would require some sort of matrotrophic contribution. In the cases cited above, this contribution appeared to be from a mucoid secretion or histotroph from the uterus that could be ingested or absorbed by the developing embryo. Thus, in some groups, the line between yolk-sac viviparity and limited histotrophy may be difficult to discern without data on the organic content of the eggs and term embryos. Consequently, the term "ovoviviparity" was abandoned and replaced by the unfortunate term "aplacental viviparity", which includes three major modes of elasmobranch reproduction: yolk-sac viviparity, histotrophy, and oophagy (see below). The term "aplacental viviparity" obfuscates the true diversity of elasmobranch reproduction and through implication elevates the importance of placental viviparity, which is restricted to a small number of families at the terminal nodes of the Carcharhiniformes. In addition, "aplacental viviparity" describes a mode by what it is not instead of what it is, and is uninformative. The term "aplacental viviparity" would best be abandoned, and the four modes of chondrichthyan viviparity recognized above should be used instead (Table 3.1).

Table 3.1 Chondrichthyan modes of reproduction.

	<i>Lecithotrophic</i>	<i>Matrotrophic</i>
<b>Oviparity</b>		
Single	+	
Multiple	+	
<b>Viviparity</b>		
Yolk-sac	+	
Limited Histotrophy		+
Lipid Histotrophy		+
Carcharhinid Oophagy		+
Lamnoid Oophagy		+
Placental		+

### 3.1.4 Histotrophy

Histotrophy reaches its zenith in the batoid Myliobatiformes, which produce a protein- and lipid-rich histotroph from highly developed trophonemata. Embryos in this group unequivocally obtain matrotrophic nutrition and exhibit an increase in organic content of 1680-4900 percent (Needham 1942). Lipid histotrophy is clearly different from the limited "mucoid" histotrophy cited above and results in term embryos that may have gained one to two orders of magnitude more in mass than embryos of limited histotrophs. It is useful to recognize these modes separately (Table 3.1) in order to gain greater insights into the reproductive ecology and evolution of elasmobranchs.

### 3.1.5 Oophagy

Oophagy is a form of matrotrophic viviparity where, after initial yolk-sac nutrition, developing embryos ingest unfertilized eggs to support further development. Oophagy may result in very large (> 100 cm TL) neonates in some species (Hamlett and Koob 1999). Oophagy is the mode of reproduction in all members of the Lamniformes, and has evolved in one small family of carcharhiniform sharks, the Pseudotriakidae (Yano 1992, 1993). The mechanisms of oophagy are different in the two groups: the lamniforms, throughout most of their pregnancy, continuously produce unfertilized eggs which the developing embryos ingest and store in a large bulging yolk-stomach; the carcharhiniforms include a multitude of apparently unfertilized ova within the same egg envelope as the developing embryo, which then ingests this self-contained food source and stores it in the external yolk sac. Adelphophagy is a form of lamniform oophagy in which the largest developing embryo in each uterus consumes all the smaller embryos then relies on maternal production of unfertilized eggs for the duration of development. This reproductive mode is definitively known for only one species, *Carcharias taurus* (Gilmore *et al.* 1983; Gilmore 1991; Hamlett and Koob 1999).

### 3.1.6 Placental Viviparity

Placental viviparity has evolved only in five families of higher carcharhiniform sharks (Compagno 1988). In the vast majority of placental sharks, early development is supported by the yolk. The timing of placentation varies among species, occurring later in some than in others. In addition, limited histotrophy may function to support embryonic growth before and perhaps even after placentation (Hamlett 1989; Hamlett and Hysell 1998, Hamlett and Koob 1999; Chapter 15 of this volume.)

### 3.1.7 The Plesiomorphic Reproductive State

In virtually all previous analyses of the evolution of reproduction in modern elasmobranchs, oviparity has been assumed to represent the plesiomorphic state (Wourms 1977; Compagno 1990; Wourms and Lombardi 1992; Callard *et al.* 1995; Dulvy and Reynolds 1997). However, no empirical evidence has been offered to support this dogmatic assumption. Dulvy and Reynolds (1997) concluded from a cladistic analysis that oviparity was the plesiomorphic reproductive mode in modern elasmobranchs, but their use of the Holocephali as an outgroup in their phylogenetic analysis pre-ordained their conclusion. All the living holocephalans for which information is available are oviparous. However, the living holocephalans are a relic of a once diverse and dynamic group of Paleozoic chondrichthyans (Grogan 1993; Grogan and Lund 2000) with reproductive modes that included viviparity (Lund 1990). In addition, recently Grogan and Lund (2004) have argued that viviparity was the dominant mode of reproduction in most of the chondrichthyans (both elasmobranch and holocephalan) in the well-known Mississippian Bear Gulch deposit of Montana (USA). (This site includes a wide diversity of very well preserved chondrichthyan fossils and is one of the most intensely studied in the world.) Therefore, although the living holocephalans are oviparous, the Paleozoic chondrichthyans from which they evolved, and also the distant ancestors of the neoselachians, already included viviparous forms. The present paper examines the hypothesis that yolk-sac viviparity, not oviparity, is the plesiomorphic mode of reproduction in the Neoselachii and perhaps for the Chondrichthyes as a whole.

## 3.2 PHYLOGENETIC PATTERNS

### 3.2.1 Neoselachii

All living elasmobranchs are considered to be monophyletic and within the sub-class Neoselachii (Compagno 1977; Maisey *et al.* 2004). This group also includes a scattering of extinct but modern level fossils from the Mesozoic and perhaps a small number of Paleozoic forms (Maisey *et al.* 2004). The sister group of neoselachians are the hybodonts, which arose during the Paleozoic, radiated widely with a diversity of ecomorphotypes in the Mesozoic and became extinct in the Cretaceous (Maisey *et al.* 2004). Extant clades of neoselachians have historically been separated into two cohorts,

batoids (Batoidea) and sharks (Selachii) (Bigelow and Schroeder 1948, 1953). However, morphological analyses during the 1990s suggested that the batoids were a terminal group among the squallean sharks, and they were included in the clade Hypnosqualea along with the Squatiniformes and Pristiophoriformes (Shirai 1992, 1996; Carvalho 1996). Recent molecular analyses including both nuclear and mitochondrial genes (Douady *et al.* 2003; Maisey *et al.* 2004; Chapter 1 of this volume) contradict this phylogeny and recognize the traditional arrangement where the batoids are the sister group of the sharks, which in turn are comprised of two major superorders, the Galeomorphii and Squalomorphii (Maisey *et al.* 2004; Chapter 1 of this volume) (Fig. 3.1). This arrangement is supported by the paleontological data which show that the batoids were already separated from the other neoselachians by the early Jurassic if not earlier (Thies 1983; Maisey *et al.* 2004). In this section, I will revisit the patterns of the major modes of reproduction among the Batoidea, the Squalomorphii, and the Galeomorphii using the most recent phylogenetic information for each group and including paleontological information.

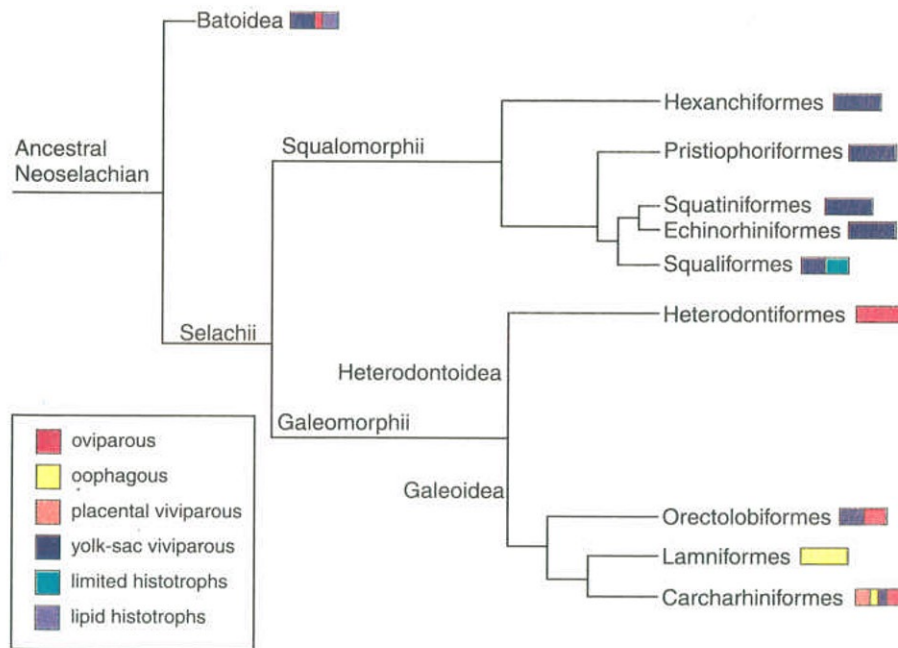


Fig. 3.1 Phylogeny of the elasmobranchs with reproductive modes. Modified after Musick *et al.* 2004.

### 3.2.2 Cohort Batoidea

The following discussion is based on the recent batoid phylogeny by McEachran and Aschliman (2004) who found that the Torpediniformes are basal to the rest of the living batoids followed by the Pristiiformes (Fig. 3.2).

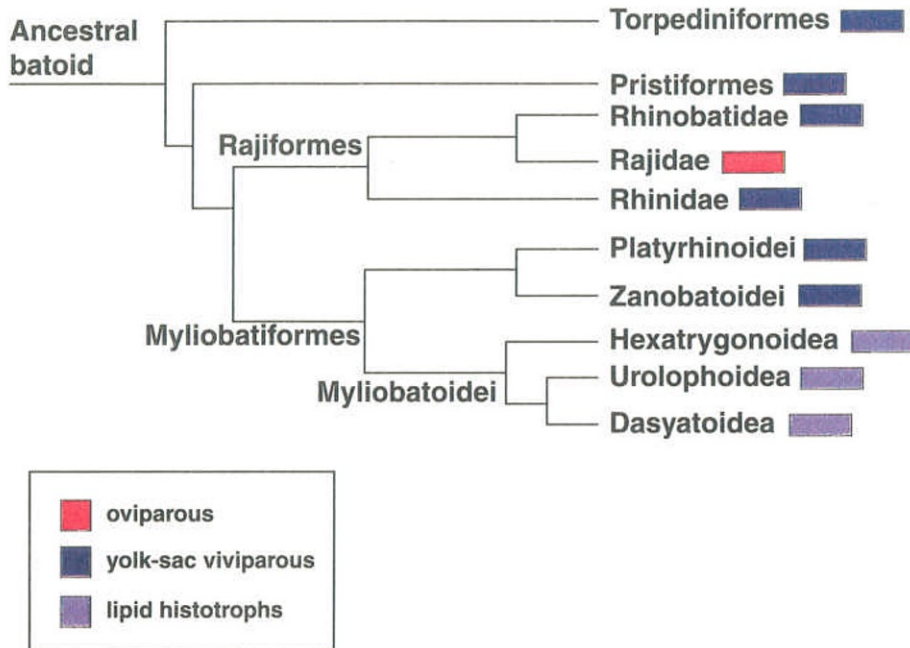


Fig. 3.2 Phylogeny of the Batoidea with reproductive modes. Modified after McEachran and Aschliman 2004.

The torpedoes exhibit yolk-sac viviparity (Ranzi 1932, 1934). The Pristiformes also exhibit yolk-sac viviparity (Thorson *et al.* 1983; Compagno 1990) and perhaps limited histotrophy. Observations by Setna and Sarangdhar (1949) of a “milky secretion” in the uterus of *Pristis cuspidatus* should not be misconstrued to mean that *Pristis* is histotrophic in the same way as the Myliobatiformes, which produce a histotroph rich in lipids. However, limited histotrophy, which involves production of mucoproteins in the uterus, is widespread among viviparous elasmobranchs (Chapter 13 of this volume) and may occur in the Pristiformes.

The next node in the batoid classification leads to two orders, one, the Rajiformes, with the Rajidae (skates) at its terminus and the other, the Myliobatiformes, with the Myliobatoidei (stingrays) as most derived (Fig. 3.2). Thus the depressed disc-shaped morphology in these two taxa evolved through separate ancestral taxa, the rhinobatoids and platyrhinids, respectively (McEachran and Aschliman 2004). Both of the latter two taxa had been placed formerly in the guitarfish order Rhinobatiformes (Compagno 1999), and both have yolk-sac viviparity as their mode of reproduction (Compagno 1990; Ebert 2003; Chapter 13 of this volume). The earliest known batoid fossils are rhinobatoids from the lower Jurassic (Cappetta *et al.* 1993). The Rajidae have single oviparity and deposit large numbers of leathery eggs. The Myliobatoidei produce a lipid-rich histotroph and bear a small number of large young (Hamlett and Koob 1999). The organic content of developing



embryos in this group increases up to 4900% and is higher than that in most placental sharks (Chapter 13 of this volume). Lipid histotrophy is apparently limited to the Myliobatoidea, although limited histotrophy may be widespread among batoids as in other groups. All of the basal clades within the Batoidea, including the oldest, have yolk-sac viviparity, and the plesiomorphic reproductive mode in the cohort Batoidea is unequivocally yolk-sac viviparity.

### 3.2.3 Superorder Squalomorphii

The Squalomorphii comprise five extant orders (Fig. 3.1): the Hexanchiformes, Pristiophoriformes, Squatiniformes, Echinorhiniformes, and Squaliformes. All of these orders, except the Squaliformes, are depauperate with few lower taxa. The Hexanchiformes is basal and also is the oldest order dating at least back to the lower Jurassic. All squalomorphs exhibit yolk-sac viviparity with limited histotrophy present in many species, particularly among the Squaliformes. Oviparity is unknown in this entire superorder and yolk-sac viviparity is obviously the plesiomorphic reproductive mode.

### 3.2.4 Superorder Galeomorphii

The galeomorphs are a morphologically diverse group of sharks that consists of four extant orders: Heterodontiformes, Orectolobiformes, Lamniformes and Carcharhiniformes. The Heterodontiformes had been placed close to hybodont sharks by early workers (Smith 1942), but both recent morphological (Maisey 1984; de Carvalho 1996; Shirai 1996) and molecular (Maisey *et al.* 2004; Chapter 1 of this volume) evidence agree that the heterodontiforms are most closely allied with the galeomorphs, if distantly. The separation between the superorder Heterodontoidea and the Galeoidea—which comprises the Orectolobiformes, Lamniformes and Carcharhiniformes (de Carvalho 1996)—dates back to the lower Jurassic at least (Cappetta *et al.* 1993). The extant Heterodontiformes are a very small group of small benthic species all of which are oviparous (Compagno 2001).

The Orectolobiformes are basal to the Galeoidea (Fig. 3.1). Recent molecular (Maisey *et al.* 2004) and morphological (Goto 2001) cladistic analyses of the orectolobiforms concur (Fig. 3.3) and suggest that the order may be subdivided into two suborders, the Parascylloidei and Orectoloboidei. The parascylloids include only one family of small benthic oviparous sharks (Compagno 2001). The Orectoloboidei includes two superfamilies, the Orectoloboidea and Ginglymostoidea. The superfamily Orectoloboidea contains two families, the Orectolobidae and Brachaeluridae, both of which have a form of yolk-sac viviparity (Compagno 2001). The Ginglymostoidea includes the Hemiscylliidae, a group of small benthic oviparous sharks, and a second clade, including the Ginglymostomidae, Rhincodontidae and Stegostomatidae (Compagno 2001). All of the ginglymostomids and *Rhincodon* have yolk-sac viviparity, whereas *Stegostoma fasciatum* is a large oviparous species (Compagno 2001, 2002). The oldest fossil orectolobiforms are within

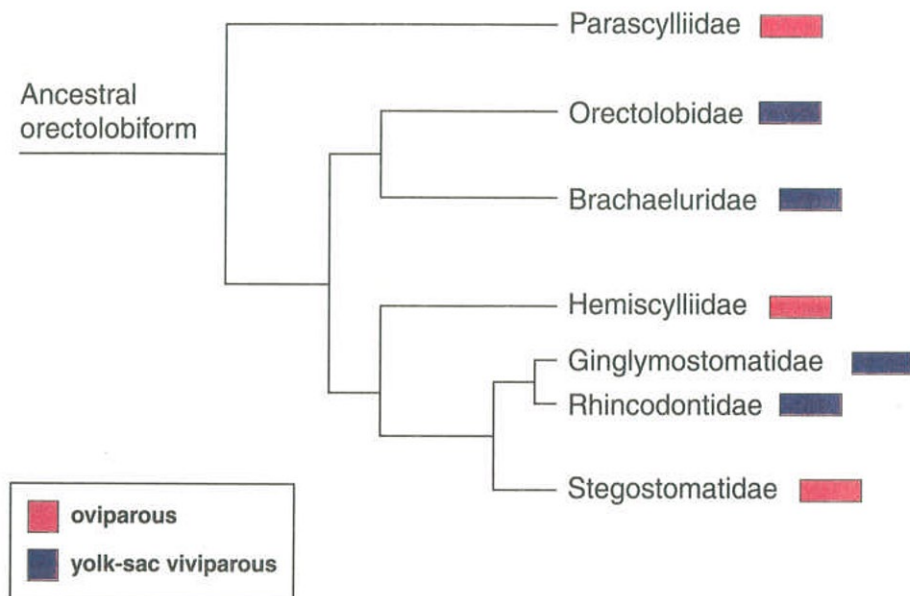


Fig. 3.3 Phylogeny of the Orectolobiformes with reproductive modes. Modified after Compagno 1988 and Goto 2001.

the Brachaeluridae (lower Jurassic, 180 mya), and Orectolobidae (middle Jurassic, 160 mya) (Cappetta *et al.* 1992), families with yolk-sac viviparity. The oviparous parascylliids and hemiscylliids did not appear until the middle Cretaceous (125 mya), although cladistic analysis suggests the parascylliids may be older. The oldest Orectolobiformes were contemporaneous with the oldest Heterodontiformes.

The relationships of the remaining two orders of galeoid sharks, the Lamniformes and the Carcharhiniformes, have been debated for many years. White (1937) considered the Lamniformes to be more closely related to the Orectolobiformes than the Carcharhiniformes, and Applegate (1974) believed both Lamniformes and Carcharhiniformes were derived from Orectolobiformes. More recent studies, both morphological and molecular, recognize the Lamniformes and Carcharhiniformes to be sister groups (Maisey 1984; de Carvalho 1996; Shirai 1996; Maisey *et al.* 2004).

All of the Lamniformes for which reproductive modes are known are viviparous with oophagy. Most recent classifications place *Mitsukurina* and *Carcharias* as the two most primitive clades within the order (Shirai 1996; Martin and Naylor 1997). Nothing is known about reproduction in *Mitsukurina*, but *Carcharias taurus* appears to be unique among elasmobranchs in that it exhibits adelphophagy (see above) (Gilmore *et al.* 1983; Gilmore 1991; Chapter 14 of this volume). Adelphophagy results in two very large (= 100 cm) neonates and represents the extreme in the alternative reproductive strategy of investing in large young with high survivorship (versus a large number of small young with low survivorship) (Stearns 1992; Cortés 2004).



It is unclear whether adelphophagy is a plesiomorphic stage in the evolution of pure oophagy or an autapomorphic condition confined to *C. taurus*. Information on reproduction of *Mitsukurina* should shed light on this question. In oophagous species the initial stages of embryonic development are supported solely by the yolk-sac, and oophagy most probably evolved from simple yolk-sac viviparity.

Compagno (1988) divided the Carcharhiniformes into two suborders: the Scyliorhinoidei, containing the families Scyliorhinidae, Proscylliidae and Pseudotriakidae and the Carcharhinoidei, including the Leptochariidae, Triakidae, Hemigaleidae and Carcharhinidae (here including the Sphyrnidae). Recent molecular analysis (Maisey *et al.* 2004) placed the Pseudotriakidae closer to the Carcharhinidae (Fig. 3.4) but did not include any proscylliids in the study. (They used *Gollum*, previously classified as a proscylliid but now included in the Pseudotriakidae (Compagno 1999)). The Scyliorhinidae have been considered to be the most primitive carcharhiniforms (White 1937) because of their posteriorly placed dorsal fins and reduced vertebral calcifications. However, posterior dorsals are typical of benthic morphotypes (Compagno 1988, 1990), and reduced calcification is widespread among several orders of elasmobranchs which are found primarily in bathyal habitats (as are most scyliorhinids) (Compagno 1984). Compagno (1988) concluded "if lamnoids are the immediate sister group of carcharhinoids [as recent studies have concluded]... the proscylliid or even triakid habitus with the first dorsal forwards might be primitive for carcharhinoids and scyliorhinoids derived...."

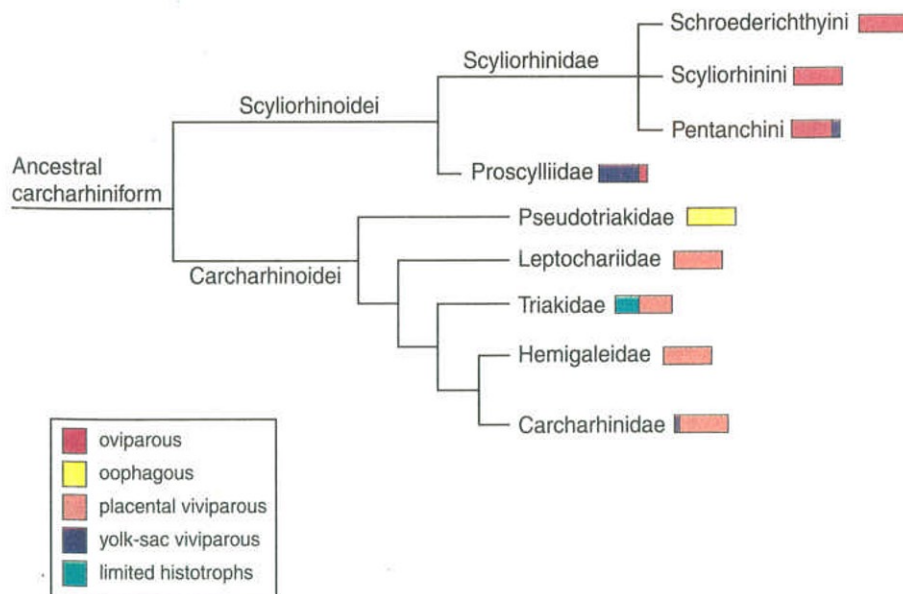


Fig. 3.4 Phylogeny of the Carcharhiniformes with reproductive modes. Modified after Compagno 1988 and Maisey *et al.* 2004.

The earliest proposed scyliorhinid fossil is *Macrourogaleus hassei* from the upper Jurassic of Europe (Cappetta *et al.* 1992). However, this specimen is in very poor condition, lacks its dentition, and consists of only a vague impression of its body outline (Cappetta 1987). The next earliest fossil scyliorhinid is *Scyliorhinus destombedii* from the lower Cretaceous of northern France (Cappetta 1987). No fewer than 18 species of *Scyliorhinus* have been recognized from early Cretaceous to Eocene deposits, most based on teeth. Cappetta (1987) contended that nearly all scyliorhinid fossils have been placed in the genus *Scyliorhinus* out of ignorance of the dentition of modern genera, and that "undoubtedly several fossil genera exist." He continued to note that "the genus *Scyliorhinus* as used by paleontologists is heterogeneous." Compagno (1988) suggested that some of the early fossil "scyliorhinids" may actually be proscylliids (which have similar dentition). Regardless, an upper Jurassic origin for the Carcharhiniformes (with the appearance of the Scyliorhinoidea) fits well with their phylogenetic position as sister group to the Lamniformes. The oldest lamniform fossil appears to be *Paleocarcharias* from the upper Jurassic of Europe (Duffin 1988).

Following Compagno's (1988) conclusions that the proscylliids are the primitive sister group of the scyliorhinids and thus the most primitive of living carcharhiniforms (Fig. 3.4), their modes of reproduction may provide particular insight into the plesiomorphic state in the order. Of the three genera of proscylliids, *Eridacnis* and *Ctenacis* both have yolk-sac viviparity, whereas *Proscyllium* is oviparous. Compagno (1988) pointed out that *Eridacnis* and *Ctenacis* were more closely related to each other than either was to *Proscyllium*, and that of the three genera, *Proscyllium* was the closest to the Scyliorhinidae, particularly the genus *Schroederichthys*. Given *Proscyllium*'s position close to the Scyliorhinidae, the characters which ally it to *Ctenacis* and *Eridacnis* should be more closely examined to determine whether they are principally plesiomorphic. If so, *Proscyllium* should be allied with the Scyliorhinidae as its most primitive member, thus clearly defining yolk-sac viviparity in the *Ctenacis-Eridacnis* clade as plesiomorphic relative to the rest of the Carcharhiniformes (Fig. 3.5). Regardless, oviparity in the Scyliorhinidae is derived. Yolk-sac viviparity is indicated as the plesiomorphic state in carcharhiniforms not only by its presence in *Ctenacis* and *Eridacnis*, but also by the sister group relationship between Carcharhiniformes and Lamniformes in which the plesiomorphic state is unambiguously yolk-sac viviparity.

All of the scyliorhinids are small benthic sharks and most have single oviparity (Compagno 1988). Multiple oviparity is present in the five species of *Halaelurus* (Nakaya 1975; Compagno 1988; Francis pers. comm.). However, in the closely related genus *Bythaelurus*, species are either single oviparous or yolk-sac viviparous with only two young (Compagno 1988; Francis pers. comm.). The appearance of yolk-sac viviparity in a group with single oviparity (Compagno 1988) contradicts the suggestion that yolk-sac viviparity has evolved from single oviparity through an intermediate stage of multiple oviparity (Nakaya 1975; Wourms *et al.* 1988; Compagno 1990). Multiple oviparity has also evolved in *Galeus melastomus*. The genus *Galeus* also includes



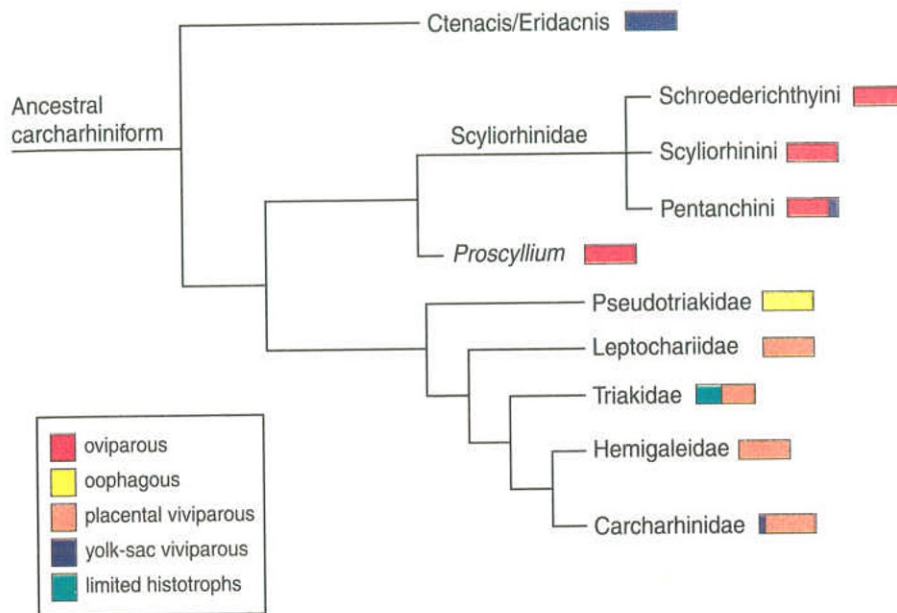


Fig. 3.5 Alternate phylogeny of the Carcharhiniformes with reproductive modes.

five apparently single oviparous species and two species with yolk-sac viviparity. All of the genera that have yolk-sac viviparity (*Bythaelurus*, *Galeus*, and *Cephalurus*) are closely related and within the subtribe Galeini (Compagno 1988). Apparently the mode of reproduction in the subtribe has remained evolutionarily labile. Springer (1979) suggested within the subspecies of *Galeus arae*, *G. arae arae* was yolk-sac viviparous, whereas *Galeus arae antillensis* was oviparous. Although the interrelationships among the sub-families of scyliorhinids are unresolved, the appearance of yolk-sac viviparity among the Galeini probably represents an evolutionary reversal in an oviparous family (Scyliorhinidae) that is an offshoot from the main line of carcharhiniform evolution.

The Pseudotriakidae fall somewhere between the Scyliorhinoidei and higher Carcharhinoidea (Compagno 1988; Maisey *et al.* 2004). The two genera in this family, *Gollum* and *Pseudotriakis*, exhibit a unique form of oophagy quite different from that in the Lamniformes (see above). As in other viviparous groups, early development of embryos is supported by the yolk sac and oophagy commences as development proceeds.

The Leptochariidae appears to be an ancient carcharhiniform clade (Compagno 1988), and has been classified as the sister group to a clade that includes the Triakidae and the Hemigaleidae and Carcharhinidae (including Sphyrnidae) together (Fig. 3.5). Alternatively, it might also be placed within the Triakidae as the sister group to all other triakids (Compagno 1988). Placental viviparity first appears in the Leptochariidae, is present along with limited histotrophy in the triakids and is found in all hemigaleids and

carcharhinids (except *Galeocerdo cuvier*, a primitive carcharhinid which is yolk-sac viviparous). The absence of placental viviparity in some triakids may represent a loss and evolutionary reversal, or Leptochariidae may have evolved its unique globular placenta (Compagno 1988) independently. Triakids without a placenta still retain the uterine compartments and persistent egg envelope (Storrie 2004) that are the hallmarks of all placental species. In addition, non-placental triakids produce a copious mucoid histotroph and may exhibit embryonic mass increases that approach those of some placental species (Needham 1942; Hamlett and Koob 1999; Storrie 2004).

### 3.3 MORPHOLOGICAL AND PHYSIOLOGICAL PATTERNS

#### 3.3.1 Oviducal Gland

The oviducal gland (= nidamental or shell gland) is a complex structure located just below the anterior oviduct and above the uterus in virtually all living chondrichthyans (Hamlett *et al.* 1998; Hamlett and Koob 1999). Fertilization takes place in the oviducal gland or just anterior to it. Histologically, four distinct zones can be discerned within this structure, a proximal club zone, papillary zone, baffle zone, and terminal zone (Hamlett *et al.* 1998; Chapter 10 of this volume). The club and papillary zones produce the various jelly coats that surround and protect the egg and developing embryos (Koob and Straus 1998). The baffle zone forms the egg envelope, capsule or membrane that encloses egg and jelly. In oviparous species, the baffle zone produces the leathery shell. The terminal zone is where sperm storage may occur in many species. Although the basic four zone structure of oviducal glands seems to be nearly universal, among most elasmobranch reproductive modes, the size of the gland is considerably larger in oviparous species (Hamlett and Koob 1999) and more elaborate at least in the Heterodontiformes (Hamlett pers. comm.). Hamlett *et al.* (1998) have characterized the oviducal gland of oviparous species as "specialized".

#### 3.3.2 Uterus

The uterus in all elasmobranchs is a complex structure that may provide many roles in protecting and supporting the developing embryos, most importantly structural accommodation of the eggs and embryos, supplying oxygen to the uterine lumen and biosynthesis and secretion of structural or nutritional materials (Hamlett and Koob 1998). In oviparous species the uterus harbors the egg capsule during capsule sclerotization and thereafter until oviposition (up to several days) (Hamlett and Hysell 1998). Regardless of earlier characterization of the oviparous uterus as a simple conduit to the outside (Wourms *et al.* 1988), it is very sophisticated (Koob and Hamlett 1998) with structural specializations. In rajids the uterus has vascularized longitudinal folds lined with cilia and microvilli and with branched tubular glands. In scyliorhinids the intrauterine mucosa is folded, vascularized, and highly secretory in structure (Otake 1990). The oviparous uterus contributes



to capsule surface structure and chemistry, and may facilitate biochemical processes associated with capsule polymerization, including provision of oxygen and absorption of water (Koob and Hamlett 1998; Hamlett and Koob 1999).

In yolk-sac viviparous species, the uterus specializes in regulating the intrauterine milieu, including supplying oxygen, water, and minerals (but not organic material) for the developing embryo, and regulating wastes (Hamlett and Koob 1999). The uterine wall in yolk-sac viviparous species is vascularized and folded with non-secretory villi. This arrangement with minor variations is similar in Squaliformes, Squatiniformes, Pristiophoriformes, primitive Rajiformes and primitive Carcharhiniformes (Ranzi 1932, 1934; Needham 1942; Compagno 1988; Otake 1990; Chapter 13 of this volume). Fine structure of the uterus in the Hexanchiformes has not been described but is probably similar to that in the Squaliformes. Limited histotrophy is a natural progression from yolk-sac viviparity and there is a thin line between the two (see above). This progression involves a proliferation of secretory cells that produce a nutritive mucous, and perhaps other organic substances, that may be ingested or absorbed by the developing embryo. Limited histotrophy has been reported in the Squaliformes, Rajiformes, and among the Carcharhiniformes in the families Pseudotriakidae (where limited histotrophy may support oophagy, (Yano 1992, 1993) and Triakidae. The uterus in the latter group is quite unlike that in the other taxa with limited histotrophy and has uterine compartments similar to those in the placental members of the family and in all other placental carcharhiniforms (Otake 1990). Uterine compartments isolate each embryo from its siblings and greatly increase the surface area available for metabolic exchange between the mother and fetus (Hamlett 1989). All placental species pass through a histotrophic stage after absorption of the yolk sac and before placental implantation (Hamlett and Koob 1999; Chapter 15 of this volume).

In the stingrays (Myliobatoidei), all of which have lipid histotrophy, the uterus develops large villous projections termed trophonemata (Hamlett *et al.* 1996a, b; Hamlett and Hysell 1998), which increase the surface area for histotrophic secretions and respiratory exchange. The oophagous lamniforms initially have a uterus with a smooth epithelium, but as embryos grow and require more oxygen, the uterus forms highly vascularized longitudinal folds. There is no provision for uterine secretion (Hamlett and Hysell 1998).

The evolutionary patterns of uterine structure suggest that species with yolk-sac viviparity and oophagy have the simplest condition with some folding and vascularization and minimal development of non-secretory villi. In the oviparous state, large secretory crypts are present along with cilia, both absent in the yolk-sac viviparous state. In the histotrophic species there is a progression in the development of secretory structures from modest development in limited histotrophs, culminating in the trophonemata found in the lipid histotrophs. In placental species, the development of uterine compartments was probably a necessary stage before placentation evolved.

### 3.3.3 Claspers

Claspers (mixopterygii) are paired, grooved extensions of the posterior base of the pelvic fins and are supported by an endoskeleton. They serve as intromittent organs to introduce sperm into the female's reproductive system thus facilitating internal fertilization (Compagno 1999a). The evolution of claspers has involved the coordinated development of the muscles required to pump sperm and to maneuver the claspers during copulation. Claspers are one of two principal synapomorphies which tie the Chondrichthyes together as a monophyletic group (Grogan and Lund 2004). All male chondrichthyans have claspers despite arguments to the contrary based on upper Devonian fossils of *Cladoseleache*. Grogan and Lund (2004) have pointed out that these fossils were likely to be female. They base their conclusion on the well-known habit of extant elasmobranchs to be sexually segregated temporally and geographically. Also, other upper Devonian elasmobranchs such as *Diademodus* from the same deposit as *Cladoseleache* had pelvic claspers, and all other male members of the cladodont group had claspers. Therefore, *Cladoseleache* cannot be used as evidence that the plesiomorphic state within male chondrichthyans was unmodified pelvic fins (Dulvy and Reynolds 1997). Thus, claspers and internal fertilization probably have been defining features of all Chondrichthyes since the earliest evolution of the group. With internal fertilization comes the strong potential if not the probability of viviparity.

### 3.3.4 Urea Retention

All Chondrichthyes retain urea while in sea water so that they can be in approximate osmotic equilibrium with the environment and at the same time can maintain characteristic low vertebrate ion levels (Smith 1953). Ureosmotic regulation was thought to be unique to Chondrichthyes before its discovery in the living coelacanth, *Latimeria chalumnae* (Pickford and Grant 1967). Urea is mostly generated by the ornithine-urea cycle when used as a significant osmolyte and as the principal form for excreting nitrogenous waste (Griffith 1991). A complete ornithine-urea cycle has been shown in representatives of all gnathostome classes except birds in which it has been lost. As an osmotic regulator urea retention has now been confirmed not only in elasmobranchs and coelacanths but also in some marine adapted amphibians and reptiles and in some other marine and freshwater fishes (Griffith 1991). Extrapolating from living fishes to the Devonian and before, by which time the ureogenic elasmobranchs, coelacanths and other major vertebrate groups had diverged, Griffith (1991) proposed a hypothesis for the evolution of ureosmotic regulation:

1. A functional ornithine-urea cycle was absent in early agnathans (as with extant agnathans), but all component enzymes were present.
2. A complete ornithine-urea cycle evolved in early gnathostomes as a means for detoxifying ammonia during early embryogenesis.

Depeche *et al.* (1979) found high levels of urea in the developing embryos of the viviparous teleost, *Poecilia reticulata* (the guppy). Griffith (1991)

concluded that urea synthesis was important in internal embryonic development where there was a restricted opportunity to exchange ammonia with the environment combined with high protein catabolism (of ovovitelline from the yolk). Following this logic, we would suggest that urea retention in early chondrichthyans evolved along with internal fertilization and yolk-sac viviparity initially as an embryonic adaptation to avoid ammonia toxicity. Urea retention into the adult stage would involve simple paedomorphosis (Griffith, 1991) and would allow early chondrichthyans to osmoregulate more efficiently in the marine environment, thus increasing their ability to occupy a broad diversity of niches.

### 3.4 EVOLUTIONARY IMPLICATIONS

#### 3.4.1 Oviparity

Single oviparity has evolved in taxonomic groups whose members are mostly of small body size (< 100 cm TL) (Callard *et al.* 1995) and therefore would

**Table 3.2** Available data on shark fecundity for species of  $\leq 100$  cm TL with single oviparous and viviparous modes of reproduction.

Species	Size	Fecundity	References
Single Oviparous	Total Length (cm)	Eggs/Year	
<i>Hemiscyllium ocellatum</i>	100	22	Bennett and Kyne 2003
<i>Scyliorhinus canicula</i>	100	29-190	Mellinger, 1983; Compagno 1984; Capape <i>et al.</i> 1991; Ellis and Shackley 1997
<i>Scyliorhinus retifer</i>	50	44-53	Castro <i>et al.</i> 1988
Average Fecundity		60.0	
Viviparous		Litter Size	
<i>Aculeola nigra</i>	60	$\geq 3$	Compagno 1984
<i>Centrophorus moluccensis</i>	98	2	Compagno 1984
<i>Centrophorus uyato</i>	100	1	Compagno 1984
<i>Centroscymnus crepidater</i>	90	4-8	Cox and Francis 1997
<i>Deania profundurum</i>	76	5-7	Compagno <i>et al.</i> 1989
<i>Etmopterus brachyurus</i>	22.7	2	Compagno <i>et al.</i> 1989
<i>Etmopterus granulosus</i>	38	10-13	Last and Stevens 1994
<i>Etmopterus hillanus</i>	50	4-5	Compagno 1984
<i>Euprotomicrus bispinatus</i>	27	8	Compagno 1984
<i>Isistius brasiliensis</i>	50	6-12	Ebert 2003
<i>Oxynotus bruniensis</i>	72	7	Compagno 1984
<i>Squalus blainville</i>	95	3-4	Compagno 1984
<i>Squalus japonicus</i>	95	4.08	Chen <i>et al.</i> 1981
<i>Squalus megalops</i>	71	2-4	Compagno 1984; Last and Stevens 1994
<i>Squalus rancureli</i>	77	3	Compagno 1984
Average Fecundity		4.6	

## 60 Reproductive Biology and Phylogeny of Chondrichthyes

**Table 3.3** Available data on batoid fecundity for species with single oviparous and viviparous modes of reproduction. Parentheses indicate average fecundity.

Species	Size	Fecundity	References
Oviparous	Total Length (cm)	Eggs/Year	
<i>Amblyraja radiata</i>	102	2-88	del Rio Iglesias 2001
<i>Dipturus batis</i>	250	40	du Buit 1977; Walker and Hislop 1998
<i>Leucoraja erinacea</i>	54	30	Johnson 1979
<i>Leucoraja naevus</i>	70	90	du Buit 1976
<i>Raja asterias</i>	70	34-112	Capape 1977
<i>Raja brachyura</i>	120	40-90	Holden <i>et al.</i> 1971; Walker and Hislop 1998
<i>Raja clavata</i>	90	60-140	Holden 1975; Ryland and Ajayi 1984
<i>Raja eglanteria</i>	79	60	Luer and Gilbert 1985
<i>Raja miraletus</i>	60	32-90	Abd El Aziz <i>et al.</i> 1987
<i>Raja montagui</i>	80	25-60	Holden <i>et al.</i> 1971
<i>Raja polystigma</i>	53	20-62	Capape 1978
Average Fecundity		58.9	
Viviparous (histotroph)	Disc Width (cm)	Litter Size	
<i>Dasyatis americana</i>	200	2-10 (4.2)	Henningsen 2000
<i>Dasyatis centroura</i>	220	2-6	Capape 1993
<i>Dasyatis dipterura</i>	88	1-4	Ebert 2003
<i>Dasyatis longus</i>	156	1-3	Villavicencio Garayzar <i>et al.</i> 1994
<i>Dasyatis marmorata</i>	440	2-4	Capape and Zaouali 1995
<i>Dasyatis pastinaca</i>	60	6	Capape 1983
<i>Dasyatis sabina</i>	37	1-4 (2.6)	Snelson <i>et al.</i> 1988
<i>Dasyatis sayi</i>	73	1-6	Snelson <i>et al.</i> 1987
<i>Dasyatis tortonesei</i>	80	(4)	Capape 1978
<i>Potamotrygon circularis</i>	59.5	4-11 (5.8)	Thorson <i>et al.</i> 1983
<i>Potamotrygon motoro</i>	46	(6.3)	Thorson <i>et al.</i> 1983
<i>Pteroplatytrygon violacea</i>	80	4-13	Ebert 2003
Average Fecundity		4.4	
Viviparous (yolk-sac)	Total Length (cm)	Litter Size	
<i>Platyrhinoides triseriata</i>	91	1-15	Ebert 2003
<i>Rhinobatos cemiculus</i>	230	5-12 (7.5)	Capape and Zaouali 1994
<i>Rhinobatos granulatus</i>	280 SL	3-5	Prasad 1951
<i>Rhinobatos horkelii</i>	130	4-12	Lessa <i>et al.</i> 1986
<i>Rhinobatos hynnicephalus</i>	44	2-9 (4.6)	Wenbin and Shuyan 1993
<i>Rhinobatos lentiginosus</i>	75	6	Bigelow and Schroeder 1953
<i>Rhinobatos productus</i>	170	6-28 (9-11)	Ebert 2003
<i>Rhinobatos rhinobatos</i>	162	6-8	Capape <i>et al.</i> 1997
<i>Rhyncobatus djiddensis</i>	310	3-5	Prasad 1951; Compagno <i>et al.</i> 1989
<i>Zaptryx exasperata</i>	97	4-11	Ebert 2003
Average Fecundity		6.7	



have very limited fecundity if viviparous. Therefore, oviparity appears to be an adaptation in small species to increase fecundity (Holden 1973) contrary to the assertion of Wourms and Lombardi (1992). They claimed that brood sizes were similar in oviparous and viviparous species and attempted to prove their point by comparing the fecundity in *Prionace glauca* and *Hexanchus griseus*, two very large (> 300 cm TL) viviparous species, with scyliorhinids and rajids, most of which are small (< 100 cm TL) (Musick *et al.* 2004; Appendix 3.1). When small oviparous species are compared to small viviparous species, the differences are striking, with fecundity in oviparous forms averaging at least an order of magnitude higher than that in viviparous forms (Tables 3.2 and 3.3). The average annual fecundity in the scyliorhinids is 60.0 (eggs/year) compared to 4.6 (pups/year) in small squaliforms (Table 3.2), and the average fecundity in the rajids is 58.9 (eggs/year) compared to 5.5 (pups/year) in the myliobatiforms and rhinobatiforms (Table 3.3).

The disk-shaped batoid morphology appears to closely restrict the coelomic space and thus further restrict uterine capacity. The average *annual* fecundity for some species in the viviparous groups may be even smaller because they may not breed every year (Dodd 1983). Another selective advantage accrues to small species of oviparous sharks and rays through "bet hedging" (Stearns 1992). Small individuals are subject to proportionately higher predation than larger individuals (Peterson and Wroblewski 1984; Chen and Watanabe 1989; Cortés 2004), and if a pregnant viviparous shark is eaten, her evolutionary fitness equals zero. Species with simple oviparity avoid that problem, and even with egg predation rates of 20-60 percent (Frisk *et al.* 2002), their evolutionary fitness may be insured. These predation rates on cleidoic elasmobranch eggs are far lower than on non-cleidoic Actinopterygian eggs (Winemiller and Rose 1993). Multiple oviparity, where a moderate number of eggs are retained in the mother's uterus for a substantial portion of the developmental period before deposition (Nakaya 1975), has probably evolved from single oviparity, where and when egg predation rates may be very high particularly during the early stages of development. Likewise, the reversal to yolk-sac viviparity in two species of small scyliorhinids of the genus *Bythaelurus* also may have been selected for because of high egg predation rates. The evolution of cleidoic oviparity among chondrichthyans may have appeared in some taxa as early as the Paleozoic, but the evidence is sparse (Grogan and Lund 2004).

### 3.4.2 Parsimony

Past studies of the evolution of reproductive modes in modern elasmobranchs have been predicated on oviparity as the plesiomorphic reproductive state (Wourms 1977; Wourms and Lombardi 1992; Dulvy and Reynolds 2002). Wourms and Lombardi (1992) estimated that viviparity evolved from oviparity 18-20 times. Dulvy and Reynolds' analysis suggested that there were 9 to 10 transitions from oviparity to viviparity, and two "reversals" back to oviparity in the Rajidae and the orectolobiform *Stegostoma*. In contrast, hypothesizing that yolk-sac viviparity is the plesiomorphic state in living

elasmobranchs requires the evolution of oviparity once each in the Heterodontiformes, Rajidae, and Scyliorhinidae (including *Proscyllium*) and three times in the Orectolobiformes for a total of six transitions, and reversals to viviparity in some species of the Galeini among the oviparous scyliorhinids. Thus plesiomorphic yolk-sac viviparity is more parsimonious because it requires three to four fewer transitions and fewer reversals than in the alternate hypothesis (Table 3.4).

**Table 3.4** Hypotheses of plesiomorphic and apomorphic elasmobranch reproductive states with numbers of transitions and reversals.

State		Transitions	Reversals	Source
Plesiomorphic?	Apomorphic			
Oviparity	Viviparity	18-20	No reversals cited	Wourms, 1977
Oviparity	Viviparity	9-10	2	Dulvy and Reynolds 2002
Viviparity	Oviparity	6	1	This paper

Yolk-sac viviparity is clearly the plesiomorphic state in all orders of Batoidea and all squalomorphs. The situation in the galeomorphs may be a bit more equivocal because the Heterodontiformes are an old oviparous group that is the sister group of the remainder of the galeomorphs. However, the fossil record shows that the oldest Heterodontiformes were concurrent with the oldest yolk-sac viviparous Orectolobiformes (Brachaeluridae). In addition, the sister group relationship between the viviparous batoids and the selachians, of which the viviparous squalomorph Hexanchiformes are the oldest clade, would dictate that the ancestral neoselachians also had yolk-sac viviparity. Limited histotrophy has evolved from yolk-sac viviparity in several lineages and might be expected in virtually all major taxa in which yolk-sac viviparity is found. Lipid histotrophy has evolved once in the myliobatoid stingrays. Likewise, placental viviparity has evolved once in the higher carcharhiniforms. There are two independently derived forms of oophagy, lamniform oophagy and carcharhiniform oophagy, each of which has evolved one time. Recognizing that yolk-sac viviparity is plesiomorphic simplifies the pattern of reproductive evolution in living elasmobranchs and provides a straightforward sequence leading to other modes of reproduction.

The Chondrichthyes appear to be the oldest gnathostome group (Miller *et al.* 2003; Kikugawa *et al.* 2004) and may have evolved from some thelodont agnath ancestor in the Silurian (Marss *et al.* 2002). Early gnathostome evolution was apparently rapid with divergence into chondrichthyan and placoderm, and osteichthyan clades. Chondrichthyans and placoderms (Miles 1967) apparently evolved intromittent organs and internal fertilization and viviparity early on probably in response to high egg predation by the newly evolved gnathostomes. Viviparity is widespread among invertebrate groups (Marshall *et al.* 2003), including the ascidians, a chordate group basal to the vertebrates (Young, 1950). Sarcopterygian reproductive evolution is equivocal, with the living Dipnoi having benthic non-cleidoic eggs and the living coelacanth

having yolk-sac viviparity. However, in contrast to Chondrichthyes, actinopterygian reproduction evolved in another direction predicated on non-cleidoic eggs. Within that evolutionary trajectory several adaptations have evolved to decrease egg predation or to increase fitness in spite of predation. These include nest building and parental protection on one hand, and the production of very large numbers of small pelagic eggs on the other. It is significant that these adaptations never evolved in the Chondrichthyes, probably because they had already evolved a successful strategy (viviparity) to avoid egg predation.

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## APPENDIX 3.1

Skate total length (mean =  $71.6 \pm 41.9$ ), habitat and FAO region for 230 species of skates. FAO Regions are designated as follows: ANE = Indian Ocean, Antarctic, ANW = Pacific Ocean, Antarctic, ANC = Atlantic Ocean, Antarctic; EIO = Eastern Indian Ocean, WIO = Western Indian Ocean. For remaining FAO Region codes, first letter indicates western (W) or eastern (E); second letter indicates central (C), north (N) or south (S); and third letter indicates Atlantic (A) or Pacific (P).

Species	Total Length (cm)	Habitat	FAO Regions	Source
<b>Anacanthobatidae</b>				
<i>Anacanthobatis americanus</i>	38	183-915 m	WCA	McEachran and de Carvalho 2002
<i>Anacanthobatis borneensis</i>	38	600-1700 m	WNP	Hatooka <i>et al.</i> 2002
<i>Anacanthobatis donghaiensis</i>	44	200-1000 m	WNP	Deng <i>et al.</i> 1983
<i>Anacanthobatis folirostris</i>	62	300-512 m	WCA	McEachran and Fechhelm 1998; McEachran and de Carvalho 2002
<i>Anacanthobatis longirostris</i>	75	520-1052 m	WCA	McEachran and de Carvalho 2002
<i>Anacanthobatis marmoratus</i>	25	230-322 m	ESA, WIO	Compagno <i>et al.</i> 1989
<i>Anacanthobatis melanosoma</i>	59	900-1100 m	WNP, WCP	Last and Compagno 1999a
<i>Anacanthobatis ori</i>	21	1000-1725 m	WIO	Compagno <i>et al.</i> 1989
<i>Anacanthobatis</i> sp. A	54	420-1120 m	EIO	Last and Stevens 1994
<i>Anacanthobatis</i> sp. B	57	680-880 m	WEP	Last and Stevens 1994
<i>Cruriraja andamanica</i>	21	510 m	WIO	Misra 1969
<i>Cruriraja atlantis</i>	34	512-777 m	WCA	McEachran and de Carvalho 2002
<i>Cruriraja cadenati</i>	38	457-896 m	WCA	McEachran and de Carvalho 2002
<i>Cruriraja durbanensis</i>	31	859 m	ESA	Compagno <i>et al.</i> 1989
<i>Cruriraja parcomaculata</i>	55	195-620 m	ESA	Compagno <i>et al.</i> 1989
<i>Cruriraja poeyi</i>	34	366-870 m	WCA	McEachran and de Carvalho 2002
<i>Cruriraja rugosa</i>	49	366-1007 m	WCA	McEachran and de Carvalho 2002
<i>Cruriraja triangularis</i>	41	220-675 m	WIO	Compagno <i>et al.</i> 1989
<b>Arhynchobatidae</b>				
<i>Arynhobatis asperrimus</i>	75	90-1070 m	WSP	Cox and Francis 1997
<i>Bathyraja abyssicola</i>	157	362-2906 m	WNP, ENP	Hatooka <i>et al.</i> 2002; Mecklenburg <i>et al.</i> 2002; Ebert 2003
<i>Bathyraja aleutica</i>	154	148-900 m	WNP	Ishiyama 1967; Hatooka <i>et al.</i> 2002; Ebert 2003
<i>Bathyraja andriashevi</i>	120	1390-1480 m	WNP	Hatooka <i>et al.</i> 2002
<i>Bathyraja bergi</i>	95	100-500 m	WNP	Hatooka <i>et al.</i> 2002

<i>Bathyrāja brachyurops</i>	64	81-313 m	ESP	Lloris and Rucabado 1991
<i>Bathyrāja diplotaenia</i>	85	300-1000 m	WNP	Hatooka <i>et al.</i> 2002
<i>Bathyrāja eatonii</i>	100	15-800 m	ANE, ANW, ANE	Stehmann and Burkel 1990
<i>Bathyrāja fedorovi</i>	73	1370-1550 m	WNP	Hatooka <i>et al.</i> 2002
<i>Bathyrāja griseocauda</i>	49	94-585 m	ESP	Miller 1993
<i>Bathyrāja hesperatrica</i>	34.2	750-2000	ECA	Stehmann 1995
<i>Bathyrāja irrassa</i>	120	300-1200 m	ANE	Stehmann and Burkel 1990
<i>Bathyrāja isotrachys</i>	75	100-1480 m	WNP	Ishiyama 1967; Hatooka <i>et al.</i> 2002
<i>Bathyrāja kincaidi</i>	56	200-500 m	ECP, ENP	Ebert 2003
<i>Bathyrāja lindbergi</i>	93	120-950 (possibly 2000) m	WNP, ENP	Hatooka <i>et al.</i> 2002; Mecklenburg <i>et al.</i> 2002
<i>Bathyrāja longicauda</i>	80	605-735 m	ESP	McEachran and Miyake 1984; Chirichigno Fonseca 2001
<i>Bathyrāja maccaini</i>	120	to 500 m	ANC, ANE	Stehmann and Burkel 1990
<i>Bathyrāja maculata</i>	120	73-1110 (usually 100-650) m	WNP, ENP	Mecklenburg <i>et al.</i> 2002
<i>Bathyrāja matsubara</i>	120	200-1205 m	WNP	Hatooka <i>et al.</i> 2002
<i>Bathyrāja meridionalis</i>	120	760-800 m	ANC	Stehmann and Burkel 1990
<i>Bathyrāja microtrachys</i>	70	1995-2900 m	ECP, ENP	Ebert 2003
<i>Bathyrāja minispinosa</i>	83	150-1420 (usually 200-800) m	WNP, ENP	Mecklenburg <i>et al.</i> 2002
<i>Bathyrāja pallida</i>	160	2400-2950 m	ENA	Stehmann and Burkel 1984
<i>Bathyrāja parmaifera</i>	150	15-1602 m	WNP, ENP	Mecklenburg <i>et al.</i> 2002
<i>Bathyrāja radiata</i>	105	735-1060 m	ESP	McEachran and Miyake 1984
<i>Bathyrāja richardsoni</i>	186	0-2500 m	WSP, WNA, ENA, ESP	McEachran and Miyake 1984; Scott and Scott 1988; Stehmann and Burkel 1984; Cox and Francis 1997
<i>Bathyrāja shuntovi</i>	140	300-1470 m	WSP	Cox and Francis 1997
<i>Bathyrāja simoterus</i>	94	300- m	WNP	Ishiyama 1967; Hatooka <i>et al.</i> 2002
<i>Bathyrāja smirnovi</i>	100	100-950 m	WNP	Hatooka <i>et al.</i> 2002
<i>Bathyrāja smithii</i>	120	440-1020 m	ESA	Compagno <i>et al.</i> 1989
<i>Bathyrāja sp. A</i>	120	2300 m		Last and Stevens 1994
<i>Bathyrāja spinicauda</i>	170	140-800 m	WNA, ENA	Stehmann and Burkel 1984; Scott and Scott 1988
<i>Bathyrāja spinosissima</i>	150	800-2938 m	ECP	Ebert 2003
<i>Bathyrāja trachouros</i>	90		WNP	Hatooka <i>et al.</i> 2002
<i>Bathyrāja trachura</i>	89	400-2550 m	WNP, ENP, ECP	Mecklenburg <i>et al.</i> 2002; Ebert 2003
<i>Bathyrāja tzinovskii</i>	71	2500 m	WNP	Hatooka <i>et al.</i> 2002
<i>Bathyrāja violacea</i>	73	20-1100 m (usually 100-800 m)	WNP, ENP	Mecklenburg <i>et al.</i> 2002
<i>Irolita sp. A</i>	42	150-200 m	EIO	Last and Stevens 1994

#### 74 Reproductive Biology and Phylogeny of Chondrichthyes

<i>Irolita waitei</i>	52	50-200 m		Last and Stevens 1994
<i>Notoraja asperula</i>	51	200-1300 m	WSP	Cox and Francis 1997
<i>Notoraja ochroderma</i>	36	400-465 m	WCP	Last and Compagno 1999b
<i>Notoraja</i> sp. A	60	840-1120 m		Last and Stevens 1994
<i>Notoraja</i> sp. B	36	400-465 m	WEP	Last and Stevens 1994
<i>Notoraja</i> sp. C	45	590-760 m	EIO	Last and Stevens 1994
<i>Notoraja</i> sp. D	53	820-930 m	EIO	Last and Stevens 1994
<i>Notoraja spinefera</i>	80	170-1460 m	WSP	Cox and Francis 1997
<i>Notoraja tobitukai</i>	50	300-1000 m	WNP	Hatooka <i>et al.</i> 2002
<i>Pavoraja alleni</i>	35	200-460 m	EIO	Last and Stevens 1994
<i>Pavoraja nitida</i>	35	30-390 m	WSP	Last and Stevens 1994
<i>Pavoraja</i> sp. A	57	800-880 m	WEP	Last and Stevens 1994
<i>Pavoraja</i> sp. B	54	610-1200 m	EIO	Last and Stevens 1994
<i>Pavoraja</i> sp. C	33	200-520 m	EIO	Last and Stevens 1994
<i>Pavoraja</i> sp. D	30	300-400 m	WEP	Last and Stevens 1994
<i>Pavoraja</i> sp. E	37	210-500 m	WEP	Last and Stevens 1994
<i>Pavoraja</i> sp. F	37	360-739 m	WEP, WSP	Last and Stevens 1994
<i>Psammobatis extenta</i>	24.5	shelves	ESP, WSA	de Carvalho and de Figueiredo 1994
<i>Pseudoraja fischeri</i>	58	412-576 m	WCA	McEachran and de Carvalho 2002
<i>Rhinoraja albomaculata</i>	14.4	130-434 m	ESP, WSA	Lloris and Rucabado 1991
<i>Rhinoraja interrupta</i>	86	55-1372 m	WNP, ENP, ECP	Mecklenburg <i>et al.</i> 2002
<i>Rhinoraja kujiensis</i>	100	600-800 m	WNP	Ishiyama 1967
<i>Rhinoraja longi</i>	70	300-980 m	WNP	Hatooka <i>et al.</i> 2002
<i>Rhinoraja longicauda</i>	70	549-914 m	WNP	Ishiyama 1967
<i>Rhinoraja murrayi</i>	60	30-650 m	ANE	Stehmann and Burkel 1990
<i>Rhinoraja odai</i>	60	330-350 m	WNP	Ishiyama 1967; Hatooka <i>et al.</i> 2002
<i>Rhinoraja taranetzi</i>	70	15-550 m	WNP, ENP	Mecklenburg <i>et al.</i> 2002
<i>Sympterygia acuta</i>	42.3	shelves	ESP	McEachran 1982
<i>Sympterygia bonapartei</i>	61	shelves	ESP	McEachran 1982
<i>Sympterygia brevipinna</i>	47	shelves	ESP	McEachran 1982
<i>Sympterygia lima</i>	53.7	shelves	ESP	McEachran 1982
<b>Rajidae</b>				
<i>Amblyraja badia</i>	100	1100-2300 m	WNP, ENP, ECP	Hatooka <i>et al.</i> 2002
<i>Amblyraja freerichsi</i>	120	800-2500 m	ESP	Lamilla 2003
<i>Amblyraja georgiana</i>	100	20-250, 660, 1130 m	ANC, ANW	Stehmann and Burkel 1990
<i>Amblyraja hyperborea</i>	106	300-1500 m	EIO, WSP, WEP, WNP, ENA	Stehmann and Burkel 1984; Last and Stevens 1994; Cox and Francis 1997
<i>Amblyraja jenseni</i>	85	1907 m	WNA	Bigelow and Schroeder 1953
<i>Amblyraja radiata</i>	62	20-1000 m	ESA, WIO	Compagno <i>et al.</i> 1989
<i>Amblyraja radiata</i>	102	18-1000 m	WNA, WCA	Stehmann and Burkel 1984; Scott and Scott 1998; McEachran and de Carvalho 2002

<i>Amblyraja reversa</i>	60	1499 m	WIO	Misra 1969
<i>Amblyraja robertsi</i>	77	1350 m	ESA, WIO	Compagno <i>et al.</i> 1989
<i>Amblyraja taaf</i>	90	150-600 m	ANE	Stehmann and Burkel 1990
<i>Breviraja claramaculata</i>	29	293-896 m	WCA	McEachran and de Carvalho 2002
<i>Breviraja colesi</i>	40	220-415 m	WCA	McEachran and de Carvalho 2002
<i>Breviraja marklei</i>	45.1	443-988 m		McEachran and Miyake 1987
<i>Breviraja mouldi</i>	41	353-776 m	WCA	McEachran and de Carvalho 2002
<i>Breviraja nigriventralis</i>	44	546-776 m	WCA, WSA	McEachran and de Carvalho 2002
<i>Breviraja spinosa</i>	33	366-671 m	WCA	McEachran and de Carvalho 2002
<i>Dactylobatus armatus</i>	32	338-685 m	WCA	McEachran and de Carvalho 2002
<i>Dactylobatus clarki</i>	75	366-915 m	WCA	McEachran and de Carvalho 2002
<i>Dipturus batis</i>	250	100-1000 m	ECA, ENA	Stehmann and Burkel 1984; Stehmann 1990
<i>Dipturus bullisi</i>	77	183-549 m	WCA	McEachran and de Carvalho 2002
<i>Dipturus campbelli</i>	66	137-403 m	ESA, WIO	Compagno <i>et al.</i> 1989
<i>Dipturus doutrei</i>	100	450-600 m	ESA, WIO	Compagno <i>et al.</i> 1989
<i>Dipturus garricki</i>	107	275-476 m	WCA	McEachran and de Carvalho 2002
<i>Dipturus gigas</i>	140	300-400 m	WNP	Ishiyama 1967; Hatooka <i>et al.</i> 2002
<i>Dipturus gudgeri</i>	140	160-700 m	EIO, WSP	Last and Stevens 1994
<i>Dipturus innominatus</i>	240	15-1310 m	WSP	Cox and Francis 1997
<i>Dipturus johannisdavesi</i>	26.3	220-549 m	WIO	Misra 1969
<i>Dipturus kwangtungensis</i>	65	20-80 m	WNP	Hatooka <i>et al.</i> 2002
<i>Dipturus laevis</i>	152	0-750 m	WNA	Bigelow and Schroeder 1953; Scott and Scott 1988
<i>Dipturus lancerostratus</i>	82	430-439 m	WIO	Compagno <i>et al.</i> 1989
<i>Dipturus linteus</i>	112	55-1371 m	WNA, ENA	Stehmann and Burkel 1984; Scott and Scott 1988
<i>Dipturus macrocaudus</i>	120	300-400 m	WNP	Hatooka <i>et al.</i> 2002
<i>Dipturus nasulus</i>	118	10-1500 m	WSP	Cox and Francis 1997
<i>Dipturus nidarosiensis</i>	200	200-1000 m	ENA	Stehmann and Burkel 1984; Stehmann 1990
<i>Dipturus olseni</i>	57	55-384 m	WCA	McEachran and de Carvalho 2002
<i>Dipturus oregoni</i>	144	475-1079 m	WCA	McEachran and de Carvalho 2002
<i>Dipturus oxyrhynchus</i>	150	90-900 m	ENA, MED	Stehmann and Burkel 1984; Stehmann 1990
<i>Dipturus pullopunctatus</i>	130	50-457 m	ESA	Compagno <i>et al.</i> 1989
<i>Dipturus springeri</i>	160	88-740 m	ESA, WIO	Compagno <i>et al.</i> 1989
<i>Dipturus stenorhynchus</i>	90	625-741 m	WIO	Compagno <i>et al.</i> 1989



## 76 Reproductive Biology and Phylogeny of Chondrichthyes

<i>Dipturus teevani</i>	84	311-732 m	WCA	McEachran and de Carvalho 2002
<i>Dipturus tengu</i>	100	60-150 m	WNP	Ishiyama 1967; Hatooka <i>et al.</i> 2002
<i>Fenestraja atripinna</i>	29	366-951 m	WCA	McEachran and de Carvalho 2002
<i>Fenestraja cubensis</i>	23	440-869 m	WCA	McEachran and de Carvalho 2002
<i>Fenestraja ishiyamai</i>	36	503-950 m	WCA	McEachran and de Carvalho 2002
<i>Fenestraja mamillidens</i>	29.2	1091 m	WIO	Misra 1969
<i>Fenestraja plutonia</i>	27	293-1024 m	WCA	McEachran and de Carvalho 2002
<i>Fenestraja sibogae</i>	31	290 m	WCP	Last and Compagno 1999c
<i>Fenestraja sinismexicanus</i>	36	56-1096 m	WCA	McEachran and de Carvalho 2002
<i>Genus A (Formerly Raja) binoculata</i>	244	3-800 m	ENP, ECP	Mecklenburg <i>et al.</i> 2002
<i>Genus A (Formerly Raja) cortezensis</i>	35.8	to 80 m	ECP	McEachran 1995
<i>Genus A (Formerly Raja) inornata</i>	76	17-67	ECP, ENP	Ebert 2003
<i>Genus A (Formerly Raja) pulchra</i>	100	50-100 m	WNP	Hatooka <i>et al.</i> 2002
<i>Genus A (Formerly Raja) rhina</i>	137	20-1000 m	ENP, ECP	Mecklenburg <i>et al.</i> 2002; Ebert 2003
<i>Genus A (Formerly Raja) stellulata</i>	76	to 732 m (usually <100 m)	ECP, ENP	Ebert 2003
<i>Genus B (Formerly Raja) ackleyi</i>	41	32-384 m	WCA	McEachran and de Carvalho 2002
<i>Genus B (Formerly Raja) bahamensis</i>	54	366-411 m	WCA	McEachran and de Carvalho 2002
<i>Genus B (Formerly Raja) cervigoni</i>	51	37-174 m	WCA	McEachran and de Carvalho 2002
<i>Genus B (Formerly Raja) eglanteria</i>	79	0-111 m	WNA, WCA	Bigelow and Schroeder 1953; McEachran and de Carvalho 2002
<i>Genus B (Formerly Raja) equitorialis</i>	50	shelvs	ECP, ESP	McEachran 1995
<i>Genus B (Formerly Raja) texana</i>	53.7	0-91 m	WCA	McEachran and de Carvalho 2002
<i>Genus B (Formerly Raja) velezi</i>	75.6	35-140 m	ECP, ESP	McEachran 1995
<i>Gurgesiella atlantica</i>	49	247-960 m	WCA	McEachran and de Carvalho 2002
<i>Gurgesiella dorsalifera</i>	53	500-800 m	WSA	McEachran and de Carvalho 2002
<i>Gurgesiella furvenscens</i>	52	slopes	ESP	Grove and Lavenberg 1997
<i>Leucoraja circularis</i>	120	70-300 m	ENA, MED	Stehmann and Burkel 1984; Stehmann 1990

<i>Leucoraja compagno</i>	29.2	550 m	ESA	Stehmann 1995
<i>Leucoraja erinacea</i>	54	26-111 m; 329 m (Scott and Scott 1988)	WNA	Bigelow and Schroeder 1953; Scott and Scott 1988
<i>Leucoraja fullonica</i>	100	30-600 m	ECA, MED, ENA	Stehmann and Burkel 1984; Stehmann 1990
<i>Leucoraja garmani</i>	44	37-366 m	WNA, WCA	McEachran and de Carvalho 2002
<i>Leucoraja lentiginosa</i>	44	53-588 m	WCA	Bigelow and Schroeder 1953; McEachran and de Carvalho 2002
<i>Leucoraja leucosticta</i>	80	70-600 m	ECA	Stehmann 1990
<i>Leucoraja melitensis</i>	50	60-600 m	MED	Stehmann and Burkel 1984
<i>Leucoraja naevus</i>	70	20-250 m, 400 m	ENA, ECA	Stehmann and Burkel 1984; Stehmann 1990
<i>Leucoraja ocellata</i>	109	0-73 m	WNA, WCA	Bigelow and Schroeder 1953; Frisk <i>et al.</i> 2002
<i>Leucoraja wallacei</i>	92	95-432 m	ESA, WIO	Compagno <i>et al.</i> 1989
<i>Leucoraja yucatanensis</i>	30	192-457 m	WCA	McEachran and de Carvalho 2002
<i>Malacoraja kreftli</i>	70	1200 m	ENA	Stehmann and Burkel 1984
<i>Malacoraja senta</i>	61	46-874 m	WNA	McEachran and de Carvalho 2002
<i>Malacoraja spinacidervis</i>	70	864-1350 m (juvies); Adults >1500 m	ECA, ESA, ENA	Stehmann and Burkel 1984; Compagno <i>et al.</i> 1989; Stehmann 1990
<i>Neoraja africana</i>	30	900-1030 m	ECA	Stehmann 1990
<i>Neoraja caerulea</i>	30	600-1260 m	ENA	Stehmann and Burkel 1984
<i>Neoraja carolinensis</i>	29	695-1010 m	WCA	McEachran and de Carvalho 2002
<i>Neoraja stehmanni</i>	35	292-1025 m	ESA	Compagno <i>et al.</i> 1989
<i>Okamejei acutispina</i>	45	50-100 m	WNP	Ishiyama 1967; Hatooka <i>et al.</i> 2002
<i>Okamejei australis</i>	50	50-180 cm	WEP, WSP	Last and Stevens 1994
<i>Okamejei boesmani</i>	55	70-90 m	WNP	Hatooka <i>et al.</i> 2002
<i>Okamejei cerva</i>	60	20-470 m	EIO, WSP	Last and Stevens 1994
<i>Okamejei heemstrai</i>	51.5	500 m	WIO	McEachran and Fechtelm 1982
<i>Okamejei hollandi</i>	55	60-90 m	WNP	Ishiyama 1967
<i>Okamejei kenojei</i>	66	30-100 m	WNP	Ishiyama 1967; Hatooka <i>et al.</i> 2002
<i>Okamejei lemprieri</i>	52	0-170 m	EIO, WSP	Last and Stevens 1994
<i>Okamejei meerdervoorti</i>	33	80-90 cm	WNP	Hatooka <i>et al.</i> 2002
<i>Okamejei pita</i>	46	shallow	WIO	Carpenter <i>et al.</i> 1997
<i>Okamejei powelli</i>	36	122-237 m	WIO	Misra 1969
<i>Okamejei schmidtii</i>	50	20-50 m	WNP	Hatooka <i>et al.</i> 2002
<i>Raja africana</i>	80	50-400 m	ESA, MED	Stehmann and Burkel 1984; Stehmann 1990

## 78 Reproductive Biology and Phylogeny of Chondrichthyes

<i>Raja asterias</i>	70	to 170 m	ECA, MED	Stehmann and Burkel 1984; Stehmann 1990
<i>Raja brachyura</i>	120	to 100 m	ENA, ECA, MED	Stehmann and Burkel 1984; Stehmann 1990
<i>Raja clavata</i>	90	to 300 m	ENA, ECA, MED, ESA, WIO	Stehmann 1990
<i>Raja herwigi</i>	50	55-102 m	ECA	Stehmann 1990
<i>Raja maderensis</i>	80	to 150 m	ENA, ECA	Stehmann and Burkel 1984; Stehmann 1990
<i>Raja microocellata</i>	80	to 100 m	ENA, ECA	Stehmann and Burkel 1984; Stehmann 1990
<i>Raja miraletus</i>	60	17-306 m	ENA, ECA, MED, ESA, WIO	Stehmann and Burkel 1984; Compagno <i>et al.</i> 1989; Stehmann 1990
<i>Raja montagui</i>	80	to 100 m	ENA, MED, ECA	Stehmann and Burkel 1984; Stehmann 1990
<i>Raja polystigma</i>	53	100-400 m	MED	Capape 1978; Stehmann and Burkel 1984
<i>Raja radula</i>	70	to 300 m	MED	Stehmann and Burkel 1984; Stehmann 1990
<i>Raja rondeleti</i>	50	moderate depths		MED Stehmann and Burkel 1984
<i>Raja</i> sp. A	70	40-250 m	EIO, WSP	Last and Stevens 1994
<i>Raja</i> sp. B	90	450-600 m	EIO, WSP	Last and Stevens 1994
<i>Raja</i> sp. C	63	70-450 m	WSP	Last and Stevens 1994
<i>Raja</i> sp. D	48	20-200 m	EIO	Last and Stevens 1994
<i>Raja</i> sp. E	58	200-250 m	EIO	Last and Stevens 1994
<i>Raja</i> sp. F	72	200-440 m	EIO	Last and Stevens 1994
<i>Raja</i> sp. G	77	225-550 m	WEP	Last and Stevens 1994
<i>Raja</i> sp. H	76	240-650 m	WEP, WSP	Last and Stevens 1994
<i>Raja</i> sp. I	115	400-1030 m	EIO, WEP, WSP	Last and Stevens 1994
<i>Raja</i> sp. J	133	800-1400 m	EIO, WSP	Last and Stevens 1994
<i>Raja</i> sp. K	76	440-650 m	WEP	Last and Stevens 1994
<i>Raja</i> sp. L	67	5 m	EIO	Last and Stevens 1994
<i>Raja</i> sp. M	36	20-35 m	EIO	Last and Stevens 1994
<i>Raja</i> sp. N	56	400-735 m	EIO	Last and Stevens 1994
<i>Raja</i> sp. O	40	350-420 m	EIO	Last and Stevens 1994
<i>Raja</i> sp. P	55	860-1500 m	EIO, WSP	Last and Stevens 1994
<i>Raja straeleni</i>	91	0-690 m	ECA, ESA	Compagno <i>et al.</i> 1989
<i>Raja undulata</i>	100	to 200 m	ENA, ECA, MED	Stehmann and Burkel 1984; Stehmann 1990
<i>Rajella annandalei</i>	33	400-830 m	WCP	Last and Compagno 1999c
<i>Rajella barnardi</i>	68	170-913 m	ESA	Compagno <i>et al.</i> 1989 (entry for <i>Rajella confundens</i> )
<i>Rajella bathyphila</i>	90	600-2173 m	WNA, ENA, ECA	Bigelow and Schroeder 1948; Stehmann and Burkel 1984; Stehmann 1990; Stehmann 1995

<i>Rajella bigelowi</i>	55	650-4156 m	WNA, WCA, ENA, ECA	Stehmann and Burkel 1984; Stehmann 1990
<i>Rajella caudaspinosa</i>	58	310-718 m	ESA	Compagno <i>et al.</i> 1989
<i>Rajella dissimilis</i>	70	719-1016 m (1620 m, Stehmann)	ECA, ESA	Compagno <i>et al.</i> 1989; Stehmann 1990
<i>Rajella fuliginea</i>	45	731-1280 m	WCA	McEachran and de Carvalho 2002
<i>Rajella lyllae</i>	60	170-2050 m	WNA, ENA	Bigelow and Schroeder 1953; Stehmann 1990; Muus <i>et al.</i> 1999
<i>Rajella leopardus</i>	95	300-923 m; 170-1920 m (Stehmann)	ECA, ESA	Compagno <i>et al.</i> 1989; Stehmann 1990
<i>Rajella nigerrima</i>	45.7	590-1000	ESP	McEachran and Miyake 1984; Lamilla 2003
<i>Rajella purpuriventralis</i>	51	732-2010 m	WCA	McEachran and de Carvalho 2002
<i>Rajella ravidula</i>	67	496-1016 m	ECA, ESA	Compagno <i>et al.</i> 1989, Stehamann 1995
<i>Rajella sadowskyii</i>	75	1200 m	ESP	Lamilla 2003
<i>RostroRaja alba</i>	230	30-366 m	ENA, ECA, MED, ESA, WIO	Compagno <i>et al.</i> 1989; Stehmann 1990
<i>Western Pacific species (Formerly Raja) koreana</i>	74	30-120 m	WNP	Halooka <i>et al.</i> 2002
<i>Western Pacific species (Formerly Raja) polyommata</i>	36	140-310 m	WEP	Last and Stevens 1994
<i>Western Pacific species (Formerly Raja) whitleyi</i>	170	0-170 m	EIO, WSP	Last and Stevens 1994