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Reproduction and Lifespan

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PART M, CHAPTER 5: REPRODUCTION AND LIFESPAN

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INTRODUCTION

The reproductive habits of living coleoids vary widely and are best known for a few, mainly coastal species. The paucity of information is apparent in the first volume of *Cephalopod Life Cycles* (Boyle, 1983a), since it includes details for just 20 species, about 3% of living species. In her review of reproduction in the second volume, Mangold (1987, p. 197) commented that "we are far from having filled all the gaps in our knowledge," and this remains so, especially among oceanic forms (Arnold & Williams-Arnold, 1977; Wells & Wells, 1977; Arnold, 1984; von Boletzky, 1986; Mangold, 1989c).

SEXUAL DIMORPHISM

The sexes are separate (gonochristic) in all Recent Cephalopoda, and external sexual dimorphism is widespread (Arnold & Williams-Arnold, 1977; Wells & Wells, 1977; Arnold, 1984; Mangold, 1987, 1989b). In most species, the male develops a special protrusible terminal organ, or penis, through which the spermatophores are extruded to the hectocotylus. This specialized structure is present on the arm(s) of the male of many species and is used for the transfer of spermatophores to the female. In the only spirulid, *Spirula spirula,* the hectocotylus is most distinctive, as both arms IV are modified, and their distal tips are morphologically quite different from each other (Kerr, 1931). In histioteuthid squids, both arms I are hectocotylized, and in the sepiolid *Heteroteuthis dispar,* both arms III are modified, but in most, only one arm is hectocotylized (Mangold, 1989b). The males of the epipelagic octopods are not only dwarf, but all possess a relatively huge hectocotylus, which is autotomized or self-amputated to be left within the female. Once the production of spermatozoa and spermatophores is initiated, it continues over a considerable period of time while the animals are still growing (Mangold, 1987).

Dimorphism is often apparent in the disparity in size of the two sexes. The male of the smallest known coleoid, *Idiosepius pygmaeus,* is mature at 10.3 mm mantle length, but the female is not mature until 17.6 mm mantle length (Jackson, 1989). The male of the giant squid, *Architeuthis,* is also smaller than the female at maturity (Roeleveld & Lipinski, 1991). In contrast, in the largest of the loliginid squids, *Loligo forbesi,* the mature male has a mantle length more than twice that of the mature female (Martins, 1982). In most of the species investigated, males have been found to mature earlier than females (Mangold, 1987). The epipelagic octopods *Tremoctopus violaceus, Ocythoe tuberculata,* and *Argonauta* (Fig. 1) show extreme sexual dimorphism, as in each, the male is a dwarf.

Secondary sexual features are found and are varied. A visceral photophore develops in the male of the oceanic squid *Chtenopteryx (Ctenopteryx) sicula,* presumably to provide a visual signal to the female; this is also the largest light organ yet known among living coleoids (Herring, 1988). Mature females of two octopods, *Eledonella pygmaea* and *Japetella diaphana,* develop a circumoral ring of luminescent tissue prior to mating (Robison & Young, 1981; Herring, Dilly, & Cope, 1987). Two species of the loliginid *Loligo (Alloteuthis)* develop a tail as they approach maturity; in both, that of the male is longer (Naef, 1923). A broad tail and lateral organ develop in the male of one cuttlefish, *Sepia confusa* (Massy & Robson, 1923). Males

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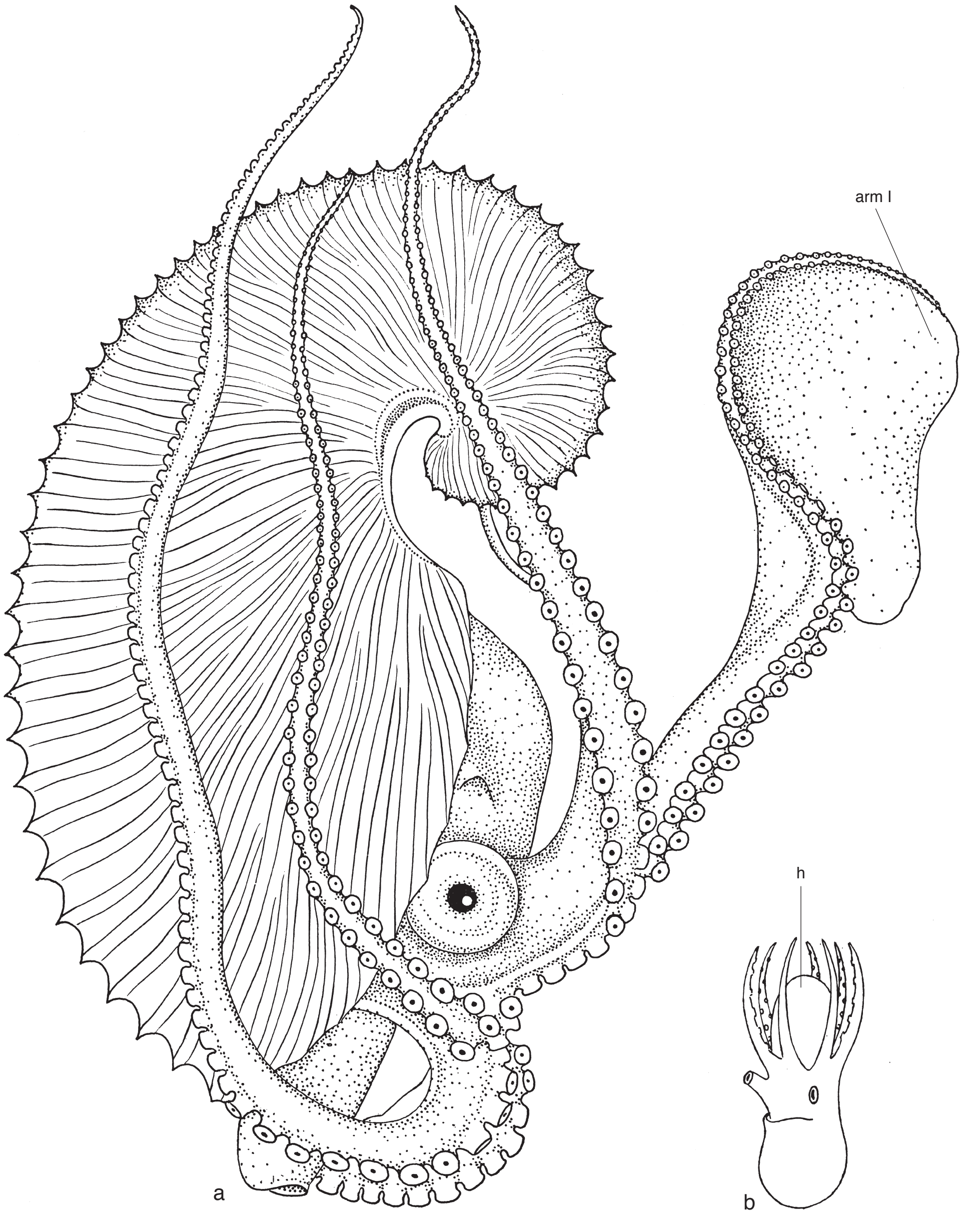

FIG. 1. *Argonauta argo*; *a,* female, with thin shell or brood chamber, which is secreted by the tissues of the large, silvery flaps of the dorsal arms; *b,* male grows only to 15 mm mantle length and is much smaller than female, and its hectocotylus (*h*) is relatively huge; both are drawn to same scale (Voss & Williamson, 1971).

of some species develop enlarged suckers (PACKARD, 1961; SINGLEY, 1983).

Hard tissue is rare in sexually dimorphic structures of living coleoids. The female alone of the pelagic octopod *Argonauta* has a thin external shell forming a brood chamber (Fig. 1). The shell is secreted by the dorsal arms, which have broad, expandable, membranous, glandular flaps. It is of calcite, with a thick upper and a thinner under layer,

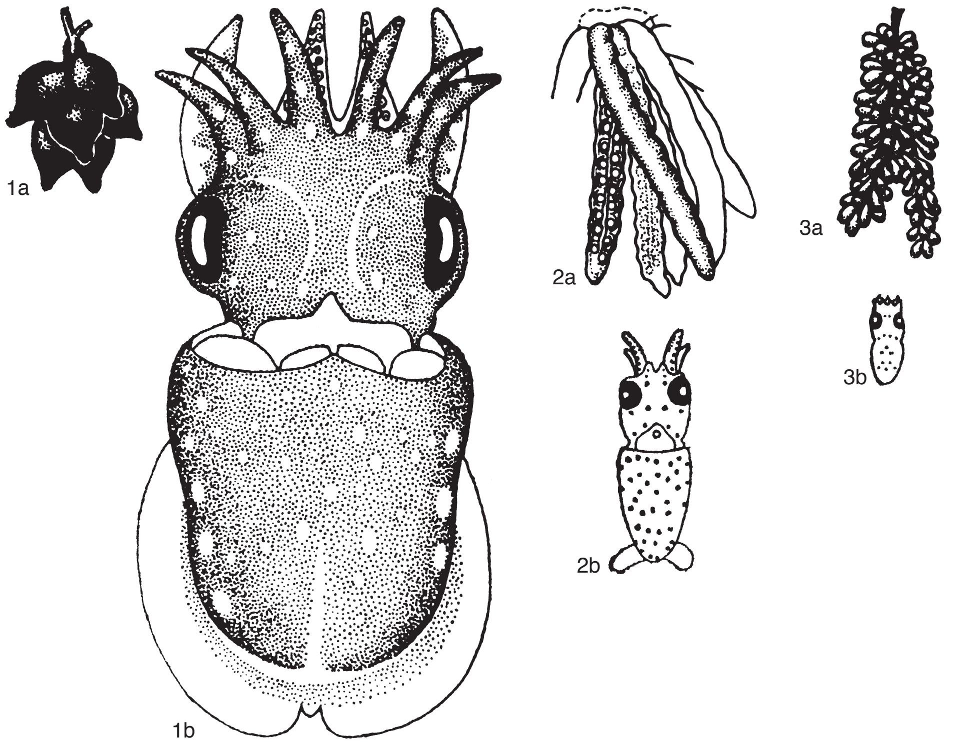

FIG. 2. Eggs and newly hatched young of *1, Sepia officinalis, 2, Loligo vulgaris,* and *3, Octopus vulgaris,* showing how they differ in size; all drawn to same scale (Fioroni, 1981).

and is finely prismatic in structure. Between is a very thin layer of very fine, irregularly grained calcite (BØGGILD, 1930), and the matrix is organic (NAEF, 1923).

MATURITY AND MATING

Sexual maturity can be followed in the development of the gonads. In the ovary, the number and sizes of the oocytes formed depend on the species. The oocytes may be all of the same size and at the same stage of development in the ovary, may range from early developmental stages to mature eggs, or there may be batches of equally sized eggs, each batch at a different stage. The number of eggs produced by a single female ranges from some 25 to as many as 3 to 5 million (FIORONI, 1982b; BOYLE, 1983a; MANGOLD, 1989c; HOCHBERG, NIXON, & TOLL, 1992; MANGOLD, YOUNG, & NIXON, 1993). The eggs are rich in yolk, spherical to elongated ovoid, and range from 0.6 to 35.0 mm in length (Fig. 2) (FIORONI, 1981, 1990; ARNOLD, 1984; SWEENEY & others, 1992).

There are significant differences in reproductive behavior in mating, in the site of sperm storage, in fertilization, and in spawning among coleoids (MANGOLD, 1987). Mating has been observed in a number of species (DREW, 1911; BOYLE, 1983a). Copulation takes place in the head-to-head position in some sepiids and loliginids (Fig. 3), and an early description was given by ARISTOTLE (384 to 322 BCE, translation by THOMPSON, 1910). The pair swim together slowly, maintaining their positions, and the spermatophores, which contain spermatozoa, are transferred to a special pouch below the buccal mass of the female. In one of the sepiolids, *Euprymna*

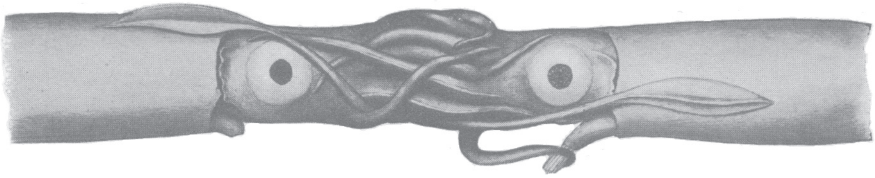

FIG. 3. *Loligo pealei*; position adopted during copulation when spermatophores are placed so that they become attached to outer buccal membrane of female (Drew, 1911).

scolopes, the female is grasped from below around the margin of the mantle by the arms of the male, and the spermatophores maneuvered by the hectocotylus into the aperture of the oviduct (SINGLEY, 1983). In some octopods, the female is mounted by the male, while the hectocotylized arm enters the mantle to insert the spermatophores in or near the oviduct. Others mate *à distance* (MANGOLD-WIRZ, 1963), as the male greatly elongates the hectocotylized arm to extend a considerable distance (J. Z. YOUNG, 1962) to insert the distal tip into the mantle of the female (Fig. 4). The spermatophores may be stored in the seminal receptacle, or spermatheca, or may be attached to the female. Spermatophores can remain viable for long periods, at least five months in the cold-water octopod *Bathypolypus arcticus* (O'DOR & MACALASTER, 1983).

SPAWNING

Spawning may be a single event when all or most oocytes develop simultaneously to maturity. Then, usually shortly after mating, spawning follows, and this may be a terminal event for the adult (semelparous reproduction) (MANGOLD, 1987; MANGOLD, YOUNG, & NIXON, 1993). Alternatively, spawning may be intermittent (iteroparous), wherein eggs are shed either in batches or singly as they mature.

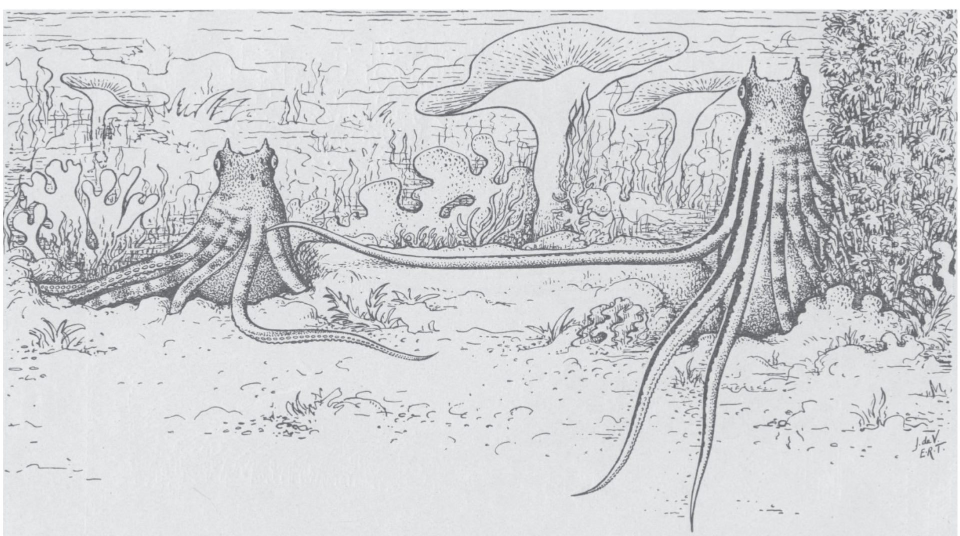

FIG. 4. *Octopus horridus*; male stretches its hectocotylized arm to reach the female (J. Z. Young, 1962).

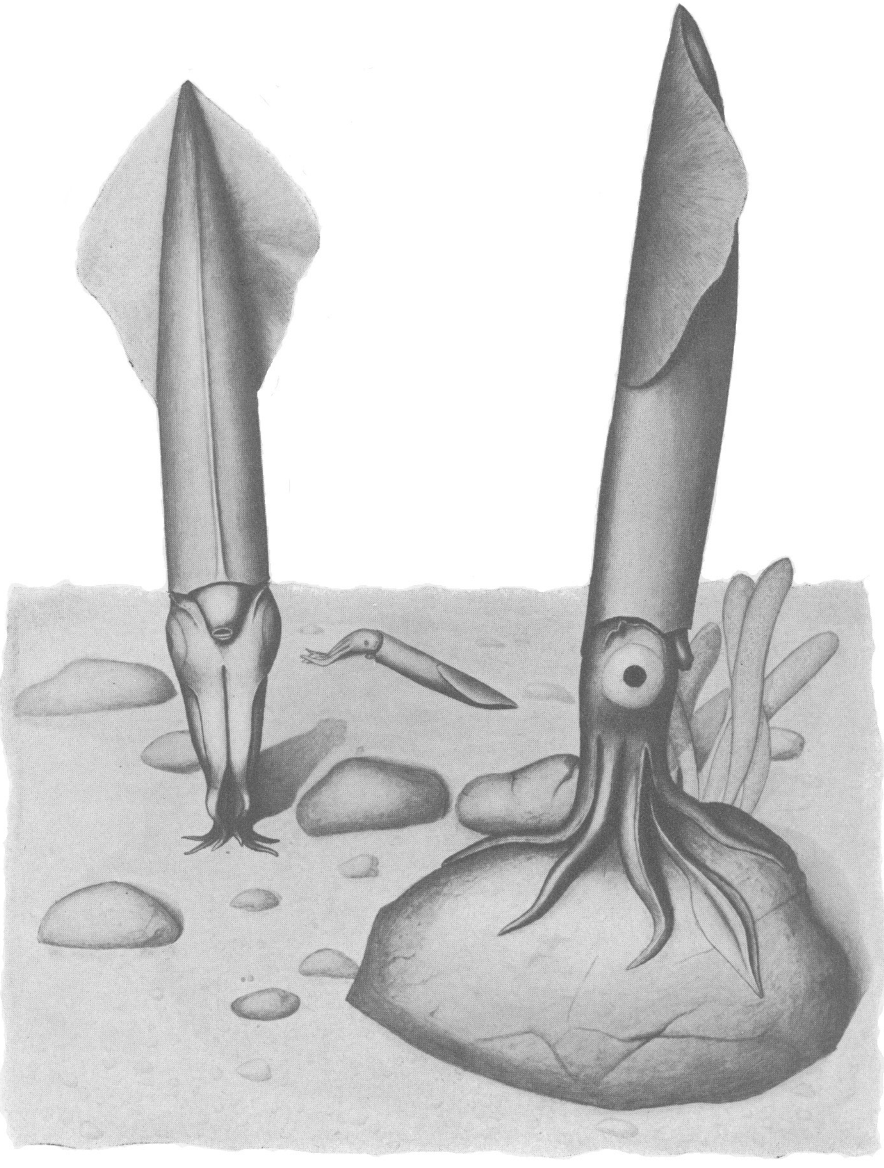

FIG. 5. *Loligo pealei*; female is positioned to select a site for the eggs (left) and attaches them to a rock (right) (Drew, 1911).

Individual eggs belonging to some oegopsid squids have been taken in plankton nets, indicating that adults spawn single eggs (R. E. YOUNG, HARMAN, & MANGOLD, 1985b). This has been found in species of the Enoploteuthidae (R. E. YOUNG & HARMAN, 1985) and in a species of *Brachioteuthis* (Brachioteuthidae) (R. E. YOUNG, HARMAN, & MANGOLD, 1985a). Among other oegopsids, some are known to shed their eggs in a single batch, forming a mass. One mass collected from the surface (63 to 94 cm long, 13 to 21 cm in diameter) consisted of semisolid, translucent jelly with

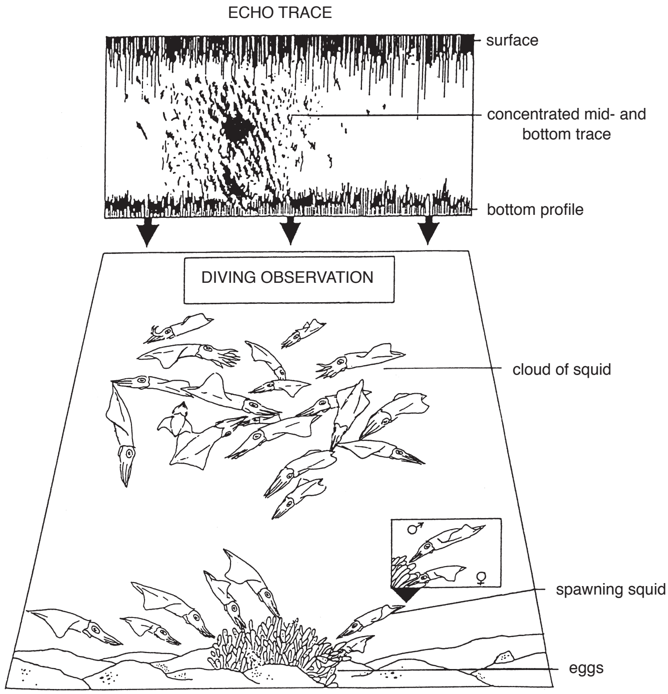

FIG. 6. *Loligo vulgaris reynaudii*; diagram of echo traces (above), and observations by divers, made at the same time and at the same site (below); mass spawning takes place on the bottom and in midwater aggregations made up of pairing squids moving in dense groups above egg masses (Sauer, Smale, & Lipinski, 1992).

numerous egg sacs, each with an active little squid, embedded in single rows. Another (about 75 cm long) also contained developing coleoid embryos; other such masses have also been reported (CLARKE, 1966). One ommastrephid, *Illex illecebrosus,* spawns in midwater: the female appears to preform a concentrated package of gel, eggs, and broken spermatophores in the mantle; once expelled, the mass swells and then sinks (O'DOR, 1983). Another member of the family, *Todarodes pacificus,* spawns a spherical egg mass (80 cm diameter), a gelatinous, neutrally buoyant, and contained some 200,000 eggs (BOWER & SAKURAI, 1996). A floating egg mass (130 cm long, 20 cm in diameter) was photographed by divers off the coast of Japan. When hatched, the young were identified as *Thysanoteuthis rhombus,* a large oceanic squid (SUZUKI, MISAKI, & OKUTANI, 1979).

Many living coastal coleoids attach their eggs, either singly to rocks, plants, coral, or other firm structures, or in masses to the substrate or to rocks, after selecting a suitable site (Fig. 5) (DREW, 1911; GRISWOLD & PREZIOSO, 1981). *Loligo vulgaris reynaudii* concentrate in large numbers above a spawning ground (Fig. 6) (FIELDS, 1965; SAUER, SMALE, & LIPINSKI, 1992). One spawning bed of *Loligo* sp. was about 40 m in length and covered with groups of egg capsules (VECCHIONE, 1988). Many coastal octopods brood their eggs in a den or in crevices in the rocks (WELLS, 1978; BOYLE, 1983a). Two species, *Octopus defilippi* and *O. burryi,* carry their eggs with them (HANLON, 1988). The epipelagic octopods

FIG. 7. *Cirrothauma murrayi*; egg mass from ovary of a specimen with a mantle length of 130 mm (Aldred, Nixon, & Young, 1983).

of open waters brood their eggs in various ways. *Tremoctopus violaceus* spawns its eggs in batches, each batch being held in a sector of the female's web (HAMABE, 1973); the female *Argonauta* secretes a brood chamber (Fig. 1) (NAEF, 1923; ARNOLD, 1984); and *Ocythoe tuberculata* is ovoviviparous, as the young develop within the female, to be released only when fully developed (STEENSTRUP, 1880; NAEF, 1923, 1928). The eggs of these octopods presumably hatch at different times, so the movement of the female disperses the hatchlings horizontally. At least one species of bathypelagic octopod is known to brood its young (R. E. YOUNG, 1972b).

The ovaries of intermittent spawners contain oocytes of various sizes at different stages of development (MANGOLD, YOUNG, & NIXON, 1993). In 1832, OWEN carefully depicted eggs of widely different sizes in the ovary of *Nautilus* (Nautilida) and then in 1835 in *Rossia* (Sepiolida). A similar condition was illustrated in one octopod by REINHARDT and PROSCH (1846) and in the ovary of *Spirula* (Spirulida) by OWEN (1879) and by CHUN (1910b). *Nautilus* is now known to

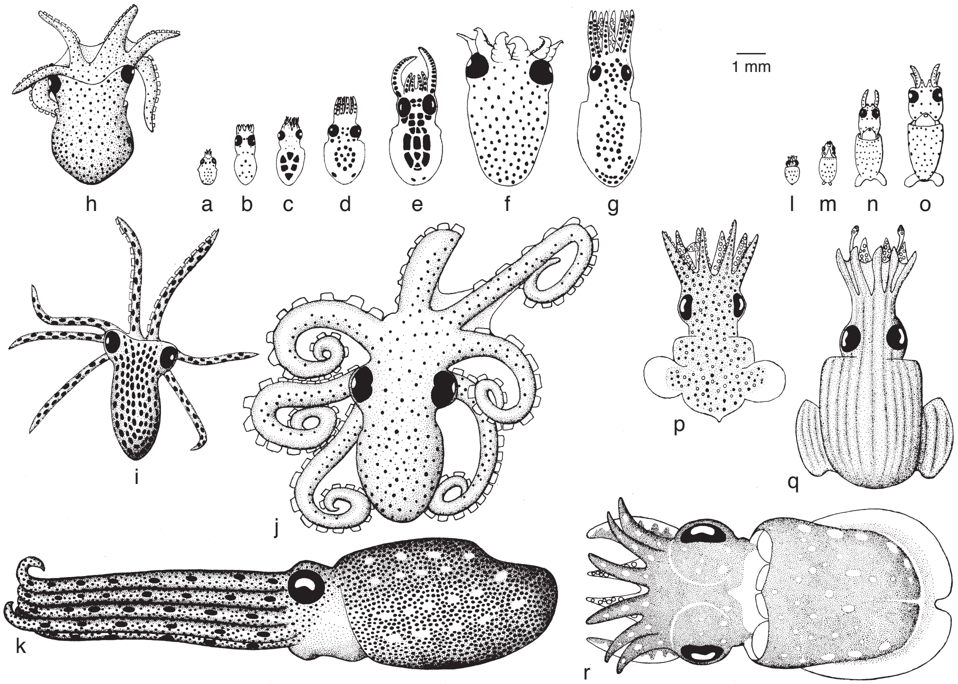

FIG. 8. Newly hatched young of Octopoda: *a, Argonauta argo; b, Octopus vulgaris; c, Octopus cyanea; d, Robsonella australis; e, Octopus defilippi; f, Eledone cirrhosa; g, Octopus maorum; h, Hapalochlaena maculosa; i, Octopus joubini; j, Octopus briareus; k, Eledone moschata;* Teuthida: *l, Ommastrephes sloani pacificus; m, Ommastrephes sp.; n, Alloteuthis media; o, Loligo vulgaris;* Sepiolida: *p, Sepietta oweniana; q, Sepioloidea lineolata;* and Sepiida: *r, Sepia officinalis* (Fioroni, 1982b).

shed one to a few eggs at intervals (ARNOLD, 1987) over a long period of time and so is iteroparous. The eggs of the vampyromorph *Vampyroteuthis infernalis* range widely in size in the ovary; and in the sea, single eggs are found (PICKFORD, 1949b). Laboratory studies of *Sepia officinalis* (Sepiida) have shown that it too spawns eggs at intervals, while continuing to grow between each spawning (VON BOLETZKY, 1983, 1987). Iteroparity has recently been found among some oegopsid squids, including the enoploteuthines (R. E. YOUNG & HARMAN, 1985), the ommastrephid, *Sthenoteuthis oualaniensis* (HARMAN & others, 1989), and the brachioteuthid, *Brachioteuthis* sp. (R. E. YOUNG, HARMAN, & MANGOLD, 1985a). Other species are known to be iteroparous, including *Opisthoteuthis* (BERRY, 1952; VILLANUEVA, 1992b) and *Cirrothauma murrayi* (Fig. 7) (ALDRED, NIXON, & YOUNG, 1983) and the octopods *Benthoctopus piscatorum* (NIXON, 1991) and *Octopus chierchiae* (RODANICHE, 1984). These coleoids all have ovarian eggs of differing sizes and spawn at intervals, probably for a considerable portion of their lives. The largest eggs yet recorded have a capsule 35 mm in length and belong to an octopod, *Graneledone* sp. (HOCHBERG, NIXON, & TOLL, 1992).

At least one species from each order of Recent Cephalopoda, including Nautilida, is iteroparous, suggesting that perhaps this mode of reproduction is primitive in this class of mollusks. Reproductive strategies among living coleoids are, from current evidence, at their most diverse in Octopoda, as species in this order range from being

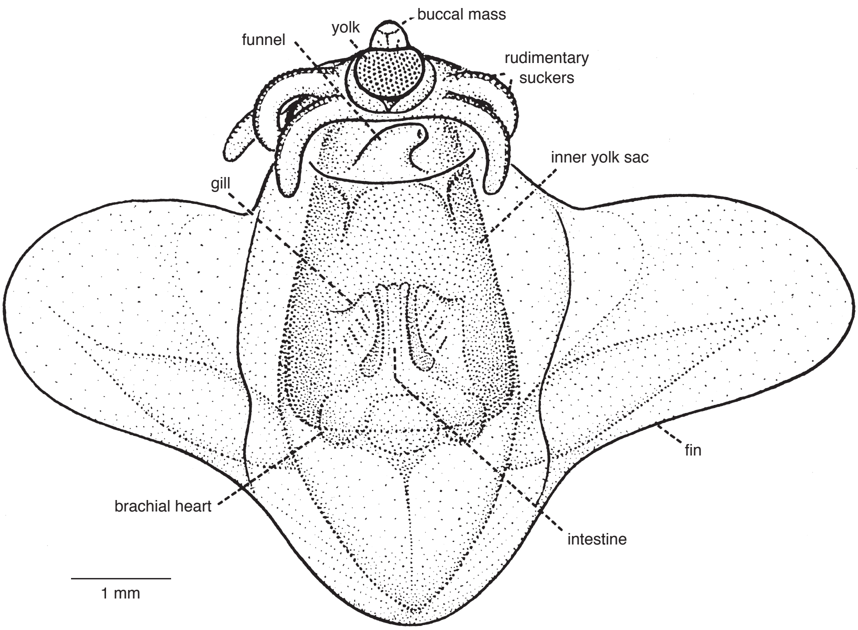

FIG. 9. Cirroctopoda; late embryo showing relatively huge fins, short arms, and prominent buccal mass at this stage (von Boletzky, 1982).

iteroparous to semelparous with various intermediate types. The female pelagic octopod *Ocythoe tuberculata* retains her eggs (STEENSTRUP, 1880; NAEF, 1923). When the embryo is fully developed, the young are expelled by the female; this is termed ovoviviparity.

HATCHLINGS

The young vary in size at hatching (Fig. 8) (FIORONI, 1982b) and range from 0.74 mm mantle length in *Todarodes* (an ommastrephid) (OKUTANI, 1983a) to 13.5 mm mantle length in a sepiid, *Sepia latimanus* (CORNER & MOORE, 1980). This may be exceeded by the hatchlings of cirrate octopods (Fig. 9) (VON BOLETZKY, 1982) and some octopods with relatively very large eggs.

Depending upon the species, the newly hatched young can settle on the bottom, be benthopelagic, or join the plankton. Benthic and benthopelagic hatchlings are often closely similar in shape and form to the adult. In contrast, planktonic hatchlings differ, often considerably, from the adult form they later achieve (Fig. 10–12) (OKUTANI, 1987; VON BOLETZKY, 1977, 1989; VECCHIONE, 1987). These young are now referred to as paralarvae (R. E. YOUNG & HARMAN, 1988). The difference in appearance between the paralarva and adult of a species is so marked in some oceanic coleoids that early stages have been described as one species, only to be found later to belong to another that has already been described from the juvenile or adult stage (SWEENEY & others, 1992; NIXON & MANGOLD, 1996). Unusual paralarval forms include the so-called rhynchoteuthion stage of ommastrephid squids, in which the two tentacles are joined longitudinally and bear a ring of suckers on the flattened distal tip (Fig. 10) (ROPER & LU, 1979; HARMAN & YOUNG, 1985). That of *Brachioteuthis* has an elongated neck (R. E. YOUNG, HARMAN,

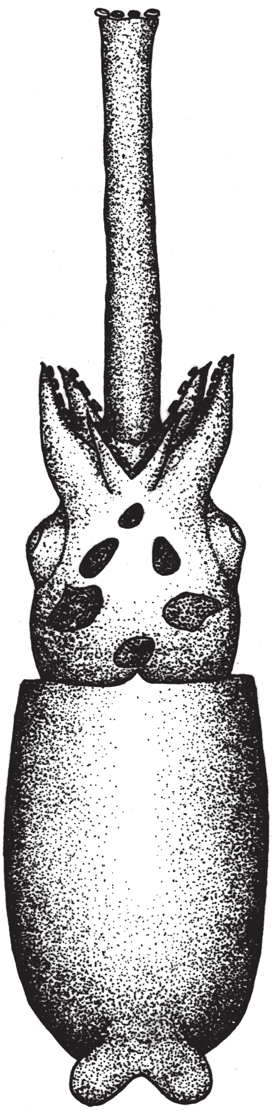

Fig. 10. Ommastrephidae; rhynchoteuthion paralarva of *Ornithoteuthis antillarum*, showing extremely long, joined tentacles with suckers on a flattened distal tip; 2 to 2.9 mm mantle length (Roper & Lu, 1979).

& Mangold, 1985a), and some cranchiid squids have eyes on long stalks (N. A. Voss, 1980).

The newly hatched young of some coastal species are expelled into the plankton, but later, after a period of growth, they settle to the sea floor, where they spend the rest of their lives. While in the plankton, such hatchlings often undergo changes in proportion of the arms and body, and in behavior. An example is found in the coastal octopod, *Octopus vulgaris*, which is initially planktonic; at this stage, its arms are short, and the funnel and the buccal mass are large relative to the length of the mantle (Rees, 1950; Nixon & Mangold, 1996). This contrasts with the adult, which has long arms, a moderate-sized funnel, and small buccal mass relative to the mantle length. Another example is *Eledone cirrhosa*, the young of which join the plankton initially and only later settle to the bottom habitat of the adult (Fig. 8f). At hatching, the young of *Eledone moschata* crawls away and settles on the bottom in the same habitat as the adult, which it resembles in appearance (Fig. 8k). It has long, well-developed arms with many suckers and is large in size relative to the adult; its appearance contrasts markedly with the planktonic hatchling of *E. cirrhosa* (von Boletzky, 1977; Fioroni, 1982b). Young sepiids, like many octopods, take up benthic habits immediately after hatching, but some enter the water column for part of each day. This behavior occurs in *Sepia officinalis* (Nixon & Mangold, 1998).

ONTOGENY

The ontogenetic development from hatching to maturity is known for a number of coastal and a few oceanic species (Clarke, 1966; Boyle, 1983a). This paucity of information for all stages of the life cycle of most coleoids is because of difficulties in capturing and identifying specimens that form an ontogenetic series of one species; often neither the very early stages nor the fully mature adults are known. External changes in shape and form during ontogeny may be few or numerous and occur in many or only a few features. The changes may be subtle, one stage merging imperceptibly into the next, or rapid and obvious, especially

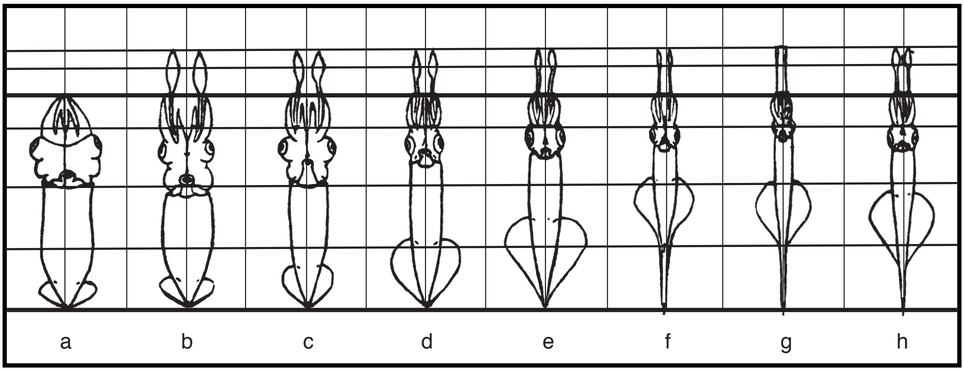

FIG. 11. *Alloteuthis subulata*; ontogenetic series, from late embryonic stage to maturity, showing differential development, especially of arm crown, fins, and tail, which differs in length in the two sexes; *a,* embryo, 5:1; *b,* nectopelagic paralarva, 3:1; *c,* nectobenthonic paralarva, 2:1; *d,* young nectobenthonic stage, 0.7:1; *e,* older nectobenthonic stage, 1:3; and adults *f,* 1:9; *g,* male with longer tail than female, 1:10; *h,* female 1:9 (Grimpe, 1925).

in species that move from the plankton to deeper water or to the bottom (Fig. 11–12). The planktonic young of benthic octopods are small, and their arms are short and bear few suckers compared with the adult (VON BOLETZKY, 1977). The hatchling of *Vampyroteuthis infernalis* (Vampyromorpha) initially has one pair of small fins, but later a second pair develop and become the adult fins; meanwhile the larval fins are resorbed (PICKFORD, 1949a). Embryonic cirrate octopods have very large fins relative to the mantle (Fig. 9) (VON BOLETZKY, 1982). There is considerable diversity in the changes that take place with growth among oegopsid squids (CLARKE, 1966). In some, virtually no change in form occurs, whereas in others, the body may become relatively wider or

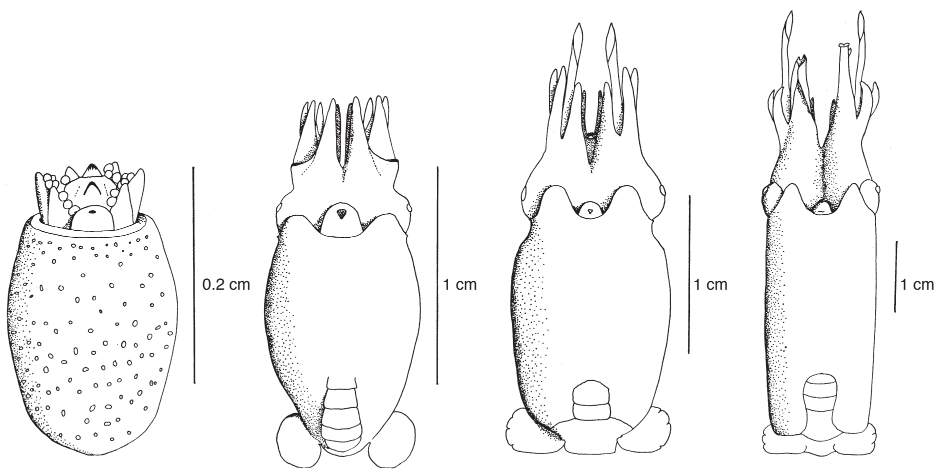

FIG. 12. *Spirula spirula;* changes in shape and form, with growth from posthatching to adult (Clarke, 1970).

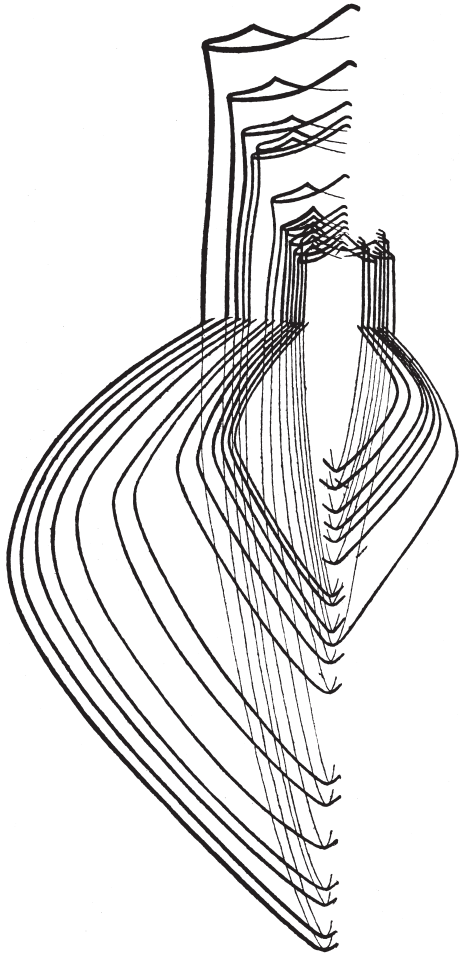

FIG. 13. *Loligo forbesi*; changes in mantle and fins with growth; reduced here to 1/4 natural size (Grimpe, 1925).

narrower, and the arms, tentacles, head, and fins may become relatively longer or shorter. Growth may take place at one rate in one part of the animal but at a different rate in other parts, resulting in changes in proportions. The fins of some teuthids are small initially and increase progressively in size (Fig. 13) (GRIMPE, 1925) or change shape during development (Fig. 11–12, Fig. 14). *Thysanoteuthis rhombus,* a large oceanic squid, has fins extending the length of the mantle in the adult, yet, at hatching, they are tiny lobes on either side of the wide, saclike mantle; similar anterior extensions of the fins also occur in *Chtenopteryx (Ctenopteryx) siculus* (SWEENEY & others, 1992).

LIFESPAN

The length of life of coleoids has been estimated in numerous species by using one or more methods, and a few species have been cultured through one or more generations. Commercial catches of some species have allowed analyses of modal length frequencies to estimate lifespan (BOYLE, 1983a; MANGOLD, 1989c). The deposition of organic or calcareous material in some of the hard tissues with growth, such as the statolith, can result in the development of periodic rings or lines, making it possible to estimate age. The beak and radula of *Octopus vulgaris* (NIXON, 1969) and of *Teuthowenia (Taonius) megalops* (DILLY & NIXON, 1976a) show changes with growth, as do the chitinous rings of the arms and tentacles in *Gonatus* (KUBODERA & OKUTANI, 1977, 1981), and the central hook of the tentacular club of *G. fabricii* (KRISTENSEN, 1977). The beak of *Moroteuthis ingens* shows periodic lines of growth, but their relationship to age is elusive (CLARKE, 1965). The microstructure of the statoliths (e.g., YANG & others, 1986; JACKSON & CHOAT, 1992) and the gladius (BIZIKOV, 1995; BIZIKOV & ARKHIPKIN, 1997) provide evidence of age and lifespan (Table 1). Longevity ranges from several months in small sepiolids such as *Euprymna scolopes* (SINGLEY, 1983) and *Idiosepius pygmaeus*

FIG. 14. *Teuthowenia (Taonius) megalops;* changes in shape and form with growth, from posthatching until near maturity; dorsal mantle lengths: *a,* 6.3 mm, *b,* 11.4 mm, *c,* 22 mm, *d,* 46 mm, *e,* 69 mm, *f,* 85 mm, *g,* 100 mm, *h,* 134 mm, *i,* 180 mm (Dilly & Nixon, 1976c).

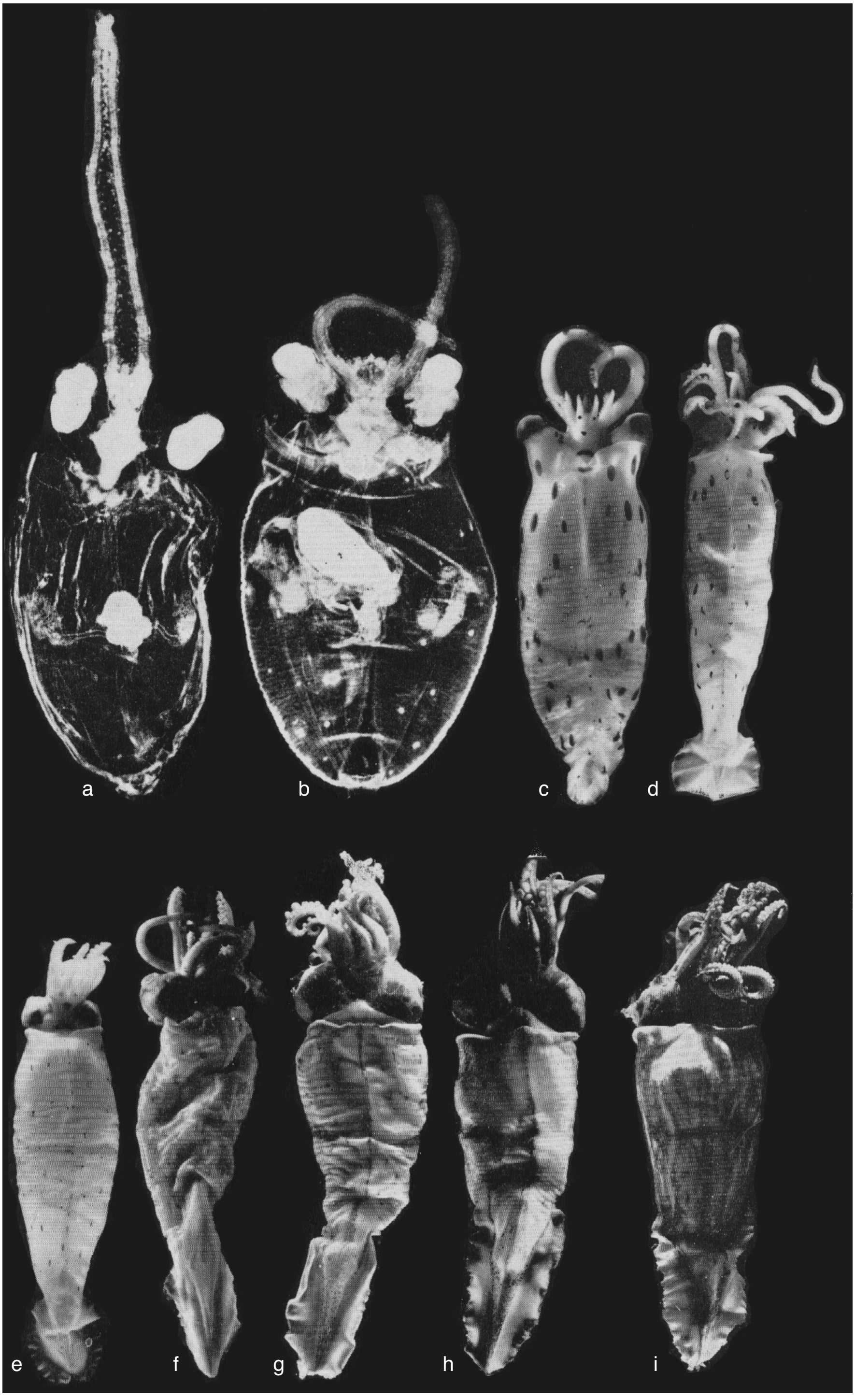

FIG. 14. *For explanation, see facing page.*

TABLE 1. Lifespan of a number of Recent Coleoidea estimated from incremental growth or laboratory culture studies (Boyle, 1983a) and of recent *Nautilus* (Landman & Cochran, 1987) for comparison; *F,* female; *M,* male.

Order and species	Lifespan
Nautilida	
Nautilus	20 years or more
Sepiida	
Sepia officinalis	18–24 months
Sepiolida	
Sepiola robusta	6–8 months
Sepietta oweniana	6–9 months
Myopsida	
Loligo pealei	>12 months
Loligo opalescens	14–36 months
Loligo vulgaris	F: 18–24 months M: 36–42 months
Oegopsida	
Illex illecebrosus	>12 months
Todarodes pacificus	>12 months
Dosidicus gigas	F: 12–36 months M: 9–12 months
Octopoda	
Octopus briareus	10–17 months
Octopus cyanea	12–15 months
Octopus dofleini	F: 36 months M: 48–60 months
Octopus joubini	6.5–11 months
Octopus maya	10 months
Octopus vulgaris	12–24 months
Eledone cirrhosa	18–24 months
Eledone moschata	10–18 months
Bathypolypus arcticus	24–36 months

(JACKSON, 1989), to three years in the teuthid *Gonatus fabricii* (KRISTENSEN, 1984), and to four years in the octopod *Bathypolypus arcticus* (O'DOR & MACALASTER, 1983). The last two are cold-water species and contrast with tropical forms, some of which apparently have a shorter lifespan (JACKSON & CHOAT, 1992). The lifespan of one octopod, *Eledone cirrhosa,* is of one year duration in the Mediterranean and almost two years in the cold waters of the North Sea (BOYLE, MANGOLD, & NGOILE, 1988). The lifespans of coleoids are relatively short when compared with *Nautilus,* which takes many years to mature, continues to live for several years while spawning at intervals, and has a lifespan of some 20 years (LANDMAN & COCHRAN, 1987).

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