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Origin and evolution of animal life cycles

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ABSTRACT

The 'origin of larvae' has been widely discussed over the years, almost invariably with the tacit understanding that larvae are secondary specializations of early stages in a holobenthic life cycle.

Considerations of the origin and early radiation of the metazoan phyla have led to the conclusion that the ancestral animal (= metazoan) was a holopelagic organism, and that pelago-benthic life cycles evolved when adult stages of holopelagic ancestors became benthic, thereby changing their life style, including their feeding biology.

The literature on the larval development and phylogeny of animal phyla is reviewed in an attempt to infer the ancestral life cycles of the major animal groups. The quite detailed understanding of larval evolution in some echinoderms indicates that ciliary filter-feeding was ancestral within the phylum, and that planktotrophy has been lost in many clades. Similarly, recent studies of the developmental biology of ascidians have demonstrated that a larval structure, such as the tail of the tadpole larva, can easily be lost, *viz.* through a change in only one gene. Conversely, the evolution of complex structures, such as the ciliary bands of trochophore larvae, must involve numerous genes and numerous adaptations.

The following steps of early metazoan evolution have been inferred from the review.

The holopelagic ancestor, blastaea, probably consisted mainly of choanocytes, which were the feeding organs of the organism. Sponges may have evolved when blastaea-like organisms settled and became reorganized with the choanocytes in collar chambers.

The eumetazoan ancestor was probably the gastraea, as suggested previously by Haeckel. It was holopelagic and digestion of captured particles took place in the archenteron. Cnidarians and ctenophores are living representatives of this type of organization. The cnidarians have become pelago-benthic with the addition of a sessile, adult polyp stage; the pelagic gastraea-like planula larva is retained in almost all major groups, but only anthozoans have feeding larvae.

Within the Bilateria, two major lines of evolution can be recognized: Protostomia and Deuterostomia. In protostomes, trochophores or similar types are found in most spiralian phyla; trochophore-like ciliary bands are found in some rotifers, whereas all other aschelminths lack ciliated larvae. It seems probable that the trochophore was the larval type of the ancestral, pelago-benthic spiralian and possible that it was ancestral in all protostomes. Most of the non-chordate deuterostome phyla have ciliary filter-feeding larvae of the dipleurula type, and this strongly indicates that the ancestral deuterostome had this type of larva.

Key words: Metazoa, phylogeny, larvae, planktotrophic, lecithotrophic.

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I. INTRODUCTION

All animals (= metazoans) have a life cycle with a series of characteristic ontogenetic stages leading to the adult. Some of these life cycles appear simple, with the adult morphology developing directly, whereas others are more complicated, with sometimes very elaborate larval stages and a complicated metamorphosis preceding the adult stage. A central question is of course whether the various types of larvae, especially the characteristic larval types of the marine invertebrates, are phylogenetically old and therefore of importance for the understanding of interrelationships of phyla or whether the planktotrophic, filter-feeding larvae have evolved convergently in the many smaller clades. Of course, it can never be ruled out that similar structures in distant clades are the result of convergent evolution. However, it is my general attitude that if detailed studies of such structures do not reveal specific differences, convergence should not be invoked.

The 'origin of larvae' has been discussed by many authors, often coupled with the question 'why have larvae evolved?' (Wray, 1995*a*), implying that the ancestral life cycle was holobenthic. Wolpert (1994) regarded direct development as ancestral because he found it improbable – if not impossible – that an ancestral larva could evolve the ability to metamorphose into an adult (see below). However, most authors do not regard the larvae as ancestors from which the adults have evolved, but discuss whether a larval stage has evolved secondarily in direct developers. Several advantages of a pelagic larval stage have been pointed out, especially increased potential for dispersal, but it seems always to have been taken for granted that the pelagic larval stage was added to the life cycle secondarily.

Early authors used characters of all stages in the life cycles in their considerations of animal systematics, and Hatschek (1891) was probably the first to emphasize the importance of the trochophore for the understanding of protostomian (zygoneuran) evolution. Many systematic studies emphasized either larval or adult stages, but several authors, one of the earliest being Jägersten (1972), have emphasized the importance of considering whole life cycles in phylogenetic considerations. Many recent authors point out that planktotrophic larval types are ancient and that lecithotrophic (non-feeding) larvae have evolved many times (Strathmann, 1978*a*, 1985, 1993; Wray, 1995*a*; Davidson, Peterson & Cameron, 1995). After a general discussion of evolution of larval development, Wray (1995*a*, p. 434) concluded that: 'A more plausible interpretation [of the persistence of planktotrophic larvae over such immense spans of time] is that feeding larvae, as well as their particular morphologies, developmental histories, and methods of feeding, have persisted because they work well under a wide variety of circumstances.' Ontogeny and morphology of planktotrophic larvae are therefore central in many modern studies on animal phylogeny (Nielsen, 1985, 1987, 1995; Brusca & Brusca, 1990; Meglitsch & Schram, 1991; Schram, 1991).

On the other hand, authors such as Salvini-Plawen (1980), Ivanova-Kazas (1987), Ivanova-Kazas & Ivanov (1988), Willmer (1990) and Haszprunar, Salvini-Plawen & Rieger (1995) regard, for example, the planktotrophic trochophores of annelids, molluscs and entoprocts as having evolved convergently from gutless, lecithotrophic larvae. These authors consequently disregard larval characters in their phylogenetic considerations of higher levels.

The variation in developmental types has been studied from an ecological point of view, for example by Thorson (1950), and through mathematical modelling, for example by Roughgarden (1989), but although these approaches demonstrate a number of biological correlations they do not throw light on the question of larval origins.

Much new information about larval types and about the genetic regulation of development has appeared during the last few years, and it is hoped that a review of the available information can throw light on the evolution of the life cycles, and lead to more general phylogenetic conclusions.

II. SURVEY OF ANIMAL DEVELOPMENTAL TYPES

The Animal Kingdom (= Metazoa) is now generally regarded as a monophyletic group which is quite well defined (Brusca & Brusca, 1990; Storch & Welsch, 1991; Morris, 1993; Ruppert & Barnes, 1994; Nielsen, 1995; Müller, 1995). A number of very early fossils have only very few informative characters and are therefore difficult to classify; their metazoan nature is generally not questioned, but their relationships with the living phyla are in many cases very uncertain (Wills & Sepkoski, 1993). The Ediacaran faunas and their possible survivors in the Early Cambrian (Conway Morris, 1993; Runnegar, 1995) appear to be below the bilaterian level of organization, and some of them may even be algae; their development is unknown and they are not relevant for the discussion of larval types. The following survey deals only with the living phyla.

(1) Phylum Porifera

Fossil remains of sponges are known from the Upper Ediacaran (Gehling & Rigby, 1996; Brasier, Green & Shields, 1997), but both the gross classification and the delimitation of the phylum are still somewhat uncertain (Rigby *et al.*, 1993). The three living classes are sometimes classified with the Hexactinellida (Symplasma) as the sister group of Demospongiae + Calcarea (Cellularia), but it cannot be excluded that the hexactinellids are highly specialized demosponges. All living sponges have sexual reproduction with ciliated larvae lacking a gut (Fell, 1989).

Calcarean larvae are generally small with an outer layer of tall, monociliate cells at the anterior part of the larva and larger unciliated cells at the posterior pole; the inner cavity may contain nurse cells of extraembryonal origin (Franzen, 1988; Gallissian & Vacelet, 1992). At settling, the ciliated anterior epithelium invaginates and the cells presumably become the choanocytes of the collar chambers (= flagellated chambers) (Lemche & Tendal, 1977), but modern investigations are lacking.

Demosponge larvae are ovoid with an outer layer of monociliate cells, except at the posterior pole which lacks cilia; some species have a ring of compound cilia encircling the unciliated pole (Woollacott, 1993). A few species have compact larvae with inner archaeocytes and sclerocytes secreting siliceous spicules; in other species a cavity is formed inside the larva and collar chambers differentiate during late phases of the development (Saller & Weissenfels, 1985). The larvae settle with the ciliated anterior pole and undergo a metamorphosis with profound rearrangement of the cells. The ciliated cells lose the cilia, become amoeboid and can be recognized in the collar chambers of the small sponge (Amano & Hori, 1996); however, choanocytes may also differentiate from archaeocytes (Bergquist & Glasgow, 1986).

Hexactinellid larvae are very poorly known, but the larva of *Oopsacus minuta* (Boury-Esnault & Vacelet, 1994) is ovoid with a rounded anterior pole without cilia, a median region with multiciliate cells, and a pointed posterior pole without cilia; the ciliated cells are covered by a thin layer of cells which is penetrated by the cilia. The ciliated cells surround a mass of cells with various inclusions, cells which secrete spicules, and developing collar chambers. The metamorphosis is undescribed.

It appears that all sponges have pelago-benthic life cycles, and that this was probably the case in the ancestral sponge. The larvae never show any sign of particle feeding or of choanocytes, and they must be described as blastulae, either coeloblastulae or sterroblastulae. Some calcarean larvae invaginate the ciliated anterior pole at settling, but an archenteron is not formed and the process cannot be homologized with a gastrulation. The larvae have a polarity, but it is lost at metamorphosis.

(2) Phylum Placozoa

Sexual reproduction and development of *Trichoplax adhaerens* are almost undescribed, so the developmental type cannot be ascertained.

(3) Phylum Cnidaria

Most of the earliest fossils sometimes interpreted as cnidarians are of rather uncertain nature, and they give very little information about the radiation of the phylum.

Four living classes are generally recognized, and the anthozoans are often regarded as the sister group of the remaining classes (Werner, 1984; Schuchert, 1993; Nielsen, 1995). Almost all cnidarians have pelago-benthic life cycles with planula larvae; only a few clades of scyphozoans and hydrozoans are holopelagic. The planula larvae are ovoid, usually ciliated larvae with an ectoderm and endoderm. They develop through a wide variety of gastrulation types and the free-swimming larvae are either compact or have an archenteron, sometimes with a blastopore (Nielsen, 1995). Planktotrophic larvae are apparently only found in anthozoans, but the development and general biology of cnidarian larvae are poorly known.

Planktotrophic larvae are found in many hexacorals. Widersten (1968) reported planktotrophic larvae of a number of actiniarians, but the method of feeding was not studied. Siebert (1974) observed that larvae of sea anemone *Anthopleura* spp. secreted mucus strings and that food particles caught by the strings were ingested together with the strings. Nyholm (1949) observed that newly settled planula larvae of *Halcampa duodecimcirrata* ingest detritus particles caught from the weak currents created by the cilia of the stomadaeal area and that this type of ciliary feeding is essential to survival and growth. Fadlallah (1983) reviewed larval types in scleractinian corals and found very few detailed observations of the structure of the larvae; presence of an oral pore has been reported in larvae of a number of genera, but only larvae of *Caryophyllia smithi*, *Fungia scutaria* and *Porites porites* have actually been observed to feed. Larvae of *Caryophyllia smithi* have been observed to capture food particles (homogenized prawns!) with mucus strings which were ingested, but ciliary currents were also seen to pass particles along the body to the mouth (Tranter, Nicholson & Kinchington, 1982).

Ciliary bands engaged in filter-feeding have not been reported from cnidarians.

The pelago-benthic life cycle is almost universal among cnidarians. The occurrence of larval types in the various groups gives no indication of the ancestral larval type, but the planktotrophic anthozoan larvae feeding from the currents set up by the general ciliation of the ectoderm may represent the ancestral type. On the other hand, it also seems possible that the earliest cnidarians were raptorial, using the nematocysts to capture small organisms.

(4) Phylum Sipuncula

The Sipuncula are a small phylum without a reliable fossil record. A considerable diversity in developmental types has been observed, ranging from complicated life cycles with teleplanic (long distance) larvae to direct development, with the whole range observed within genera such as *Golfingia* (Rice, 1985). *Sipunculus nudus* has a pericalymma larva with a serosa extending from the prototrochal area. The serosa is shed at an early stage exposing the hyposphere with mouth, buccal organ, and a ring of compound cilia which is used in swimming (Hatschek, 1883; Rice, 1988). The ring of compound cilia is usually called a metatroch, but its effective stroke is directed posteriorly as opposed to the anteriorly beating metatrochs of annelid and mollusc larvae. This larva is called a pelagosphaera and it is found also in genera, such as *Golfingia*, which lack the pericalymma stage. Pelagosphaera larvae are planktotrophic, but their feeding mechanism is poorly known.

The spiral cleavage and early larval development of the pericalymma larva of *Sipunculus nudus* indicate that the sipunculan larvae are modified trochophores, but the typical ciliary filter-feeding mechanism of the trochophore is not found in any sipunculan species.

(5) Phylum Mollusca

The Mollusca have a very extensive fossil record, but unfortunately, solenogasters and caudofoveates, which are by most authors considered to be the 'primitive' sister groups of the shelled classes, have not been recorded as fossils. The shelled, living classes have representatives from the Cambrian or Ordovician. Phylogenies based on fossil evidence (see, for example, Runnegar, 1996) and on morphology (see, for example, Scheltema, 1996; Salvini-Plawen & Steiner, 1996) show some variations in relationships between the classes, but this seems of little importance for the present discussion because only Bivalvia and Gastropoda have representatives with planktotrophic larvae (see below). The Cambrian halkieriids (Conway Morris & Peel, 1995) probably represent a separate molluscan class; no character indicates a closer relationship with annelids or brachiopods (Nielsen, 1997).

Solenogasters have lecithotrophic larvae. *Epimenia verrucosa* has a modified trochophore with a preoral and a preanal ring of probably compound cilia and a rather gradual metamorphosis (Baba, 1940). *Neomenia carinata* has a pericalymma larva with the mouth in an anterior position, covered by a thin, preoral serosa; at metamorphosis, the serosa unfolds and becomes enclosed in the episphere (Thompson, 1960).

Caudofoveates are believed to be free spawners, but only *Chaetoderma nitidulum* has been studied; it has a lecithotrophic larva with an anterior and a posterior ring of probably compound cilia like many of the lecithotrophic polychaete larvae (Nielsen, 1995).

Some polyplacophorans are free spawning with lecithotrophic larvae whereas others brood the embryos and the larvae hatch at an advanced stage ready for metamorphosis. Both developmental types are found in the genus *Lepidochitona*, and the stages ready for metamorphosis are quite similar, with a well-developed prototroch of compound cilia (Eernisse, 1988).

Monoplacophoran development has not been studied, but the larval shells found on the apex of adult shells indicate that the development is lecithotrophic (Haszprunar & Schaefer, 1997).

Gastropod phylogeny has been the subject of a number of recent studies, and it seems clear that old concepts such as Prosobranchia and Archaeogastropoda do not denote monophyletic groups (Haszprunar, 1988, 1993; Ponder & Lindberg, 1996). Most authors seem to agree that the Patellogastropoda (= Docoglosa) are the sister group of all other gastropods, and that Opisthobranchia and Pulmonata are sister groups, but the phylogeny of the remaining groups seems unsettled.

Many patellogastropods and other 'archaeogastropods' are free spawners and the embryos develop into non-feeding trochophores with a prototroch of compound cilia (for example, *Tectura* (= *Notacmaea*) *scutum*, see Nielsen, 1987). Later stages are shelled veligers, but it appears that all these larvae are lecithotrophic; earlier reports of planktotrophy in 'archaeogastropods' appear to be erroneous (Haszprunar *et al.*, 1995). Planktotrophic veliger larvae with downstream-collecting ciliary bands are found in many clades of the old groups 'Mesogastropoda' (for example, in *Crepidula fornicata*, see Werner, 1955) and 'Neogastropoda' (for example, *Nassarius obsoletus*, see Strathmann & Leise, 1979) and in the opisthobranchs, but other species in the same clades have planktonic, lecithotrophic larvae or direct development.

At this point, it is important to note that terms such as lecithotrophic and direct development emphasize the ecological aspects of the developmental type rather than the morphological aspect (Levin & Bridges, 1995). Most gastropods pass through developmental stages with well-developed larval structures, such as a velum, but these structures are not active in filter feeding in lecithotrophic species and in species which develop into small juveniles inside an egg cocoon. McEdward & Janies (1993) discussed the terminology and proposed to restrict the term 'direct development' to species without a developmental stage with transient structures, i.e. structures not involved in the morphogenesis of the juvenile/adult.

The transition between planktotrophic and lecithotrophic development is very gradual in some species, such as *Conus pennaceus*, which has a 'facultatively lecithotrophic' larva. Such larvae have a short pelagic phase and are able to settle and carry through metamorphosis without feeding, but they do feed if the right type of plankton is available (Perron, 1981).

There are many Mediterranean examples of species pairs with one species having planktotrophic and the other non-planktotrophic development, and it has been proposed that Quaternary climatic fluctuations could have been the factors which created local areas in which planktotrophy became unfavourable and was lost (Oliverio, 1996).

The detailed phylogenetic analyses of littorinid gastropods by Reid (1989, 1990) strongly indicate that planktotrophy is the ancestral state, and that non-planktotrophy has evolved independently in the genera *Tectarius*, *Littoraria* and *Littorina* within the subfamily Littorininae. In the Lacuninae, which are almost exclusively non-planktotrophic, a reversal to planktotrophy is indicated by the sculpture of the larval shell in species of *Epheria*. As could be expected, this is not a *de novo* evolution of a velum with the characteristic ciliary bands; direct developing species of the sister genus *Lacuna*, such as *L. parva* (Ockelmann & Nielsen, 1981), have intracapsular embryos with almost fully developed velar structures with a beating prototroch, and it appears that the ciliary bands have simply regained their function in *Epheria* spp.

Considering the fact that planktotrophy has been lost numerous times within the gastropods (and regained a few times) and that lecithotrophic trochophore or veliger larvae are found in almost all clades, it definitely seems possible that planktotrophy was the ancestral developmental type. Page (1994) proposed that the newly hatched opisthobranch veliger is the gastropod larva which is closest to that of the gastropod ancestor.

Cephalopods all have yolk-rich eggs with discoidal cleavage; this is generally regarded as a specialization within the molluscs (e.g. Berthold & Engeser, 1987).

Bivalves are a large group with an extensive fossil record going back to the Early Cambrian; early phylogenies were based solely on shell characters, but modern studies lean heavily on the morphology of the soft parts, such as gills and muscles (Waller, 1990; Morton, 1996). It appears that two clades with extant species can be recognized: Protobranchia (with the living groups Nuculoidea, Nuculanoidea and Solemyoidea) and Autobranchia (with the living groups Pteriomorphia and Eulamellibranchia). Protobranchs have, in the main, retained the primitive ctenidium found also in other mollusc classes; they have specialized palps and palp proboscides as feeding structures and developed a characteristic pericalymma larva. Autobranchs have filibranch or eulamellibranch gills as feeding structures, have a trochophore (veliger) larva in most clades, and have developed a larval byssus; the two groups also differ in the structure of the stomach.

The protobranch pericalymma larvae have a thin ciliated praeoral extension, the serosa, covering the posterior part of the body (Drew, 1899; Gustavson & Reid, 1986). In *Yoldia limatula* and *Nucula delphinodonta*, the larval mouth is situated at the posterior edge of the serosa, so in these species it is actually the whole velar edge that is extended posteriorly (Drew, 1899). The shelled juvenile develops inside the serosa, which is shed at metamorphosis. The metamorphosing larva of *Yoldia limatula* goes through a stage strongly resembling a metamorphosing veliger larva (see Fig. 19 in Drew, 1899). In general, the autobranchs have planktotrophic veliger larvae, with exceptional leithotrophic developmental types in specialized habitats, as, for example, fresh-water species and many deep sea species, or in a few families with brooding habits (Morton, 1996). Early, non-feeding, developmental stages resemble annelid trochophores (Galtsoff, 1964), and some of the full-grown veligers have a quite small velum. Most species have veligers with a circular velum with downstream-collecting ciliary bands at the edge, but the very large velum of *Atrina* sp. is sinuous forming an anterior and a posterior plate (C. Nielsen, personal observations, Phuket, Thailand). It seems possible that the bivalve ancestor had a planktotrophic veliger larva, and that this became specialized to a pericalymma in the protobranchs.

Scaphopod larval development is poorly described, only the larva of *Dentalium entale* being illustrated (Lacaze-Duthiers, 1858, 1859); it is a lecithotrophic veliger with a narrow, circular velum.

In general, molluscs have a complicated, pelago-benthic life cycle and their development goes through a stage resembling a lecithotrophic annelid trochophore, i.e. an ovoid stage with a prototroch, possibly always with compound cilia, and some larvae have a telotroch too; later stages may be veligers, which may be planktotrophic, lecithotrophic or intracapsular with feeding on yolk, or the development may lead directly to the juvenile; only cephalopods have a truly direct development. It seems probable that the ancestral mollusc had a pelago-benthic life cycle and that its larva was a trochophore. The earliest known fossil mollusc shells are only approximately 1 mm long and show no trace of a larval shell (Runnegar, 1996). This could indicate that the earliest conchiferans had trochophores without a shell, and that the shell(s) evolved as protective structures in the benthic adult; the shelled larvae would then represent a later step in their evolution. Chaffee & Lindberg (1986) argued that the ancestral mollusc was too small to have a planktotrophic larva; this is discussed in the general discussion below.

(6) Phylum Annelida

Annelid phylogeny is completely unresolved, and it is possible that the polychaetes are in fact a paraphyletic stem group with the Clitellata as a highly specialized ingroup (Nielsen, 1995; Westheide & Purschke, 1996). The early fossil record is rather meagre; a few well-preserved species are known from the Burgess Shale (Briggs, Erwin & Collier, 1994).

In the following, the classification of Pettibone (1982) will be used, with the addition of pogonophorans and echiurans. Many of the marine 'polychaetes' have planktonic larvae, and a number of species have been studied in great detail during the last hundred years; the discussion will concentrate on orders with species having planktotrophic larvae. All the clitellates have direct development.

The very large polycheate order Phyllodocida, which includes families such as Phyllodocidae, Glyceridae, Nereididae, Nephtyidae, Aphoroditidae, Polynoidae and Sigalionidae, is predominantly pelago-benthic with lecithotrophic trochophores having a prototroch of compound cilia. However, a number of polynoid and sigalioniodlarvae are planktotrophic trochophores; they lack a metatroch and adoral ciliary zone but have, to the left of the mouth, a group of very long prototroch cilia forming a brush (or perhaps a compound cilium) which captures large particles, so these larvae are not filter feeders (Phillips & Pernet, 1996). The ciliary brush is a modified part of the prototroch used for capturing large particles, and this feeding mechanism, which handles individual particles, cannot be interpreted as a transitional stage from a non-feeding larva with only a prototroch to a filter-feeding larva with a downstream-collecting (double band) ciliary system, as suggested by Strathmann (1993). A number of species belonging to other families have planktotrophic larvae with a prototroch but without a metatroch and adoral ciliary zone; the larvae of *Nephtys ciliata* have well-developed prototroch and telotroch and are carnivores, feeding, for example, on bivalve larvae (Thorson, 1946; Mileikovsky, 1959). The feeding method is unknown in most of the other families, but filter feeding appears unlikely (Blake, 1975).

The small order Amphinomida comprises some species with a characteristic planktotrophic larva called a rostraria, which has a prototroch and metatroch extended on a pair of long, dorsal tentacles, almost resembling a pair of narrow velar lobes (Jägersten, 1972). The orders Eunicida and Orbiniida have non-planktotrophic development.

Spionida, especially the family Spionidae, comprises many species with planktotrophic trochophores having a prototroch and a telotroch of compound cilia (Nielsen, 1987); however, a metatroch is not found, and the method of feeding is not known (Hannerz, 1956). Many spionid larvae have a pair of ciliated lateral 'lips' which could perhaps be used in handling larger particles; the ciliation of the lips probably represents the adoral ciliary zone of a trochophore. Some species, such as *Pygospio elegans*, produce egg masses with nurse eggs in each cocoon, and the intracapsular larvae may ingest so much of this material that they can leave the capsule as small juveniles whereas others have a free, planktotrophic stage (Rasmussen, 1973).

Some species of the order Chaetopterida have planktotrophic larvae which feed by means of ciliary currents on the two large lips and by mucous filaments secreted by epithelial glands on certain zones of the body (Werner, 1953); this is clearly an apomorphy of the order.

The order Magelonida, with the only genus *Magelona*, have planktotrophic larvae with two feeding modes (Wilson, 1982). Early trochophores have a circular prototroch, and it soon becomes drawn out on a pair of lateral tentacles, which thus carry a double-band ciliary system (Strathmann, Jahn & Fonseca, 1972). Later, the tentacles elongate strongly with sensory papillae developing especially at their distal parts and the very flexible tentacles are used for capturing small plankton organisms, especially bivalve larvae.

The order Opheliida comprises both planktotrophic and lecithotrophic species. The well-studied larvae of *Ophelia bicornis* have a large prototroch but no metatroch and are probably non-feeding (Wilson, 1948), whereas the larva of *Armandia brevis* is a filter-feeder with a prototroch and metatroch, although larger diatoms may be ingested too (Hermans, 1978).

Within the order Capitellida, arenicolids and maldanids have direct development or lecithotrophic larvae with a short free phase but some capitellids, such as *Mediomastus fragile*, have planktotrophic trochophores which feed by means of a prototroch and metatroch (Rasmussen, 1956; Hansen, 1993).

The small order Oweniida comprises only one family with four genera, of which *Owenia* and *Myriochele* have the highly characteristic mitraria larvae. These very unusual 'blown up' trochophores have a prototroch and metatroch of single cilia (one cilium per cell in *Owenia fusiformis* and many cilia per cell in *Myriochele* sp.), but the ciliary filtering mechanism is similar to that of typical trochophores (Wilson, 1932; Smith, Ruppert & Gardiner, 1987; Emlet & Strathmann, 1994).

The order Terebellida comprises tubicolous forms and their larval development varies from planktotrophic to direct; several of the species with pelagic larvae build a small transparent tube while in the plankton. Young larvae of *Pectinaria* spp. still without a tube, have prominent proto- and telotrochs but lack a metatroch; the prototroch has a pair of large, anterior lobes (Thorson, 1946; Rasmussen, 1973); their feeding method has not been described, but the ciliated lobes appear well suited for handling larger food particles. Sabellariids have filter-feeding trochophores, which from published illustrations appear to have a prototroch, metatroch and adoral ciliary zone, although the metatroch is not mentioned specifically (Wilson, 1929; Eckelbarger & Chia, 1976; Smith & Chia, 1985; see also Strathmann, 1987).

The Sabellida consists of two main families of filter feeders with a funnel-shaped crown of bipinnate, ciliated tentacles. All sabellids apparently have non-planktotrophic larvae, with developmental types ranging from lecithotrophic to direct (Rouse & Fitzhugh, 1994), whereas a number of serpulids have planktotrophic trochophores. The phylogeny of the serpulids is unresolved; only two subfamilies, Serpulinae and Spirorbinae can be recognized (ten Hove, 1984). The spirorbines brood lecithotrophic larvae, which have a proto- and telotroch (Bailey, 1969). Serpuline phylogeny has not been resolved; ten Hove (1984) regarded the genera with an operculum as a clade, and within that the genera with apinnulate operculum stalks as a clade, but the definition of an operculum in the genera *Filograna*/*Salmacina* appears open to interpretation (Rouse & Fitzhugh, 1994). Genera without opercula or with opercula with pinnulate stalks, such as *Protula*, *Filograna* and *Salmacina* have lecithotrophic larvae (brooded or not brooded), but the larva of *S. dysteri* apparently has a prototroch, adoral ciliary zone surrounding the mouth, and metatroch (see Fig. 3c in Nishi & Yamasu, 1992). Both planktotrophic and lecithotrophic larvae are found in genera with naked opercular stalks (called Serpulinae by ten Hove, 1984). The larvae of *Serpula vermicularis* have a prototroch and metatroch of compound cilia and an adoral ciliary zone of single cilia (Nielsen, 1987); the feeding of the similar larva of *Spirobranchus spinosus* has been studied in detail by Strathmann *et al.* (1972; see also Lacalli, 1984). *Pomatoceros triqueter* (Segrove, 1941) and *Galeolaria caespitosa* (Grant, 1981) have planktotrophic larvae with similar ciliary bands, whereas *Chitinopoma* (= *Microserpula*) *inflata* broods lecithotrophic larvae (Thorson, 1946). It seems probable that the planktotrophic trochophore was ancestral of the family, and perhaps of the order.

Most of the 'archiannelid' families have now been referred to various orders with macrofaunal species, but the Polygordiida with the single genus *Polygordius* has an uncertain phylogenetic position. Larvae of a couple of species have been studied in detail and they are all filter-feeding trochophores with the characteristic complex of prototroch, metatroch and adoral ciliary zone (Hatschek, 1878; Woltereck, 1902).

The development of the Pogonophora (Frenulata + Vestimentifera) is not well known. Larvae of the frenulate *Siboglinum fiordicum* are lecithotrophic and have two ciliary rings, which probably represent a prototroch and metatroch (Bakke, 1974). The newly settled juvenile of the vestimentiferan *Ridgeia* spp. has retained an anterior ciliary band which possibly represents the prototroch (Southward, 1988).

Myzostomids have larvae which are apparently planktotrophic, but the feeding mechanism is unknown (Jägersten, 1939).

Echiurans such as *Echiurus abyssalis* (Hatschek, 1880; Baltzer, 1917) and *Urechis caupo* (Newby, 1940; see also Strathmann, 1987, p. 492) have planktotrophic, almost schematic trochophores with a prototroch, metatroch and adoral ciliary zone. *Bonellia viridis* has lecithotrophic larvae with a prototroch and telotroch (Spengel, 1879; Baltzer, 1926).

Almost all the marine annelids have pelago-benthic life cycles, and this must be an ancestral character of the whole phylum.

Filter-feeding trochophores are known from nine of the 28 orders, and almost all of these orders also include species with larvae which are not filter feeders. Some of these non-filter-feeding larvae are lecithotrophic while others are planktotrophic but specialized for capturing larger food particles. There is no indication of a transition from the large-particle-feeding trochophores without a metatroch to a filter-feeding larval type. The filter-feeding trochophores of the various families show very detailed similarities, and knowing that the transition from planktotrophy to lecithotrophy is an easy step while the opposite step is apparently very difficult (see below), it appears more likely that the filter-feeding trochophore was the ancestral larval type of the annelids than that it evolved independently one or more times within each of the nine orders.

(7) Panarthropoda

This clade, which comprises the living phyla Onychophora, Arthropoda and Tardigrada, is very well defined; the three phyla share a number of characters, such as segmentation with new segments added from a posterior growth zone, presence of a cuticle of α-chitin which is moulted and absence of locomotory cilia in all stages. The three phyla are usually regarded as the sister group of the Annelida, based on the type of segmentation and the excretory organs (Schram, 1991; Nielsen, 1995, 1997), but some morphologists and molecular biologists argue for a closer relationships with some of the aschelminths which have similar cuticles (Eernisse, Albert & Anderson, 1992). Primary, ciliated larval stages are lacking, which may be correlated with the change from a microvillous cuticle with collagen to a chitinous cuticle. Secondary larvae, such as the nauplius, are found in many of the marine arthropods. Panarthropods are among the most numerous fossils in the Cambrian faunas (Briggs *et al.*, 1994), and nauplius larvae have been recorded from Cambrian forms, such as *Bredocaris admirabilis* and *Rehbachiella kinnekullensis* (Müller & Walossek, 1988; Walossek, 1993). This indicates that ciliation was lost at an early stage in arthropod evolution, probably in association with the evolution of their special cuticle.

(8) Phylum Entoprocta

All entoproct larvae described so far (Nielsen, 1971, 1987, 1996) are more or less typical trochophores. A prototroch and metatroch of compound cilia and adoral ciliary zone of single cilia are found in larvae of all the species except *Loxosomella vivipara*, which has lecithotrophic development and lacks a metatroch and gut. Almost all species have brood protection and the advanced larvae begin filter-feeding while still attached to the embryophore of the mother zooid. Such stages of *Barentsia gracilis* have been observed to 'steal' particles from the food grove of the mother (Mariscal, 1965). The larvae of some species of the genus *Loxosomella* and of all the colonial types have the area of the gastrotroch organized as a ciliated foot and have a short planktonic stage, perhaps lasting only few hours. Larvae of genus *Loxosoma* and of some species of *Loxosomella* appear to have a long planktotrophic stage and a number of such larvae are known from the plankton (Jägersten, 1964); some of these larvae, for example *Loxosoma nung*, have a ciliated foot when released from the mother, whereas others, such as *Loxosoma pectinaricola* and *Loxosomella elegans*, lack the foot. None of the larvae with a long planktotrophic phase has been followed to metamorphosis and it is unknown whether the larvae without a foot will develop one at a later stage.

The presence of planktotrophic trochophores in all major lines clearly indicates that the ancestral entoproct had a pelago-benthic life cycle with a filter-feeding trochophore.

(9) Phylum Ectoprocta

All ectoproct bryozoans have pelago-benthic life cycles and are colonial with all polypides formed through budding. A few species have planktotrophic larvae, which lose their gut at metamorphosis. This is a very specialized life cycle and, just as in many other animals, characters of the adults in some groups are expressed already in a free-swimming larval stage, for example, in many phylactolaemate larvae which in reality are young colonies with one or more polypides.

The phylogeny of the phylum is still under debate. The traditional view holds that ectoprocts together with phoronids and brachiopods form the group Lophophorata (Brusca & Brusca, 1990; Ruppert & Barnes, 1994), which should have the archimeric body plan characteristic of the deuterostomes. The phylactolaemates are thought to represent the most primitive type with the epistome being homologous with the prosome of phoronids (Farmer, 1977), but this is not supported by embryological or histological evidence (Nielsen, 1995). Furthermore, the phylactolaemates are a fresh-water group without a long fossil record. The Jurassic fossils interpreted as phylactolaemate statoblasts appear quite dubious, and the oldest certain fossils are statoblasts from the Late Tertiary; there is only a very uncertain report (from the Upper Cretaceous) of a fossil, adult phylactolaemate (Taylor, 1993). Nothing indicates that they should be as ancient as the gymnolaemates and stenolaemates. An alternative view regards the ectoprocts as protostomes, possibly the sister group of the entoprocts (Nielsen, 1971, 1995; Nielsen, Scharff & Eibye-Jacobsen, 1996).

The earliest fossil ectoprocts are from the Lower Ordovician and there is a rich fossil record of the calcified cheilostomes and stenolaemates. The last-mentioned class flourished in Ordovician–Permian, but only members of the order Cyclostomata survived the Triassic (Taylor, 1993). All living cyclostomates have large brood chambers and polyembryony, and the larvae are lecithotrophic with no trace of a gut (Nielsen, 1970). Some of the Palaeozoic types had small chambers indicating absence of polyembryony (Schäfer, 1991), but there is no information about the larval type of the early stenolaemates. The fossil record of ctenostome gymnolaemates is meagre because of the lack of calcification of the body wall, but boring forms are known from the Upper Ordovician and encrusting forms preserved through bioimmuration from the Middle Jurassic (Taylor, 1993). The larval type of the fossil ctenostomes is unknown, but planktotrophic cyphonautes larvae are known in species of the living genera *Alcyonidium* (suborder Carnosa; see, for example, Cadman & Ryland, 1996), and *Hypophorella* and *Farrella* (suborder Stolonifera; see Prouho, 1892; Marcus, 1926). The earliest known cheilostomes, *Pyriporopsis portlandensis* (Late Jurassic) and its close relative *Pyripora catenularia* (Cretaceous to Recent) (Taylor, 1986, 1994), lack ovicels and generally resemble living malacostegan genera, such as *Conopeum* and *Electra*, which have planktotrophic cyphonautes larvae. *Cardoarachnidium* spp. (Upper Jurassic), which has been preserved through biommuration, is non-calcified but has an operculum and may represent a very early stage in the evolution of cheilostomes from ctenostomes (Taylor, 1990). Various lecithotrophic, cyphonautes-like larvae, such as the shelled larva of the ctenostome *Flustrellidra hispida*, and larvae with a narrow corona and a non-functioning gut, such as *Bulbella abscondita*, show how the planktotrophic larvae can be transformed to larvae with the corona covering almost the whole body (Zimmer & Woollacott, 1977). It appears that the 'invention' of the lecithotrophic coronate larva of cheilostomes has been one of the factors which made the strong radiation of the group possible (Taylor, 1988).

The planktotrophic cyphonautes larvae is a very special larval type; the paired chitinous shells are not found in any other larval (or adult) animal, and its ciliary feeding structure with stiff laterofrontal cilia probably functioning as a mechanical filter (Strathmann & McEdward, 1986) seems to be unique too. Its occurrence in primitive, and most probably in early, representatives of both Ctenostomata and Cheilostomata indicates that it was the ancestral larval type in the Gymnolaemata. The lecithotrophic stenolaemate larvae, developing through polyembrony, and the direct developing 'pelagic colonies' of the phylactolaemates appear highly specialized. Further investigations are needed to demonstrate whether the cyphonautes larvae is in fact a strongly modified trochophore (as is possibly indicated by the structure and embryonic development of the 'corona'), but it cannot be questioned that the ancestral ectoproct had a pelago-benthic life cycle.

(10) Phylum Platyhelminthes

The flatworms are a large phylum almost without a fossil record. A cladistic classification has been proposed by Ehlers (1985) and this is accepted by most authors. The 'class Turbellaria' is obviously a paraphyletic group, comprising free-living species.

Most free-living platyhelminths have a pelago-benthic life cycle with a free-swimming ciliated larva, and many of the parasitic flukes and tapeworms have a free-swimming, ciliated larva. Direct development occurs in a number of groups, whereas larvae which are presumed to be planktotrophic are known only from the Polycladida. Two types of such larvae have been named, Müller's larva and Götte's larva; they are both completely ciliated with an equatorial band of more prominent cilia drawn out in lobes or short tentacles (Ruppert, 1978; Lacalli, 1982; Nielsen, 1995). This band is often referred to as the prototroch, but this has not been ascertained through studies of the cell lineage, and its function in filter feeding has not been investigated.

The pelago-benthic life cycle with a ciliated larva must be considered ancestral within the phylum, but whether the presumed planktotrophic larvae are modified trochophores and represent the ancestral larval type cannot be decided from the present knowledge.

(11) Phylum Nemertini

The ribbon-worms also have a very uncertain fossil record. The phylum is usually divided in two classes each with two orders, but a cladistic classification has not been attempted. Many species have pelago-benthic life cycles with pelagic larvae, but planktotrophic pilidium larvae are found only in the order Heteronemertini, and in the problematic genus *Hubrechtella* (Cantell, 1969). Studies of cleavage patterns show that the cleavage is spiral, as in annelids and molluscs (Henry & Martindale, 1994, 1996; Martindale & Henry, 1995). Cell-lineage studies indicate that the large ciliary band is homologous with the prototroch of the trochophore (Hörstadius, 1937), but the ciliary mechanism involved in filter feeding is imperfectly known (Cantell, 1969). The very unusual metamorphosis, with the adult epithelium being formed from eight invaginations of the larval ectoderm, makes detailed comparisons with other larval types very difficult (Nielsen, 1995). Lecithotrophic larvae are found in a few species and many species have direct development (Iwata, 1960; Friedrich, 1979).

The ancestral nemertine probably had a pelago-benthic life cycle, but the type of its larval development appears difficult to deduce.

(12) Aschelminthes

The phyla Rotifera, Acanthocephala and Chaetognatha possibly form a monophyletic group and morphological characters strongly indicate that Gastrotricha, Nematoda, Nematomorpha, Priapula, Kinorhyncha and Loricifera form a monopohyletic group (Neuhaus, 1994; Nielsen, 1995; Nielsen *et al.*, 1996; Ehlers *et al.*, 1996). Whether the two clades are sister groups or whether the aschelminths is, in fact, a paraphyletic group is more uncertain. The fossil record is uncertain for most of the groups, but the Cambrian Burgess Shale fauna comprises a rich representation of priapulids (Conway Morris, 1977).

All the aschelminths have direct development, and only some of the rotifers have ciliary bands used in feeding and locomotion. These bands appear to be of the same structure and function as those of the spiralian trochophores and indicate that at least the ancestors of the rotifers had planktotrophic trochophore larvae (Nielsen, 1995).

(13) Phylum Ctenophora

The comb jellies have a scanty fossil record, but a number of remarkably well-preserved specimens have been described from the Burgess Shale and an undescribed species reported from the Lower Cambrian of Chengjiang (Conway Morris & Collins, 1996). The majority of the species are holopelagic and pass through a characteristic cydippid stage, which is ovoid with short comb rows. The few benthic genera, such as *Coeloplana* and *Tjalfiella*, have pelagic cydippid larvae, and are usually interpreted as highly specialized (Komai, 1922; Mortensen, 1912). The rather undifferentiated, parasitic larval stage of *Lampetia pancerina* (known under the name *Gastrodes parasiticum*; see Komai, 1922) is obviously another type of specialization.

It seems obvious that the ancestral ctenophore was holopelagic and that its general organization was that of a gastraea. There are no synapomorphies which indicate a sister-group relationship with the cnidarians.

(14) Phylum Phoronida

This phylum comprises only approximately 12 described, living species, and there is no unequivocal fossil record. Almost all species have planktotrophic actinotroch larvae (Zimmer, 1991); the ciliary band on the tentacles form an upstream-collecting system with single cilia on monociliate cells (Strathmann, 1973; Gilmour, 1978; Nielsen, 1987). The structure and function of the ciliary band are similar to those of the other planktotrophic deuterostome larvae (see below), but the ciliary band has the shape of an almost closed horseshoe with a small opening near the apical pole; it may correspond to the postoral part of the neotroch as seen in asteroid larvae (see below). The larval tentacles are retained in the juvenile at metamorphosis in *Phoronis vancouverensis* (Zimmer, 1964), whereas a set of new tentacles develop at metamorphosis in *P. muelleri* (Silén, 1954). Only the very small *Phoronis ovalis* has very large eggs and direct development (Silén, 1954).

It seems likely that the ancestral phoronid had a pelago-benthic life cycle with a planktotrophic actinotroch.

(15) Phylum Brachiopoda

The brachiopods can be traced back to the Early Cambrian, and the whole Palaeozoic showed a high diversity of orders and families; only three families of non-articulate type and a number of articulate families have survived to the present (Harper *et al.*, 1993). The phylogeny of the whole group is emerging (Williams *et al.*, 1996), and it seems clear that the families Disciniscidae and Lingulidae are closely related within the class Linguliformea, while their relationships with Craniidae (Craniiformea) and Articulata (= Rhynconelliformea) are still under debate (Carlson, 1995; Williams *et al.*, 1996).

Shelled disciniscid larvae resembling small juveniles have been known from the plankton for almost a century, but a younger, unshelled stage of *Discinisca* sp. with two bundles of extremely long larval setae has only been described by Chuang (1977); the embryology and early larval stages are unknown. The described larvae are planktotrophic and feed with an upstream-collecting ciliary system on tentacles resembling those of the benthic adults (Nielsen, 1987). The embryology of *Lingula anatina* was studied by Yatsu (1902) who observed that a small shell (called a protegulum by Chuang, 1977) was formed before hatching occurred from the egg membrane and a larval shell can be distinguished from the adult shell of the bottom stage. Both larvae and adults are filter feeding with upstream-collecting bands (Nielsen, 1987).

Crania (*Neocrania*) *anomala* is a free spawner and the development is lecithotrophic; shells and tentacles are formed after settling and metamorphosis (Nielsen, 1991*a*).

The development of a number of articulates has been studied and only very little variation has been observed (Conklin, 1902; Percival, 1944; Long & Stricker, 1991). The development is lecithotrophic and shells and tentacles develop after settling and metamorphosis.

Almost all species have a pelago-benthic life cycle, but the occurrence of planktotrophy and lecithotrophy does not give any indication of the plesiomorphic state within the phylum. Larval shells have not been recognized in any of the fossil craniiforms or rhynchonelliforms (Williams *et al.*, 1996), so the early representatives of these clades appear to have been lecithotrophic, like the living species. A protegulum has not with certainty been observed in fossil linguliforms, but larval shells are easily recognized in most species (Holmer, 1989; Williams *et al.*, 1996), so the ancestor of this clade probably had a planktotrophic larva like the living species.

A pelago-benthic life cycle is observed in almost all species and is probably ancestral. The planktotrophic linguliform larvae feed with an upstream-collecting system with single cilia on monociliate cells like the adults of all groups, and there is a gradual addition of tentacles after the settling. This agrees well with the idea that the ancestral larvae had a neotroch which was elaborated on tentacles in the adult (Nielsen, 1995). However, it is equally likely that the larval tentacles are precociously developed adult structures.

(16) Phylum Pterobranchia

The living pterobranchs are the few survivors of earlier, very diverse faunas. Graptolites, which flourished in Ordovician and Silurian, are now regarded as a highly diverse group of the order Rhabdopleurida, and the single surviving family Rhabdopleuridae goes back to the Lower Cambrian; the Cephalodiscida has been traced from the Ordovician (Benton, 1993). All species of the living genera *Cephalodiscus* and *Rhabdopleura* which have been studied have turned out to have brooded, lecithotrophic larvae (John, 1932; Lester, 1988), but nothing can be said about the developmental type of the early forms.

(17) Phylum Echinodermata

The Echinodermata are an old phylum with representatives already present in the Lower Cambrian. Several groups went extinct in the Palaeozoic, and the living classes (except the holothurians, which do not fossilize so easily) have been recognized already from the Lower Ordovician (Paul & Smith, 1984; Simms *et al.*, 1993). Both the more traditional phylogenies and the calcichordate theory derive the ancestral echinoderm from a *Cephalodiscus*-like ancestor which turned over on one side and lost the tentacles of the right side. The tentacles of the left side became the ambulacral system and the mesocoel of the left side became the water vascular system; pentamery evolved at a later stage (Holland, 1988; Nielsen, 1995; Jefferies, Brown & Daley, 1996). Nothing is known about the larval type of the early echinoderms, but skeletal fragments of echinopluteus larvae, probably of a spatangoid echinid, have been described from the Upper Jurassic (Deflandre-Rigaud, 1946).

The five living classes of echinoderms are very distinct and their interrelationships have been much debated; the Concentricyloidea are here regarded as asteroids (Janies & McEdward, 1994). However, it seems to be generally accepted that the crinoids are the sister group of the other four classes, and sister-group relationships of asteroids + ophiuroids (Asterozoa) and echinoids + holothurians (Echinozoa) appear to be supported both by most morphological and molecular studies (Smith, 1988; Smith *et al.*, 1993; Marshall, 1994).

Studies of echinoderm development have revealed an enormous variation of types, ranging from planktotrophic larvae with long arms, in some forms supported by elaborate calcareous endoskeletons (pluteus larvae), to direct development with brooded, globular embryos. The planktotrophic development usually passes through an early rhomboid stage, called dipleurula, with the larval mouth surrounded by a ciliary band (neotroch) used both in locomotion and filter-feeding in an upstream-collecting system; this stage can be recognized in larvae of asteroids, ophiuroids, echinoids and holothuroids (Dawydoff, 1948). Later planktotrophic stages are characteristic of the classes (Strathmann, 1971; see below). A lecithotrophic larval type called doliolaria (vitellaria) has a series of ciliary rings instead of the continuous ring seen in most planktotrophic larvae. This is the only larval type known in the crinoids and it is found also in ophiuroids and holothuroids (Fell, 1967). The pelagic development of some ophiuroids and holothurians shows that the ciliary band of the planktotrophic stage splits up and becomes transformed into the ciliary rings in the

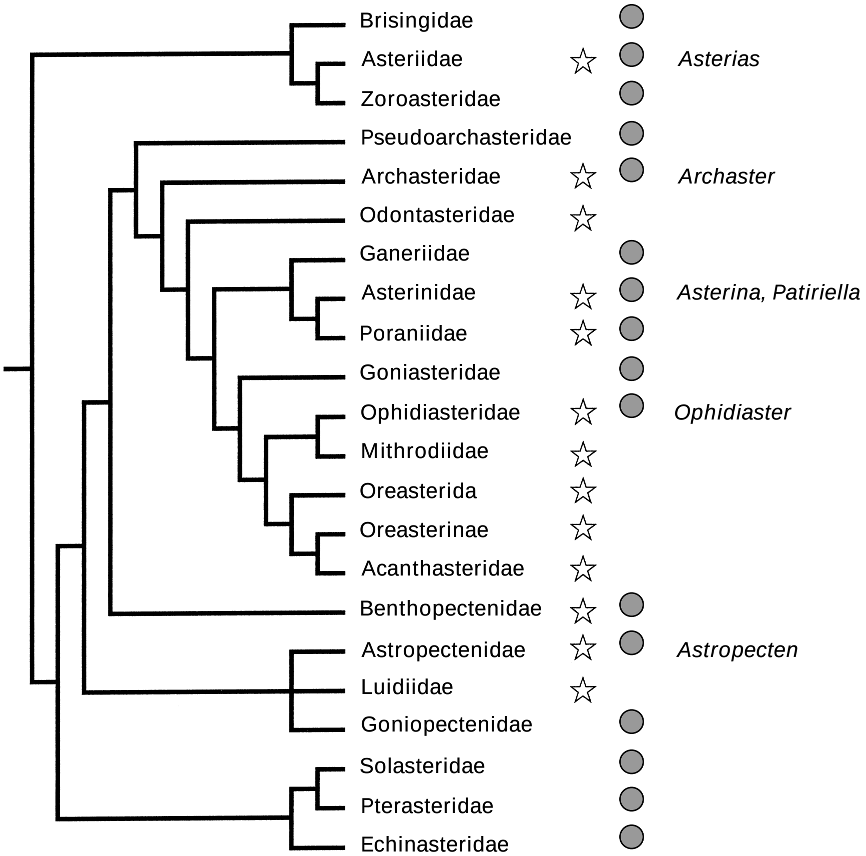

Fig. 1. Developmental types of selected asteroid families. Phylogeny based on Blake (1987); developmental types based on Emlet, McEdward & Strathmann (1987), supplemented with information from Pearse & Bosch (1994) and Byrne & Cerra (1996). Genera comprising both species with planktotrophic and species with non-planktotrophic development are indicated. ☆ planktotrophic development; ● non-planktotrophic development (lecithotrophic, direct or brooding).

subsequent doliolaria stage (see below), indicating that the doliolariae are derived from planktotrophic types.

(*a*) *Crinoidea*

The crinoids can be traced further back than any of the four other living classes, *viz.* to the Ordovician (Simms *et al.*, 1993). The living representatives are clearly only a few families remaining after massive extinctions: only the Articulata survived after the Palaeozoic, and less than half of the families of the Articulata survived the end of the Mesozoic (Paul & Smith, 1984; Simms *et al.*, 1993). The development of a few species of feather stars (order Comatulida) has been studied and all have turned out to go through a non-planktotrophic development involving a barrel-shaped doliolaria stage with five rings of locomotory cilia (McEdward, Carson & Chia, 1988). Earlier developmental stages show more complicated patterns of the differentiating ciliary bands with indications of a sinuous pattern like that in the development of holothurian larvae, but it has not been possible to homologize the bands with certainty (Lacalli & West, 1986, 1987). The development of the stalked types, the sea lilies, is almost unknown, and it cannot be excluded that some of these forms will turn out to have planktotrophic larvae. Strathmann (1978*b*) and McEdward *et al.*, (1988) suggested that the lecithotrophic developmental type could be the result of a 'historical accident' in which only one small group of crinoids survived the large extinctions and the ancestor of this group happened to have a doliolaria larva.

(*b*) *Asteroidea*

Asteroid phylogeny has been the subject of a number of recent studies, but a consensus has not been reached. Blake (1987) presented a comprehensive cladistic study of the interrelationships of the families (see Fig. 1). Lafay, Smith & Christen (1995) combined studies of morphology and ribosomal RNA and concluded that the group Paxillosida (comprising families such as Luidiidae and Astropectinidae) is the sister group of the remaining asteroids. Finally, Wada, Komatsu & Satoh (1996) studied mitochondrial DNA and concluded that the family Luidiidae is the sister group of the remaining asteroids. As can be seen from Fig. 1, the occurrence of planktotrophic and non-planktotrophic development does not follow any obvious pattern whatever phylogeny is preferred, and future studies of other species will probably reveal even more variation.

Most planktotrophic larvae go through a dipleurula stage before they reach the bipinnaria stage characterized by breaks in the band at the apical pole, so that a small, preoral and a large, postoral band are formed, and the presence of long flexible arms with extensions of the ciliary bands. Bipinnaria larvae of many species develop further into a brachiolaria stage having three preoral arms with attachment organs before they metamorphose (for example, *Asterias rubens* and *Patiriella regularis*; see Gemmill, 1914; Byrne & Barker, 1991). Larvae of paxillosidan species lack the brachiolaria stage (for example, *Astropecten auranciacus*, see Hörstadius, 1939); this has been interpreted as the ancestral condition (Wada *et al.*, 1996), but Blake (1988) argued that it should be regarded as a secondary loss. Erber (1985) suggested that traces of a brachiolaria stage can be recognized in coelomogensis of all asteroid larvae, and that this larval stage is ancestral in asteroids. Non-feeding bipinnaria larvae have apparently not been recorded (McEdward & Janies, 1993). Non-planktotrophic, pelagic development with a simple brachiolaria without bipinnaria arms is common (for example, *Solaster endeca*; see Gemmill, 1912), and larvae with an elongate, uniformly ciliated anterior region are seen in many species (for example, *Astropecten latespinosus*; see Komatsu, 1975). A pelagic development without any trace of larval structures is seen in *Pteraster tesselatus* (McEdward, 1992). Benthic development with larval stages having large brachiolaria arms has been observed in many species which brood or deposit the eggs in egg masses (for example, *Leptasterias hexactis*; see Chia, 1968). The genera *Patiriella* and *Asterina* comprise species with planktotrophic bipinnaria/brachiolaria larvae, species with short-lived, non-feeding brachiolariae, species with direct development in egg masses deposited on the substratum, and species with intraovarian, direct development (Byrne & Cerra, 1996). McEdward & Janies (1993) outlined two sequences of evolutionary changes from an ancestral life cycle with bipinnaria and brachiolaria stages to the various developmental types observed, and this interpretation appears to cover the observed types completely. There is no indication of evolution from lecithotrophy to planktotrophy, and the high number of genera and families comprising both species with planktotrophic and species with non-planktotrophic larvae (see Fig. 1) makes it very unlikely that the highly similar planktotrophic larvae have evolved independently many times. An analysis of the occurrence of planktotrophic *versus* non-planktotrophic development shows: (1) if planktotrophy was the ancestral character state, then non-planktotrophy must have evolved at least 13 times; and (2) if non-planktotrophy was the ancestral character state, then planktotrophy must have evolved at least nine times (reversals not allowed). A strict parsimony analysis would prefer the tree with the fewest steps, but because it has been shown in several groups that larval characters/structures are easily lost, it is not correct to give gain and loss equal weight.

(*c*) *Ophiuroidea*

A phylogenetic picture of the ophiuroids based on both morphological and molecular data is emerging (Smith *et al.*, 1995*a*), but the scattered observations of developmental types reveal no distinct pattern. The planktotrophic ophiopluteus larvae are well-known elements in the plankton, but Hendler (1975, 1991) estimated that the development is known for only approximately 4% of the ophiuroid species; direct development has been described for a number of brooders, and a number of unidentified ophioplutei have been described (Mortensen, 1921). Planktotrophic larvae have been described in families such as Amphiuridae, Ophiactidae, Ophiothricidae, Ophiocomidae and Ophiuridae, and non-planktotrophic development has been ascertained in many families. Species with ophiopluteus larvae as well as brooding species with direct development have been reported from genera such as *Amphiura* and *Ophiura* (Mortensen, 1921, 1936). Most ophiopluteus larvae have eight arms, but the planktotrophic larva of *Amphiura filiformis* has only six and the probably non-feeding larva of *A. chiajei* has only one pair of short, postero-lateral arms (Fenaux, 1963). *Ophiocoma pumila* develops through a normal ophiopluteus stage which gradually loses pluteus arms and skeleton and becomes a doliolaria before it metamorphoses into a juvenile brittlestar

(Mladenov, 1985). Planktonic doliolaria larvae with rudiments of the adult skeleton are known from a number of species, for example, *Ophiolepis cincta* (Mortensen, 1938), and in early doliolaria of *Ophionereis annulata*, Hendler (1982) observed skeletal rods which he regarded as homologues of the pluteus skeleton. Direct development inside the vitelline membrane has been observed in *Amphioplus abditus* where a short-armed pluteus stage with rudiments of the larval skeleton and a doliolaria-like stage are passed before the juvenile stage hatches (Hendler, 1977).

The development of a doliolaria from an ophiopluteus in *Ophiocoma pumila* indicates that the doliolaria was originally a stage in the metamorphosis of the planktotrophic larva. The planktotrophic larva must be considered the plesiomorphic type, and the scattered occurrence of planktotrophic larvae within families and genera further support this view. There seems neither to be indications of independent development of planktotrophy from lecithotrophy nor of reestablishment of planktotrophy from lecithotrophic development with dormant genetic information.

(*d*) *Echinoidea*

The traditional systematics of the class Echinoidea has been rather stable for more than half a century, and an understanding of echinoid phylogeny is now emerging, based on both morphological and molecular data (Smith, Lafay & Christen, 1992; Wray & Bely, 1994; Smith, Littlewood & Wray, 1995*b*; see Fig. 2).

Echinoplutei are always easy to recognize, so although there is some variation in the shape and number of larval arms between (and also to some extent within) families (Wray, 1992), it seems obvious that all these types are variations of one ancestral theme. This must have been established at least at the time of the split between the two oldest lineages of living echinoids, Cidaroidea and Euechinoidea, approximately 260 million years ago in the mid-Triassic (Littlewood & Smith, 1995; Smith *et al.*, 1995*b*). Non-planktotrophic developmental types, such as pelagic, lecithotrophic development and direct development in brood pouches, are believed to have evolved independently at least 20 times (Wray, 1995*b*; reviews in Emlet, McEdward & Strathmann, 1987; Emlet, 1990, 1995*a*). Four of the genital and two of the ocular plates of the adult skeleton develop from proximal parts of the skeletal rods in the echinopluteus arms (Gordon, 1926*a*, *b*, 1929; Emlet, 1985); the distal parts of the rods and the other elements of the larval skeleton degenerate at metamorphosis. The rudiment of the juvenile sea urchin with the five primary podia develops from the left side of the larva where the adult mouth finally breaks through.

Non-planktotrophic developmental types occur in almost all major echinoid groups, in some cases even within genera comprising species with planktotrophic development (Fig. 2), and all transitional types between the planktotrophic echinopluteus with long arms to direct development through an almost globular stage without any larval spicules can be recognized (see also Raff, 1987). The larvae of *Brisaster latifrons* and *Clypeaster rosaceus* are facultatively planktotrophic (Hart, 1996; Emlet, 1986). The lecithotrophic larva of *Phyllacanthus imperialis* has four rather short, club-shaped arms (Olson, Cameron & Young, 1993). *Peronella japonica* has variable lecithotrophic larvae ranging from four-armed larvae with skeletal rods to almost spherical larvae devoid of skeleton (Mortensen, 1921). The lecithotrophic larva of *Asthenosoma ijimai* has four very short larval 'arms' containing short spicules and these structures are interpreted as vestiges of the postoral and posterodorsal arms of the echinopluteus (Amemiya & Emlet, 1992). The 45 h old lecithotrophic larva of *Heliocidaris erythrogramma* is ovoid, uniformly ciliated and shows rudiments of the adult structures, including five podial buds, on the left side, but additionally has two paris of bilaterally arranged calcareous rods which by their position and fenestrated structure can be identified as rudiments of the postoral and posterodorsal rods of planktotrophic larvae (Emlet, 1995*b*). The fenestrated parts of the rods are clearly reminiscent of the larval skeleton and this is apparently also the case with the ciliary bands which develop at a slightly later stage. These characters indicate clearly that the ancestors of this species had echinopluteus larvae, and this larval type is indeed found in the sister species *H. tuberculata* (Raff, 1987; Laegdsgaard, Byrne & Anderson, 1991). Molecular studies indicate that the two species diverged approximately 10 million years ago (McMillan, Raff & Palumbi, 1992); the exact duration of the change from planktotrophic to lecithotrophic development cannot be ascertained, but it is clear that the shift from planktotrophic larval development to lecithotrophic development with a highly modified larval type can take place within a few million years (Wray & Raff, 1991).

The lecithotrophic and direct developmental types

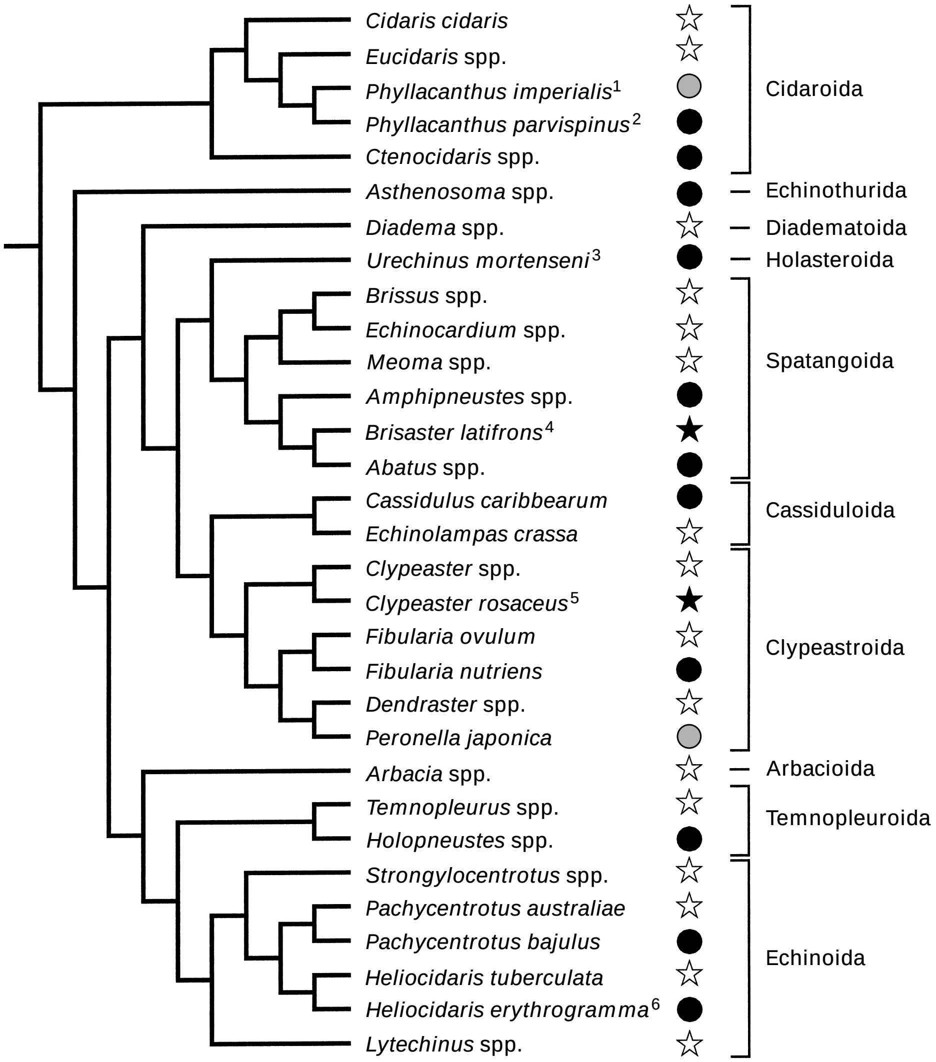

Fig. 2. Developmental types of selected echinoids. Phylogeny based on Wray & Bely (1994), Emlet, McEdward & Strathmann (1987) and Jensen (1988). Developmental types based on Emlet *et al.* (1987) and [1] Olson, Cameron & Young (1993); [2] Parks *et al.* (1989), [3] David & Mooi (1990), [4] Hart (1996), [5] Emlet (1986), and [6] Raff (1987). ☆ planktotrophic larvae; ★ facultative planktotrophic larvae; ○ lecithotrophic larvae with larval arms; ● direct development (without larval arms).

have almost always been interpreted as derived from the planktotrophic type, and it does indeed seem very unlikely that planktotrophic larvae of the echinopluteus type, which share so many detailed morphological similarities (Wray, 1992), should have evolved independently so many times within the class (Wray, 1996). In contrast, lecithotrophic larvae are quite diverse morphologically, as discussed above. The loss of larval structures appears to be the result of heterochrony and loss of larval developmental processes – possibly loss of genetic information, but perhaps just a change in the control of expression of specific gene sets – in some species coupled with a remodelling of early cell lineage and cell specification (Smith, Boom & Raff, 1990; Wray & Raff, 1990; Raff, 1992; Wray, 1994). There are no indications of 'revival' of dormant information as seen in some molluscs (littorinids, see above). In short, the larva of the ancestral echinoid was apparently a planktotrophic echinopluteus and direct development with loss of essential larval characters has evolved again and again in the various echinoid clades.

(*e*) *Holothuroidea*

The sea-cucumbers have a poor fossil record because of their usually weakly consolidated skeleton, and a phylogenetic classification has not been attempted. Six orders are usually recognized. Larval development has been studied in almost all of the 25 families, and the planktotrophic auricularia larvae have been found only in species belonging to Holothuriidae and Stichopodidae (order Aspidochirota) and Synaptidae (order Apoda) (Smiley *et al.*, 1991).

The auricularia larva resembles an early bipinnaria without arms, but can be distinguished by the continuity of the ciliary band, which in bipinnariae is divided into a preoral and a postoral band by interruptions at the apical organ (Strathmann, 1971). The auriculariae of *Labidoplax* (*Synapta*) *digitata* (Semon, 1888; Bury, 1895), *Stichopus californicus* (Smiley, 1986; Lacalli, 1993) and *Holothuria mexicana* (Lacalli, 1988) develop highly sinuous ciliary bands, which break up and subsequently rearrange as five circular bands of a non-feeding doliolaria larva; the larva soon develops five tentacles, a stage called pentactula.

Non-planktotrophic development comprises planktonic doliolaria larvae with 2–5 ciliary rings or uniform ciliation and non-planktonic development usually connected with brood protection (Smiley *et al.*, 1991). Both planktotrophic and non-planktotrophic, pelagic development have been recorded from the genus *Labidoplax* (Nyholm, 1951) and other species of the same family are viviparous with coelomic brooding (Clark, 1898).

It appears unlikely that the very similar planktotrophic auricularia larvae, developing into similar doliolariae, have evolved independently within the three families (representing two orders); so although most holothurians have non-planktotrophic development it seems probable that the ancestral form had a planktotrophic larval stage.

Thus, it appears that the latest common ancestor of the living echinoderms had a pelago-benthic life cycle with a planktotrophic larva of a type close to the dipleurula (a stage also observed in the closely related phylum Enteropneusta; see below), and it is reasonable to believe that this was the case for the ancestor of all echinoderms; this view is shared by most authors (Strathmann, 1975, 1978*a*, 1993; Nielsen, 1987; Raff, 1987; Emlet, 1994). Müller (1853) observed previously that the planktotrophic echinoderm larvae were built according to a common plan, in modern terms that the ciliary bands and oral fields of the planktotrophic echinoderm larvae are homologous. The class-specific larval types must be apomorphies of the classes, and the doliolariae and various types of direct development must have evolved independently in larger or smaller clades (see also Strathmann, 1988). There seems to be no indication that species with planktotrophic larvae have evolved from species with non-planktotrophic development.

(18) Phylum Enteropneusta

The acorn worms are a small group of animals with an uncertain fossil record. *Planctosphaera pelagica* is possibly a giant enteropneust larva (Hart, Miller & Madin, 1994). There is no understanding of the phylogeny of the group, but four families are usually recognized.

The characteristic planktotrophic tornaria larva with an upstream-collecting perioral ciliary band and a perianal band of compound cilia is known from many seas, but only a few of the larvae have been related to adult species. Tornaria larvae are known from species of *Schizocardium* and *Glandiceps* (family Spengeliidae; Ruppert & Balser, 1986; Rao, 1953) and *Ptychodera* and *Balanoglossus* (family Ptychoderidae; Strathmann & Bonar, 1976; Gilmour, 1982). Young tornariae resemble the dipleurula stage of planktotrophic echinoderm larvae, having an upstream-collecting, perioral ciliary band (neotroch) consisting of separate cilia on monociliate cells. Later stages develop elaborate sinuosities of the ciliary band and the perianal band of compound locomotory cilia (on multiciliate cells) (Gilmour, 1982; Nielsen, 1987). The metamorphosis from the tornaria larva to the juvenile bottom stage is gradual; the body changes from a rather spherical shape to an elongate shape and the ciliary bands disappear (Hadfield, 1975). Several species of *Saccoglossus* (family Harrimaniidae) have lecithotrophic development, with larvae having a short pelagic period; the larval apical organ and perianal ring of compound cilia are conspicuous structures of the embryos (Burdon-Jones, 1952).

The pelago-benthic life cycle seems to occur in all enteropneusts and must be interpreted as an ancestral character. The detailed structural and functional similarities of the neotrochs of early tornaria larvae and of the dipleurula stage of echinoderm larvae indicate that these structures are homologous and that the ancestral enteropneust had a planktotrophic larva (Strathmann, 1988).

(19) Chordata

None of the chordates has a ciliated primary larva; ciliated gastrula-stages are known from *Branchiostoma* *lanceolatum* (Conklin, 1932), but they are non-feeding and do not hatch from the egg membrane until a much later stage.

Most urochordates have a pelagic tadpole larva with a laterally compressed tail containing a chorda dorsalis (urochord, see Nielsen, 1995). This larva is not a feeding, ciliated primary larva, but it will be discussed here because recent experimental investigations on ascidian development have thrown light on the genetic control of the development of larval structures, i.e. the question of gain *versus* loss of larval organs.

The appendicularians (= larvaceans) are usually interpreted as neotenic forms which have retained the tail in the adult stage. Most ascidians have tadpole larvae with the characteristic tail, but the family Molgulidae show an enormous variation from free spawners to viviparous species and from tadpole larvae with a pigmented sensory organ (otolith) to tailless (anuran) larvae without an otolith (Berrill, 1931; Jeffery & Swalla, 1992). Some species of the family Styelidae also have tailless larvae (Millar, 1962). Studies of ribosomal DNA sequences indicate that the tailless developmental type has evolved at least four times within the family Molgulidae (Hadfield, Swalla & Jeffery, 1995). The embryos of species with tailless larvae show the same development of the urochord and neural tube as observed in species with tadpole larvae, but the zone of the urochord is very short and non-protruding (Berrill, 1931; Jeffery & Swalla, 1990). It seems generally accepted that the tailless larvae represent specializations, as indicated by their occurrence within styelids and molgulids, and it appears that the tailless larval type has evolved independently at least five times within the ascidians (Hadfield *et al.*, 1995). All urochordate larvae can in principle be considered as lecithotrophic, although the adult branchial sac has already developed by the late larval stages of some species.

Recent experimental studies of the development of the sister species *Molgula oculata* (which has a tadpole larva with an otolith) and *M. occulta* (which has a tailless larva devoid of an otolith) (Hadfield *et al.*, 1995) have demonstrated some of the genetic mechanisms which control the development of the tail (Swalla & Jeffery, 1996; Pennisi, 1996). Swalla & Jeffery (1996) showed that a gene called *Manx* is expressed in *M. oculata*, with *Manx* protein showing up in the cells which differentiate into the urochord, tail muscles and dorsal nerve tube, but is silent or absent in *M. occulta*, where the protein could not be detected. Hybrids formed from *M. occulta* eggs and *M. oculata* sperm developed a short tail, whereas the tail did not develop in embryos where the *Manx* gene was blocked so that *Manx* protein was not synthesized. It appears that the species with tailless larvae has an almost complete genetic instruction for the organization of a tadpole larva, and all the components are present but short, so that the only difference is that one (or a few) genes responsible for the elongation of the tail are lacking or silenced. This shows that a highly differentiated larval organ can be lost through a mutation in a single gene. On the other hand, it should be remembered that a complicated structure like the complex of urochord, neural tube and muscles in the tail of the ascidian larva must be organized through the functioning of a whole series of genes and that it seems highly unlikely to have evolved as one single mutation, as suggested by Pennisi (1996).

These observations throw light on the gain *versus* loss of (larval) characters and are therefore of special importance to a discussion of planktotrophy *versus* lecithotrophy. They have unequivocally demonstrated that the loss of a larval structure can be the result of one mutation, whereas the evolution of complex larval organs, such as the elongate tail with the urochord, neural tube and lateral muscles of the ascidian larva, are likely to be the results of a long evolutionary history.

III. GENERAL DISCUSSION

(1) Origin of the animal life cycle

Animal (= metazoan) origin has been discussed for more than a century, and a number of highly diverging theories have been proposed. It now seems generally accepted that the sister group of the metazoans is the choanoflagellates, and this strongly supports the colonial theory, which derives the first animals from a colony of choanoflagellate-like cells (Ruppert & Barnes, 1994; Rieger, 1996). The ancestor may actually have been a choanoflagellate, which would make the Choanoflagellata a paraphyletic group, but this is without importance to the present discussion. The syncytial theory, which derives the early animals from multinucleated ciliates which then developed cell boundaries is now seen as lacking in support (Brusca & Brusca, 1990; Nielsen, 1991*b*).

Boaden (1975) pointed out that anaerobic marine sands harbour a rich fauna of interstitial species of many phyla, and proposed that early animal radiation took place before oxidized environments became established. This is an exclusively ecological

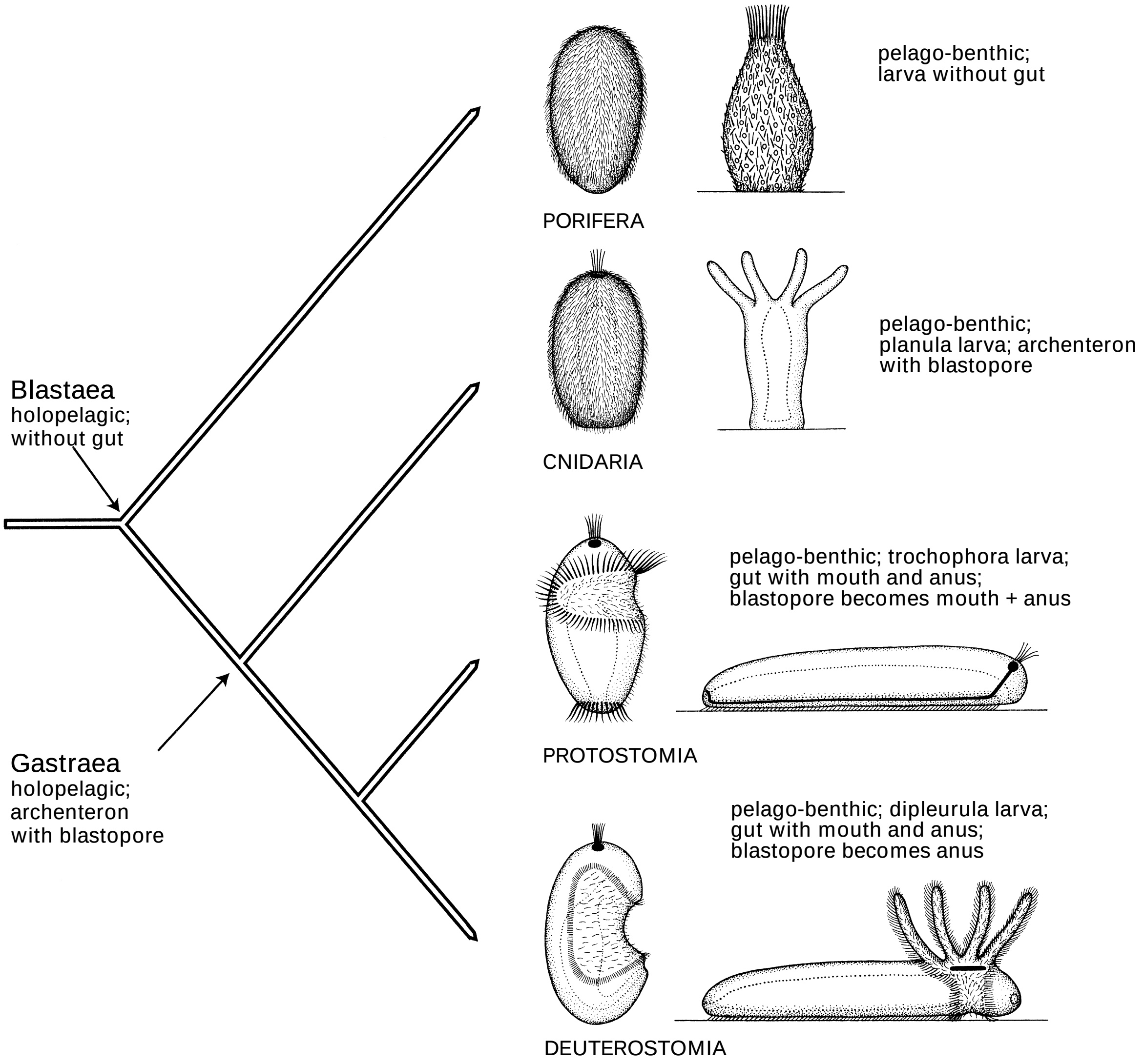

Fig. 3. Early metazoan radiation with indications of the most important characters of the hypothetical ancestors.

view which may or may not be correct, but it does not require that the early animals were interstitial/benthic as stated in his conclusions; contemporary studies indicate that living anaerobic eukaryotes are in most cases descendants of aerobic ancestors (Fenchel & Finlay, 1995). Wolpert (1994) proposed a scenario for the evolution of a spherical multicellular organism – having the shape of a blastaea – from a single cell, but this was based on non-ciliated, osmotrophic cells and is probably without relevance to animal origins.

The earliest animals were probably free-living, spherical organisms with choanocytes on the surface (blastaea); as metazoans, they were characterized by such close cell contacts that nutrients could be exchanged between cells, and this had made it possible for some cells to abandon particle feeding and, for example, to become displaced from the surface of the organism. A life cycle with sexual reproduction with haploid, choanoflagellate-like spermatozoa and eggs (perhaps with choanoflagellate-like oocytes, see Frick & Ruppert, 1996), a zygote, and an embryology leading to the adult, sexually mature stage with characteristic cell types organized in specific patterns seems to be one of the most conspicuous apomorphies of the Animal Kingdom (Margulis & Schwartz, 1988; Brusca & Brusca, 1990; Nielsen, 1995; see also Erwin, 1993). This ancestral animal life cycle could possibly resemble that of a colonial choanoflagellate, but sexual reproduction has not been described from any member of that group. Almost all colonial choanoflagellates are pelagic, only a few limnic species are attached to the substratum by a gelatinous stalk (Dr

H. A. Thomsen, University off Copenhagen, personal communication). This indicates that a holopelagic life cycle was a plesiomorphy of the metazoans. The ancestral animals may not have inhabited the open oceans, where particulate food was probably scarce, but rather have been found in the shallow ocean zones or the water layer very close to the ocean bottom where the concentration of food particles was presumably higher.

It thus appears that the ancestral animal life cycle was holopelagic, and it seems probable that the quite different adult stages observed in Porifera, Cnidaria, Protostomia and Deuterostomia, which all have pelago-benthic life cycles, have evolved independently by the addition of benthic, adult stages (Fig. 3). The metamorphoses of the early protostomes were, of course, not from fully differentiated, planktonic, filter-feeding trochophores to deposit-feeding or carnivorous, benthic adults, but from a ciliary-feeding, planktonic gastrula stage to a rather similar deposit-feeding, benthic stage. The differentiation of both larval stages, such as trochophores and dipleurula larvae, and adult stages took place after the establishment of the pelago-benthic life cycle (see below).

These early stages of animal radiation are often referred to as the Cambrian explosion (McMenamin & McMenamin, 1989; Signore & Lipps, 1992), but what we see in the Early Cambrian strata is the remains of organisms which could easily be fossilized because they had a skeleton. It seems probable that a long period of evolution comprising small, naked organisms took place much earlier (Fortey, Briggs & Wills, 1996), but the age of divergence of the major groups based on molecular data is highly controversial (Doolittle *et al.*, 1996; Wray, Levinton & Shapiro, 1996; Conway Morris, 1997).

(2) **Planktotrophy *versus* lecithotrophy**

Experimental evidence from ascidians has demonstrated, and many observations of echinoderms and molluscs have indicated, that larval characters can easily be lost, in some cases probably by only one mutation which turns off a regulatory gene. Factors influencing the change from feeding to non-feeding and from pelagic to non-pelagic development have been much discussed (summary in Havenhand, 1995), but I am not aware of any more comprehensive discussion of factors which could influence changes in the opposite direction.

Haszprunar *et al.* (1995) claimed that although the similarities of all the downstream collecting bands of the protostomes seem striking (just as the upstream ciliary bands of the deuterostomes seem strikingly similar), the types of larval feeding and locomotory structures could be the results of many convergent evolutions from non-feeding larvae. In support of this, they mention a few other structures/organs which appear to have evolved independently several times, but none of the examples can be taken as proof of multiple evolution of complicated, very similar structures: the duo-glands of several interstitial groups are structures of low complexity, consisting of only 2–3 cells; collar receptors are probably a cell type inherited from the earliest eumetazoans; and for the protonephridia, the paper cited, Ruppert & Smith (1988, p. 252), concludes that ‘if… the ancestral bilaterian was a large adult with a small larva, then both meta- and protonephridia may have been in its body plan’. Thus, the cases of parallel evolution of structures proposed by Haszprunar *et al.* (1995) are all much simpler than the complex feeding structures of the planktotrophic larvae, and some of the structures may, in fact, be conserved rather than convergent.

Ivanova-Kazas (1985, 1987) suggested that filter-feeding, planktotrophic larvae should have evolved from lecithotrophic, gutless larvae, but there is to my knowledge not a single well-documented example of an evolutionary process of that type.

There is one example which indicates ‘re-evolution’ of planktotrophy, namely the gastropod genus *Epheria* (see above); the developmental types of its relatives indicate that its closest ancestors have had intracapsular development with a fully formed but non-functioning velum and that the genetic program for a functioning velum has been ‘turned on’ again in *Epheria* spp. This cannot be compared to a *de novo* evolution of a filter-feeding ciliary organ.

Olive (1985) and Chaffee & Lindberg (1986) have documented that small eggs and planktotrophic larvae are usually found in larger species which are able to broadcast many eggs whereas small species have comparatively large eggs, brood protection and direct development. This should speak against theories which regard planktotrophic larvae as ancestral in major animal groups. I have commented previously that these characteristics of living species are the result of competition/predation in the plankton and that the ecological conditions were quite different in the Precambrian when the early radiation of the animal phyla took place (Nielsen, 1995). It is usually stated that free spawning of eggs and sperm of the ‘primitive’ type should be coupled with planktotrophic development (Jägersten, 1972), and Olive (1985) added strong seasonality of reproduction and large body size to the list of characters. This is indeed what can be observed in most species with planktotrophic filter-feeding larvae, but there are exceptions:

The entoproct *Loxosomella elegans* is microscopic (length up to 670 μm), but it has small eggs, internal fertilization and sperm with an elongate head (Nielsen & Jespersen, 1997); it has brood protection and the reproductive season is recorded to be June–January in Danish waters (Nielsen, 1964); the almost spherical larvae are approximately 90 μm in diameter, have a functioning gut and probably a long pelagic, planktotrophic phase (Nielsen, 1971). As in all entroprocts, this species has asexual reproduction through budding, which will of course increase the number of larvae produced from one zygote, but there must on the other hand be a need for an increased number of larvae because a high proportion of the larvae probably fail to find a proper host (polychaetes of the species *Praxillella praetermissa* and *Rhodine gracilior*).

Another example is the interstitial prosobranch *Caecum glabrum*, which is cylindrical, approximately 1 mm long, and lays egg capsules each containing one egg; a planktotrophic veliger with a shell length of approximately 100 μm hatches from the capsule and grows in the plankton to a size of approximately 450 μm before it settles (Götze, 1938; Thorson, 1946).

These examples show that, although there is a strong tendency towards lecithotrophy or direct development in small organisms, this is not a law without exceptions and it is indeed possible that, for example, the ancestral protostomes and deuterostomes had planktotrophic larvae.

Loss of planktotrophy has been observed in larvae of many smaller and larger clades of annelids, molluscs and echinoderms (Figs 1, 2), whereas *de novo* evolution of planktotrophy has not been documented in any clade, although some clades within non-planktotrophic clades would be likely to benefit from planktotrophy (Strathmann, 1978*b*). The general pattern is very similar to that which can be observed in the phylogenetic tree of the Animal Kingdom (Fig. 4). It therefore seems highly unlikely that planktotrophy should have evolved anew in the numerous clades with planktotrophic larvae. It seems much more probable that the highly characteristic, ciliary filter-feeding larval types, such as the trochophore and dipleurula, evolved once. Convergent evolution can, of course, not be ruled out (Willmer & Moore, 1997), but there is no indication of this from detailed observations of the structure and function of the ciliary bands (Nielsen, 1987).

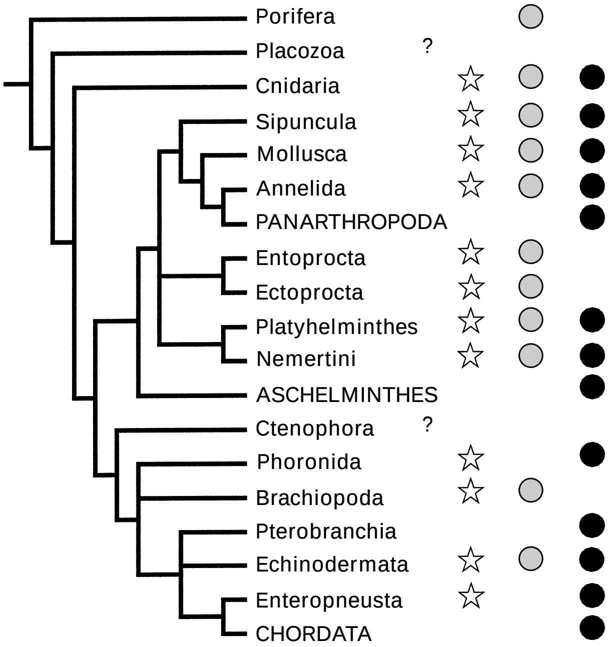

Fig. 4. Developmental types of the animal phyla. Placozoa and Ctenophora have not been allocated a developmental type because the development of *Trichoplax adhaerens* is unknown and both the phylogenetic position and the developmental type of the ctenophores are uncertain. ☆ planktotrophic larvae; ○ lecithotrophic larvae; ● direct development (no primary larvae).

I know of no general selection pressure which could favour the evolution of lecithotrophic larvae from planktotrophic larvae (or *vice versa*). However, when planktotrophy is lost in a lineage it is apparently very rarely regained, and we know no examples of *de novo* evolution of planktotrophy from lecithotrophy. The evolution of larval types thus seems to function as a 'one-way street', and this could at first sight be mistaken for the result of a general selection pressure. This is parallel to the evolution of obligatory parthenogenesis in the animal kingdom; it occurs in several smaller clades and in bdelloid rotifers, most chaetonotoid gastrotrichs and astigmate mites (Bell, 1982; Hughes, 1989). It is well established that sexual reproduction has been lost in many clades, but the only well-documented example of apparent reevolution of sexuality is found in some mites (Norton, 1994).

(3) Evolution of animal life cycles

In the above sections it was demonstrated that: (1) the ancestral animal (= metazoan) was probably a holopelagic organism, and (2) that planktotrophy has been lost many times within larger and smaller clades whereas no example of the evolution of a life cycle with ciliary filter-feeding larva from a direct-developing species has been identified. These conclusions will now be combined with information regarding the individual phyla discussed above in an attempt to follow the evolution of the life cycles in the Animalia.

There is unfortunately no generally accepted phylogeny for the Animal Kingdom. Morphological and especially molecular phylogenies show considerable variation, but there is almost complete agreement about the interrelationships of Porifera, Placozoa, Cnidaria and Bilateria; also Protostomia and Deuterostomia are often recognized, although the position of the 'lophophorates' (Ectoprocta, Phoronida, Brachiopoda) is controversial. In the following discussion, I will use the basal part of the phylogeny which was the conclusion of my recent evaluation of morphological data (Nielsen, 1995; see also Nielsen *et al.*, 1996). The basal part of the tree has the following characteristics (Fig. 3): The animal ancestor, blastaea, was a spherical, free-living organism with most of the surface covered by choanocytes. Porifera evolved a pelago-benthic life cycle by adding a benthic adult stage and retaining the gutless pelagic stage as a larva. The adult sponge reorganized the choanocytes into collar chambers, resembling the living choanoflagellate *Diaphanoeca spherica* (see Fig. 4.1 in Nielsen, 1995). The ancestor of the Eumetazoa, gastraea, was a pelagic, radially symmetrical organism with an archenteron. Cnidaria evolved a pelago-benthic life cycle by adding a sessile, radially symmetrical adult stage and retaining the gastraea-like ancestral stage in the shape of the planula larva. Protostomia and Deuterostomia evolved pelago-benthic life cycles by adding bilaterally symmetrical, benthic adult stages and retaining the pelagic larval stages, which became bilateral and specialized in the shape of the trochophore and dipleurula, respectively. This is in good accordance with the general idea of the evolution of larval types proposed by Wray (see Fig. 1, 1995*a*), although some of the phylogenetic details diverge.

Porifera have choanocytes, or collared units, as the principal feeding structure in the sessile adult stage, and can be seen as illustrations of the general organization of the earliest animals. The larvae have no choanocytes or collared units and are lecithotrophic, but the ancestral life cycle probably comprised a larva feeding using choanocytes.

Cnidaria have retained the organization of the gastraea. The nematocysts, which are the most conspicuous apomorphy of the whole phylum, may have evolved already in the holopelagic ancestor. Most groups have pelago-benthic life cycles with ciliated planula larvae and benthic polyps. A few species exhibit gastrulation by invagination, and a few larvae are known to be planktotrophic. Ciliary bands engaged in filter-feeding have not been reported. This indicates that a pelago-benthic life cycle was ancestral within the phylum and that the ancestral larva may have been planktotrophic.

Ctenophora have remained holopelagic; the very few benthic forms are clearly highly specialized. They can be interpreted as living examples of the gastraea type of organization and life cycle. The position of this phylum as a sister group of the Bilateria or of the Deuterostomia seems somewhat uncertain, but both positions are compatible with the phylogeny outlined in Fig. 3.

Bilateria show a wealth of different life cycles, but a gastrula stage can be recognized in most groups, usually being passed inside the egg membrane. Bilaterality has probably evolved twice, as indicated by the different fates of the blastopore and the different origin and organization of the adult nervous system in Protostomia and Deuterostomia (Nielsen, 1994).

Among the Protostomia, a pelago-benthic life cycle is found in species of most spiralian phyla; arthropods and aschelminths have direct development or secondary, non-ciliated larvae. Planktotrophic, filter-feeding trochophore-type larvae with a downstream-collecting ciliary system consisting of a prototroch and metatroch of compound cilia and an adoral ciliary zone of single cilia, all on multiciliate cells, are found in annelids (including echiurans), molluscs and entoprocts, and some adult rotifers have a similar feeding structure. Non-filter-feeding trochophores lack the metatroch, and such larvae are found in many species of the above-mentioned groups and in sipunculans. The planktotrophic larvae of platyhelminths and nemertines resemble trochophores, but the homology of their ciliary bands is uncertain. The larvae of ectoproct bryozoans have a circumferential ciliary band called the corona, which may be homologous with the prototroch, but the ciliary feeding structure of the planktotrophic cyphonautes larvae seems to be a unique system among the planktotrophic larvae. It seems possible that the pelago-benthic life cycle is ancestral in the Protostomia and has been lost subsequently in arthropods and aschelminths. Planktotrophic larvae of unquestioned trochophore type appear to be ancestral in a number of spiralian phyla, and as shown above the trochophore may be ancestral within the spiralians. Blastopore closures and central nervous systems in spiralian and aschelminth phyla show considerable similarity, which indicates the monophyly of the Protostomia, and the ciliary feeding structures of the planktotrophic rotifers indicate that also the aschelminths may have had an ancestor with a trochophore.

In the Deuterostomia, pelago-benthic life cycles are predominant in all phyla except the chordates. The characteristic larval feeding structure is an upstream-collecting ciliary band consisting of single cilia on monociliate cells; this type of structure is found in larvae and adults of phoronids and brachiopods, in larvae of echinoderms and enteropneusts, and in adult pterobranchs (where all species studied have direct development or lecithotrophic larvae); only the chordates, which all have direct development, have no comparable structures. Ciliary bands of this type have not been observed in any other phylum and this character must be regarded as one of the main synapomorphies of the deuterostomes. Other characters, such as the fate of the apical organ and the embryology and morphology of the coeloms, support the monophyly of the group (Nielsen, 1994). Planktotrophy has been lost in larvae of many smaller and larger clades, well documented for example in echinoderms, and also many of the adult forms, especially those attaining larger sizes, have switched to other feeding strategies. It therefore seems most likely that the ancestral deuterostome had a dipleurula larva with an upstream-collecting ciliary band and possibly an adult having tentacles with the same band. The ancestor probably evolved from a holopelagic gastraea, but how the new mouth, surrounded by the neotroch, the dorsal/ventral orientation, and the new central nervous system evolved appears quite enigmatic (Nübler-Jung & Arendt, 1994; Lacalli, 1996; Nielsen, 1997).

It appears that the pelago-benthic life cycle is ancestral in almost all the major clades and it must be concluded that it was ancestral in Porifera, Cnidaria, Protostomia and Deuterostomia. Non-planktotrophic development occurs in almost all phyla, but the occurrence of developmental types and characteristic planktotrophic larvae nevertheless indicates that a trochophore-like larva was the ancestral larval type of the Protostomia and a dipleurula-like larva was the ancestral larval type of the Deuterostomia.

IV. CONCLUSIONS

1. The animalian (= metazoan) ancestor was a holoplanktonic blastaea with an outer epithelium consisting mainly of choanocytes.
2. The eumetazoan ancestor was a holoplanktonic gastraea with a ciliated ectoderm and endoderm.
3. Pelago-benthic life cycles evolved in sponges, cnidarians, protostomes and deuterostomes, when an adult, benthic stage became established and the pelagic stage was retained as a larval stage.
4. The planktotrophic trochophore was the larval type of the ancestral protostome, and the planktotrophic dipleurula was the larval type of the ancestral deuterostome.
5. There are numerous well-documented examples of loss of larval feeding in phyla such as annelids, molluscs, entoprocts and echinoderms.
6. There are a few examples of re-evolution of larval planktotrophy through re-activation of unused feeding structures.
7. There is no well-documented example of a *de novo* origin of a ciliary feeding band within any living animal phylum, although the ciliated ridge of the cyphonautes larva may be one.
8. Gain and loss of planktotrophy should not be given same weight in cladistic analyses.

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