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LARVAL ECOLOGY OF MARINE BENTHIC INVERTEBRATES: PALEOBIOLOGICAL IMPLICATIONS

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I. INTRODUCTION

The role of larval ecology in the distribution and evolutionary history of marine benthic organisms is only now beginning to be appreciated by paleontologists. Documentation of the early ontogeny of fossil organisms has generally been considered to be

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extremely elusive, but it is now clear that types of larval development can be inferred with some confidence in well preserved molluscan shells (and perhaps some other groups as well) because the accretionary mode of growth retains a record of early developmental stages. In recent years, the analysis of such early developmental stages in fossil organisms has led to new hypotheses in paleoecology (Lutz & Jablonski, 1978*b*; Jablonski & Bottjer, in press), paleobiogeography (Kauffman, 1975; Jablonski, 1979*a*, 1980*a*; Scheltema, 1979), and evolutionary studies (Scheltema, 1977, 1978, 1979; Hansen, 1978*a*, *b*, 1980*a*; Jablonski & Lutz, 1979, 1980; Jablonski, 1979*b*, 1980*a*, 1982). Further studies along these lines should be firmly grounded in the biological processes underlying the paleontological data; the links among developmental history, the morphology of the individual, and the temporal and spatial distribution of species (and higher taxa) are complex. Here we will review criteria utilized to infer larval types in fossil material, with emphasis on bivalves and gastropods, and discuss some paleontological implications of this new dimension in our picture of the mode of life of extinct organisms.

II. DEVELOPMENTAL TYPES IN MARINE BENTHIC INVERTEBRATES

Numerous classifications have been proposed for the spectrum of developmental types found in marine benthic invertebrates (cf. Mileikovsky, 1974). The classification employed depends largely on the perspective of the individual investigator. For example, a paleobiogeographer concerned with dispersal capability might emphasize the dichotomy between those larvae that feed on plankton during development and those that do not (planktotrophy *vs.* nonplanktotrophy). Alternatively, such a worker might wish to classify larval forms according to their swimming capabilities (planktic *vs.* nonplanktic). A population ecologist might finely subdivide developmental types according to amount of reproductive effort invested by the parent, while an embryologist might be more interested in the presence or absence of a distinct larval stage (direct *vs.* indirect development). In the present study, we adopt an informal classification of general utility, a modified version of that devised by Thorson (1946, 1950) in the course of his monumental work on marine larval ecology. In such a classification scheme, the various types of larval development fall into two main categories: planktotrophic and nonplanktotrophic larvae. We stress this dichotomy in feeding type because it is readily recognizable using shell morphology in Recent and fossil material, and because planktotrophic larvae often have a prolonged planktic stage and thus high dispersal capability. Nonplanktotrophic larvae may be planktic or nonplanktic, and in either case will generally have a lower dispersal capability than planktotrophs. This classification, which is briefly discussed in the following paragraphs, is not all encompassing; intergradations, exceptions, and combinations of two or more developmental types within a single life cycle render the presented scheme as artificial as any other simple pigeonholing of the complexity of the natural world. An extreme example of difficulties encountered is found in the ascoglossan opisthobranch *Elysia cauze*, in which development varies seasonally within a single population, with planktotrophic, planktic lecithotrophic, and nonplanktic lecithotrophic ('direct') development occurring in sequence every year (Clark *et al.*, 1979) (see Eyster, 1979, and Williams, 1980, for other perplexing examples among the opisthobranchs). Furthermore, organisms with similar development can exhibit considerable variation in other life-history characteristics (e.g., Switzer-Dunlap & Hadfield, 1979).

(1) *Planktotrophic larvae*

Planktonic, or more properly ***planktic*** larvae (see Martinsson, 1975), spend a significant portion of their development time swimming freely in surface waters. *Planktotrophic* planktic larvae depend on smaller planktic organisms (and possibly organic detritus) for nutrition. This involves development of complex structures that function in locomotion and feeding, all of which are lost or resorbed during metamorphosis when the larva settles and assumes a sessile mode of life. Eggs are released with little yolk, and thus there is a minimum expenditure per egg per parent. Species having planktotrophic larvae produce them in great numbers – up to 85000 eggs per individual per spawning in the gastropod *Littorina irrorata* (Bingham, 1972), and up to 70 million eggs per individual in a single spawning of the oyster *Crassostrea virginica* (Davis & Chanley, 1956). Consequently, total parental investment in reproduction can actually be very high despite the relatively low expenditure per offspring (e.g. Chia, 1971; Grahame, 1977).

Predation, starvation, and other factors take a tremendous toll of planktotrophic larvae, with estimated mortality exceeding 99% according to Thorson (1950, 1966; Mileikovsky, 1971). However, the enormous numbers of planktic larvae produced by planktotrophic species counterbalance this extremely high larval mortality. For example, Brousseau (1978) calculated that only 0·0001% of the larvae need survive annually to maintain a population of *Mya arenaria* near Cape Ann, Massachusetts, while Vahl (1981) calculated that larval survival of 0·00005% was necessary for maintenance of a population of *Chlamys islandica* in Balsfjord, Norway.

Orians & Janzen (1974) have pointed out the rather surprising lack of toxicity or other chemical defences in vertebrate eggs. Toxic defences are also apparently rare in marine invertebrates, although a few examples are known (e.g. Lucas *et al.*, 1979; Timko, 1979), and behavioural or morphological defences may be important. Little is actually known about the presumably high mortality present in the early life histories of many marine invertebrates, and it may be that settlement and early post settlement, rather than planktic larval life, are actually the times of greatest mortality (e.g. Thorson, 1950, 1966; Muus, 1973; Turner, 1975; Strathmann, 1975*a*; Woodin, 1976, 1979; Sarver, 1979; and numerous others). This has important implications for the manner in which selective (and stochastic) forces shape benthic populations during larval development, as well as during recruitment and maturation.

A thought-provoking variation on the general pattern of high early post-settlement mortality is described by Underwood (1976) for the intertidal gastropod *Nerita atramentosa*, which appears to exhibit intraspecific competition for trophic resources. At high population densities, juveniles were able to maintain themselves, without growth, while adults were unable to acquire sufficient food for maintenance and died. Underwood thus concluded that in the event of a large settlement of planktic larvae, mortality of adults might occur while juveniles remain small on maintenance food intake until the densities of adults decline (although this means that juveniles would take longer to find a size refuge from predation and other sources of mortality – an effect that might not be evident in caging experiments such as those conducted by Underwood). By way of contrast, we can cite the intraspecific interactions of the intertidal limpet *Patella cochlear* studied by Branch (1975). Larvae (nonplanktotrophic in this species) settle throughout the intertidal zone, but only survive on the backs of adult limpets, where they are not killed by the grazing activities of the adults (see Underwood, 1979, for discussion of these and many other examples).

Scheltema (1967) divided the planktic stage of planktotrophic species into two phases: (1) growth and development (the 'pre-competent period' of Hadfield, 1978, and Jackson and Strathmann, 1981), followed by (2) a 'delay period' ('competent period') in which development is essentially completed, but larval adaptations for a planktic existence are retained until a substratum suitable for settlement is found. Scheltema (1971*a*, p. 306) further comments that "it is the delay period which gives to many species the greatest flexibility in the length of their larval life," since this stage may last from a few minutes to over 3 months, depending on the species. It is interesting to note that Pechenik (1980), in his study of gastropod larval energetics, found that the duration of the competent period was inversely related to the species' rate of growth; this effect may also be seen within species (e.g. temperature-controlled changes in growth rate; Bayne, 1965; Lutz & Jablonski, 1978*b*). Jackson & Strathmann (1981) predicted that there will be an increased competent period with increased pre-competent period among species, and that the competent period will be greater than or equal to the pre-competent period. For the most part, available data coincide with their models, supporting the hypothesis that, since transport of larvae during a lengthy pre-competent period may move them away from suitable substrata, a long delay period is required to enable the larvae to encounter suitable settlement sites once they are capable of metamorphosis. The complex process of selection of settlement sites suitable for metamorphosis is reviewed by Meadows & Campbell (1972), Scheltema (1974), Crisp (1974*a*, 1976*a*), Buss (1979), and Underwood (1979).

The ability of planktotrophic larvae to subsist on planktic food not only obviates the need for deposition of large quantities of yolk in the egg as an energy source for the developing larvae, but also allows a long planktic larval duration for many species. The evolutionary success of this mode of development is indicated by Thorson's (1950) estimate (see also Mileikovsky, 1971) that 70% of all benthic marine species undergo planktotrophic development. In temperate-water species, this planktic stage generally lasts from 2 to 6 weeks (Thorson, 1961); Scheltema (1977) has pointed out that during this period an ocean current of only 0·5 km/h could carry a larva 150–550 km. Other species, notably among the tropical benthos, can remain in the plankton for 6 months or more, and thus may be carried great distances by ocean currents. Larvae of this type have been termed *teleplanic* (Gr. *teleplanos*, 'far-wandering,' Scheltema, 1971*b*). Scheltema (1971*a*, 1977) discussed several tropical gastropod species having larvae capable of traversing trans-oceanic distances, and thus maintaining the amphi-Atlantic distribution of the adults (see also Edmunds, 1977). The ecological and evolutionary implications of a long planktic stage in essentially sessile benthic organisms will be considered in more detail later in this paper.

Demersal larvae undergo development while swimming and/or crawling in the near-bottom water layer, apparently feeding on organic detritus (or microbes?) in the water close to or on the sediment. Some benthic feeding may occur, and inclusion of this larval type within the general planktotrophic category may be inappropriate. The demersal larvae of other species may not feed at all, further invalidating the general inclusion of this mode of development within planktotrophy. Though poorly documented, demersal development is probably important in high-latitude and deep-sea faunas (Pearse, 1969; Mileikovsky, 1971; Clarke, 1979). Demersal development has been demonstrated in a number of polar echinoderms (Pearse, 1965, 1969; Pearse & Giese, 1966), as well as in mid-latitude corals (e.g. Gerrodette, 1981) and polychaetes (e.g. Hardy, 1977), but in only a few molluscan species, including the olivid gastropod *Olivella verreauxi* (which is lecithotrophic; Marcus & Marcus, 1959) and perhaps the related species, *O. biplicata* (Edwards, 1968), the rissoid *Hydrobia ulvae* (Fish & Fish, 1974, p. 696; but see Fish & Fish, 1977), and perhaps the Antarctic limpet *Nacella (patigera) concinna* (Picken, 1980). In high latitudes, this dispersal mode appears to be an adaptive compromise, retaining some of the advantages of free-swimming larvae, while reducing mortality by keeping larvae out of the polar surface waters (Pearse, 1969). Also, benthic dispersal at any latitude would expose larvae to a more stable benthic food resource and temperature–salinity regime compared to the seasonally and diurnally more variable conditions at the sea surface, particularly in nearshore waters (e.g., Levinton, 1974; Hendler, 1977; Whitlatch, 1977, p. 289; McCall, 1978).

(2) *Nonplanktotrophic larvae*

Lecithotrophic larvae are nourished by the yolk of the eggs from which they develop (and thus are nonplanktotrophic). Such larvae are either entirely nonplanktic or remain in the plankton for little more than a few hours to a few days (Thorson, 1950, 1961). Clearly, reproductive effort per offspring is generally much higher, and larval mortality much lower (assuming mortality is in some way correlated with duration of planktic period), than in planktotrophic species. Accordingly, far fewer eggs per parent are produced (4100 eggs per parent in the bivalve *Nucula proxima* and 1200 in the related species *N. annulata*: see Scheltema, 1972). Thorson (1950, p. 11) stated that this mode of development is absent in marine gastropods, but this has proven not to be the case (recorded so far in Patellidae, Acmaeidae, Trochidae, Olividae, Muricidae, and Conidae: Natarajan, 1957; Marcus & Marcus, 1959; Kohn, 1961; Fretter & Graham, 1962; Anderson 1962, 1966; Gohar & Eisawy, 1967; Eisawy, 1970; Underwood, 1972, 1979; Spight, 1977; Gallardo, 1981; Heslinga, 1981; Perron, 1981*a*, *b*; Rex & Warén, 1982).

So-called 'mixed development' occurs when early developmental stages are encapsulated but later stages emerge as free-swimming, pre-metamorphic larvae (Pechenik, 1979; see also Caswell, 1981). Mixed development is prominent in several benthic marine groups, including the polychaetes and gastropods, and capsule production may constitute a significant proportion of the reproductive effort of the parent (up to 50% in the nonplanktotrophic gastropod *Conus pennaceus*: Perron, 1981*c*). Evidence compiled by Pechenik (1979) indicates that it is not tenable to generalize that encapsulation of early molluscan growth stages serves to provide food, prevent desiccation, protect embryos against predation or bacterial attack or maintain relatively stenotopic early stages in more favorable environments than those potentially encountered by hardier later (veliger) stages. Rather, he suggests that passive, small, unshelled embryos may be significantly more susceptible to predation than active, larger, shelled veliger larvae, so that delayed release could significantly reduce the mortality of early growth stages. Planktotrophic feeding capability also increases with size, both in terms of feeding rate and size range of available particles (Strathmann & Leise, 1979); this may be an additional advantage of encapsulation of early growth stages of species undergoing planktotrophic development.

In contrast to species having lecithotrophic larvae with a planktic (or demersal) phase, oviparous species have lecithotrophic larvae that develop entirely within an egg mass or egg case, often attached to a hard substratum. Embryos pass through a lecithotrophic veliger stage, with metamorphosis taking place within the protection of the egg mass, and the offspring emerge as benthic juveniles. This mode of reproduction has been termed direct development (Thorson, 1946, 1950; Mileikovsky, 1971, 1974; Webber, 1977), but as Chia (1974) emphasized, this term should be applied only to species that do not pass through a distinct intermediate stage such as a veliger. Direct development should apply only to the embryos (which may or may not be free-living) that morphologically differentiate gradually into the adult. Certain opisthobranchs (see Bonar, 1978, who uses the term ametamorphic development), most cephalopods (e.g. Boletzky, 1974; Arnold & Williams-Arnold, 1977; Wells & Wells, 1977; but see Fioroni, 1977), the Polyplacophora (according to some authors; see Pearse, 1979), and some echinoderms (Chia, 1974) show true direct development.

Among the higher prosobranch gastropods (Neogastropoda), oviparous species may deposit, along with viable eggs, a supplementary food source in the form of nurse eggs. The ratio of nurse eggs to viable eggs may vary considerably within a species. For example, the gastropod *Buccinum undatum* deposits 50–2000 eggs per capsule, with only 10–30 of these eggs developing into juveniles (Portmann, 1925; see Fioroni & Schmekel, 1976, and Webber, 1977, for tabulations of prosobranch data). Spight (1976*a*) has shown that embryos feeding on nurse eggs show a greater range in hatching size than embryos in which the entire yolk supply is enclosed within their own egg membrane (see also Fioroni, 1966, 1967; Gallardo, 1979*a*).

Brooded larvae, characteristic of ovoviviparous species, are retained (sometimes encapsulated) within the parent throughout development, emerging as metamorphosed juveniles. Thus ovoviviparous species can be regarded as investing the greatest amount of effort in the protection of their offspring during early ontogeny (e.g. Hughes & Roberts, 1980). Accordingly, they often have the lowest fecundities. This developmental type has been termed viviparity (Thorson, 1946, 1950; Mileikovksy, 1971, 1974*a*), but Simpson (1977, p. 128) writes, "...a viviparous condition requires that the developing embryo derives nutriment by close contact with maternal tissues without interposition of egg membranes, for example, as in placental mammals. Surely this must not be the case for the invertebrates frequently listed as viviparous in the literature. Ovoviviparous is the correct term in describing embryos that develop within the maternal organism from which they derive nutriment but are separated from the parent organism by egg membranes for most or all of their development, which is at the expense of yolk. It is an important distinction."

True viviparity may be present in some marine invertebrates, e.g., the ophiuroid *Amphipolis squamata* (Fell, 1946). Perhaps most remarkable is Bartlett's (1979) description of papillae in the inner surface of the gills of brooding female *Parastarte triquetra*; these structures apparently serve to hold developing embryos within the gill chamber, preventing premature release and may play a nutritional role as well, resulting in true viviparity in these bivalves. Purchon (1968, pp. 307–313) cites a number of examples that might be regarded as intermediate between ovoviviparity and oviparity, in which eggs are attached, and developing embryos are carried, on the surface of the

Table 1. *Comparison of terminologies for marine invertebrate larvae*

	Thorson (1950), Ockelmann (1965)	Scheltema (1978), Crisp (1974*b*)	Shuto (1974), Strathmann (1978*a*)	Jablonski & Lutz (1980)
Free-swimming, feeding larvae	Planktotrophic	Pelagic	Planktotrophic	Planktotrophic
Free-swimming, non-feeding larvae	Lecithotrophic		Lecithotrophic	Nonplanktotrophic
Offspring emerge as benthic juveniles	Direct development	Non-pelagic		

shell or on the body of the parent (see Lindberg & Dobberteen, 1981, for gastropod examples). Such developing embryos might be placed, somewhat arbitrarily, in the general category of *brooded larvae* (see also Matveeva, 1978; Sastry, 1979).

(3) *Planktotrophic/nonplanktotrophic classification scheme*

Our dichotomous classification of larval types differs in some respects from those previously used, but we feel it represents a useful compromise between several conflicting sets of terminologies (see Table 1). In his classic papers on larval ecology, Thorson (1946, 1950, 1961) employed a classification based firstly on pelagic and nonpelagic categories; within the pelagic category he recognized planktotrophic and lecithotrophic development, and within the nonpelagic category direct and viviparous development. Most subsequent workers have used one or another modified version of Thorson's scheme (Mileikovsky, 1974).

A common terminology in recent years recognized three basic categories derived from Thorson's scheme: planktotrophic, lecithotrophic (meaning non-feeding but with a free-swimming stage), and direct development; widely cited papers include Ockelmann (1965) on bivalves, Thompson (1967) on opisthobranchs (see also Todd, 1981), Strathmann (1974*a*) on echinoderms (the terms planktotrophic, lecithotrophic, and brooded), and Vance (1973*a*, *b*) on theoretical models. This trichotomous division has prevailed despite the recognition that in most mollusks "direct" development is not truly direct (see above) and, in fact, "development of these species is lecithotrophic" (Sastry, 1979, p. 233). We feel that for paleontological (and many other) purposes the most useful and logical scheme can be based firstly on larval feeding capability; hence, planktotrophic *vs.* nonplanktotrophic. Our nonplanktotrophic category, then, includes the two main lecithotrophic modes under a single heading.

In adopting this dichotomy we follow Shuto (1974), except that he used the terms planktotrophic and lecithotrophic (which included "direct" development) (as did Rex & Warén, 1982 who were also studying prosobranch gastropods). Strathmann (1978*a*, *b*) also used a dichotomy in his discussion of the evolution of marine invertebrate larvae, again as planktotrophic *vs.* lecithotrophic. Because 'lecithotrophic' has long been understood to imply the presence of a planktic stage, we would replace Shuto's and Strathmann's expanded usage of the term with a more neutral term, nonplanktotrophic (although they are, we recognize, etymologically correct).

Scheltema (1977, 1978, 1979), in his models of the evolutionary significance of larval ecology, uses a pelagic/nonpelagic (planktonic/nonplanktonic) dichotomy, as does Crisp (1974*b*). Scheltema ultimately distinguishes among three kinds of species, however: (1) those having teleplanic larvae, (2) those with planktic stages of 3 to 6 weeks, and (3) "species with a very short or completely lacking pelagic stage (i.e., lecithotrophic development)" (Scheltema, 1978, p. 313; see also p. 314). Similarly, Hansen (1980*a*, p. 194) uses the term planktic for species having planktotrophic larval development, and the term nonplanktic to "indicate species whose development is lecithotrophic, direct, or ovoviviparous." Although these authors were discussing neogastropods, in which most nonplanktotrophic species are indeed nonplanktic, we feel that this terminology could be confusing since nonpelagic or nonplanktic categories as used by these authors include at least some free-swimming larvae, and that their models can readily be accommodated within the terminological scheme used here.

Finally, as mentioned previously, the planktotrophic/nonplanktotrophic dichotomy is a practical subdivision for paleontological research. Modes of larval development are recognized in fossil mollusks on the basis of larval shell morphology, and, as discussed below, this character reflects presence or absence of a yolk supply. This, in turn, is related to dispersal capability, and all evolutionary models on the significance of larval ecology ultimately recognize the importance of low-dispersal, nonplanktotrophic larvae, effectively grouping species having this mode of development into a single category.

III. RECOGNITION OF DEVELOPMENTAL TYPES IN FOSSIL ORGANISMS

(1) *Mollusca*

The best-suited organisms for inferring developmental histories from fossil material are the Mollusca. Firstly, early larval stages are calcified and retained as the organism grows. Secondly, one of the fundamental dichotomies in larval adaptation, the presence or absence of a yolky food supply during development (nonplanktotrophy *vs.* planktotrophy) affects egg size, which in turn is reflected in the morphology of the larval shell. Consequently, study of both larval and well preserved early juvenile molluscan shells permits inferences to be made concerning type of larval development present in extinct species.

(*a*) *Bivalves and gastropods*

Parallel terminologies are applied to early growth stages in bivalves and gastropods (see discussion by Jablonski & Lutz, 1980). The entire shell formed prior to metamorphosis is designated the *protoconch* in gastropods, and the *prodissoconch* in bivalves; this corresponds to the more general term 'larval shell' as used by most authors. The first shelled stage is the Protoconch I (gastropods) or Prodissoconch I (bivalves), and is apparently secreted by the shell gland, at least at first (Raven, 1966; Carriker & Palmer, 1979; Kniprath, 1979, 1981; Iwata, 1980; but see Waller, 1981). This initial shell is generally unornamented. It has a coarse-grained appearance under the optical microscope, which resolves into a granulated or punctate surface texture under the scanning electron microscope, apparently reflecting loci of shell deposition. Buckland-Nicks *et al.* (1973) suggest that the tubercules on the Protoconch I of the nonplanktic lecithotrophic gastropod *Littorina sitkana* aid in the hatching process. In gastropods, the Protoconch I, which always comprises less than two whorls, has also been called the 'embryonic shell' (e.g. Fretter, 1967; Robertson, 1971). In bivalves, the Prodissoconch I stage is equivalent to Werner's (1939) special usage of the term *veliger*,* which has been followed by many European workers, and to the protostracum of Bernard (1898); on the basis of shape, this stage is also known as the D-shaped or straight-hinged veliger (see Chanley & Andrews, 1971).

The Protoconch II and Prodissoconch II stages represent a different process of larval shell growth. During these stages, shell is added by marginal deposition by the mantle edge (Carriker & Palmer, 1979). Waller (1981), however, has emphasized that the transition from shell gland to mantle calcification is a gradual rather than an abrupt one. He considers the Prodissoconch I/II boundary in bivalves to mark the moment when the valves first completely enclose the body and close against one another. More work is still needed before we fully understand the equivalent features in gastropods.

In gastropods, the Protoconch II when present may range from 1·5 to 8 whorls, and may be smooth to heavily ornamented; in bivalves, ornamentation of the Prodissoconch II is generally restricted to comarginal growth lines (perhaps related to a diurnal endogenous rhythm: Millar, 1968). It is interesting to note that prodissoconchs and protoconchs are apparently always composed of aragonite, even in taxa having calcitic shells as adults (Stenzel, 1964; Carriker & Palmer, 1979; although dahllite has been reported in the Prodissoconch I of *Pinctada martensii* – Watabe, 1956). The post-larval shell is termed the teleoconch (sometimes misspelled 'teloconch') in gastropods and the dissoconch in bivalves. Ornamentation, surface textures, and other features of post-larval shell growth may contrast markedly with the larval shell.

Since there may be little resemblance between larval and post-larval shell morphologies, it is often difficult to place larval gastropods and bivalves in taxa founded exclusively on adult characters. Although some gastropods appear to have protoconch morphologies that are diagnostic at the species level (e.g. Fish & Fish, 1977, 1981; Hansen, 1980*b*), identification of larval or early juvenile shells must generally be based on careful comparison with species of metamorphosed juveniles that have attained an age at which diagnostic shell features are available. The protoconch is often abraded on adult specimens, so it is often necessary to assemble growth series. Excellent figures of Recent gastropod protoconchs, which are very useful for comparative purposes, have been presented in a number of scanning electron microscopic studies (e.g. Robertson, 1971; Rodriquez Babio & Thiriot-Quiévreux, 1974, 1975; Bandel, 1975 *a*, *b*, *c*; Jung, 1975; Richter & Thorson, 1975; Thiriot-Quiévreux & Rodriquez Babio, 1975; Thiriot-Quiévreux, 1980*a*, *b*).

Bivalve larval shells are often abraded in adults, and so growth series are often needed for identification and interpretation of early ontogenetic stages of these organisms (e.g. Turner, 1975; Jablonski & Lutz, 1980, and references therein). Identification of the shells of larval bivalves is facilitated by examination of the larval hinge area (*provinculum*) and associated lateral hinge system. Using optical microscopy, Rees (1950) recognized

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* We prefer to use the term veliger for a shelled molluscan larva that possesses a velum (ciliated swimming organ), an adaptation for a free-swimming existence. This velum is lost or resorbed at the time of final settlement and metamorphosis. Certain species that undergo development through metamorphosis entirely within the confines of an egg capsule nevertheless pass through a veliger phase.

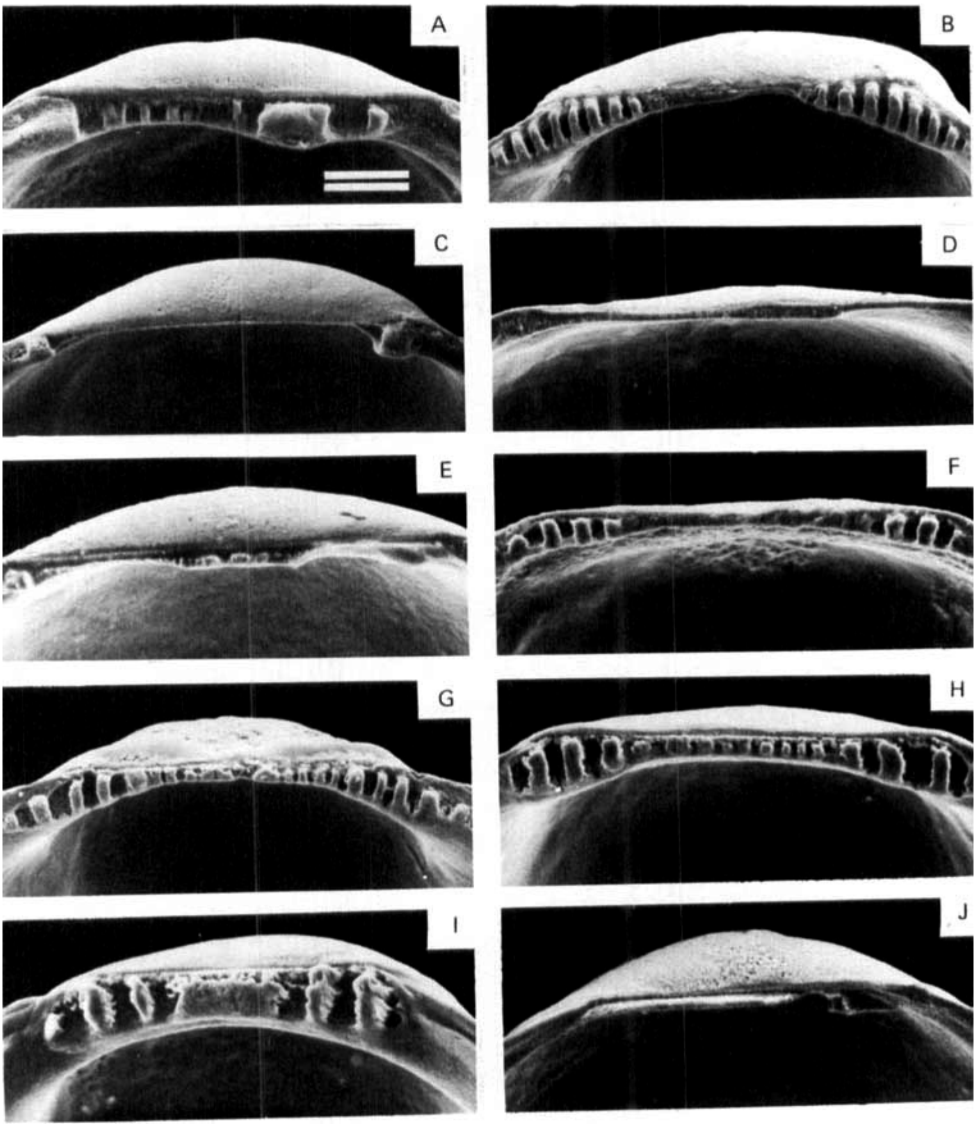

Fig. 1. Scanning electron micrographs of the hinge region of larval shells of ten species of Recent bivalve molluscs, showing characteristic morphologies for nine superfamilies. A, *Spisula solidissima* (right valve) (Mactracea); B *Arca noae* (right valve) (Arcacea); C, *Ensis directus* (right valve) (Solenacea); D, *Arctica islandica* (right valve) (Arcticacea); E, *Mercenaria mercenaria* (Right valve) (Veneracea); F, *Argopecten irradians* (right valve) (Pectinacea); G, *Mytilus californianus* (left valve) (Mytilacea); H, *Geukensia demissa* (right valve) (Mytilacea); I, *Crassostrea virginica* (right valve) (Ostreacea); J, *Mya arenaria* (right valve) (Myacea). Scale bar (= 20 μm) in A is applicable to all micrographs in this figure.

five major provinculum types that are apparently diagnostic at the familial or superfamilial level. However, structural details of the larval hinge apparatus are more readily discerned by scanning electron microscopy (Fig. 1), and may be used to identify bivalves at the generic and specific level in many instances (e.g., LaBarbera, 1974; Culliney & Turner, 1976; Turner & Boyle, 1975; Booth, 1977, 1979*a*, *b*; Le Pennec, 1978, 1980;

Lutz & Jablonski, 1978*a*, 1981; Lutz & Hidu, 1979; Stephenson & Chanley, 1979; Chanley & Chanley, 1980; Chanley & Dinamani, 1980). The phylogenetic significance of larval hinge morphology is unclear and largely unexplored. Larval hinge structures frequently bear little resemblance to the adult hinge morphologies that play such an important part in the higher classification of the Bivalvia.

Shell shape is also important in taxonomic placement of larval shells (Werner, 1939; Rees, 1950; Yoshida, 1953; Miyazaki, 1962; Le Pennec, 1973). Relative prominence of the umbo (in the Prodissoconch II stage) and height/length and length/depth ratios are particularly useful. Chanley & Andrews (1971) provide a glossary and numerous examples of species-level separation on the basis of shape (see also Loosanoff *et al.*, 1966; Stephenson & Chanley, 1979).

The key character in distinguishing between planktotrophic and nonplanktotrophic gastropod larval shells was indicated in Thorson's (1950, p. 33) 'apex theory' which states that "as a general rule, a clumsy, large apex points to a nonpelagic development, while a narrowly twisted apex, often with delicate sculpture, points to a pelagic development." That is, large, rounded, often paucispiral protoconchs indicate larvae that spent little or no time in the plankton, while narrow, polygyrate protoconchs suggest planktotrophic larvae (see also Shuto, 1974)*. Ockelmann (1965) and subsequent authors suggested similar criteria for recognition of developmental type in bivalves based on detailed examination of the morphology of the prodissoconch.

With the increasing application of the scanning electron microscope to larval shell studies (reviewed by Jablonski & Lutz, 1980; Waller, 1981), more precise criteria, with closer direct relationships to the underlying development process can be used. A small Protoconch I or Prodissoconch I (boundary readily discernable with the scanning electron microscope generally derives from a small (60–200 μm), yolk-poor egg; larval development is generally planktotrophic (Fig. 2A, C) (Ockelmann, 1965; Robertson, 1974; Shuto, 1974; Bandel, 1975*b*; Rodriguez Babio & Thiriot-Quiévreux, 1975; Clark & Goetzfried, 1978; Waller, 1981). In bivalves having planktotrophic larvae, the Prodissoconch II, deposited during the veliger stage, is large (200–600 μm in length) relative to the Prodissoconch I (Ockelmann, 1965); a similar relationship may exist in gastropods between the relative sizes of the Protoconch I and the Protoconch II stages (Shuto, 1974; Sohl, 1977).

In contrast, species with lecithotrophic pelagic larvae generally have a relatively large Protoconch I or Prodissoconch I (135–230 μm in length, depending on the species; Ockelmann, 1965; Shuto, 1974; Waller, 1981) reflecting the larger-diameter yolky eggs from which they develop. This initial growth stage may be poorly demarcated, and the Protoconch II or Prodissoconch II stage may be poorly developed (Fig. 2B, D). This probably reflects the short time lecithotrophs spend in the plankton, although a direct relationship between planktic duration and Prodissoconch II size has not been demonstrated quantitatively. Species with larvae lacking a planktic stage (e.g. brooded or encapsulated larvae) have the largest eggs of all, with a Protoconch I or a Prodissoconch I ranging in length from 230 μm to over 500 μm. The initial growth stage of such larvae is often inflated and may show irregular folds and wrinkles (Ockelmann, 1965; Chanley & Andrews, 1971; Bandel, 1975*c*; Matveeva, 1978). Perhaps well

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* Dall (1924) also recognized that protoconch morphology was related to mode of development, but his discussion is cast in terms of specifics rather than a broad generalization; see also Morton (1950, p. 458).

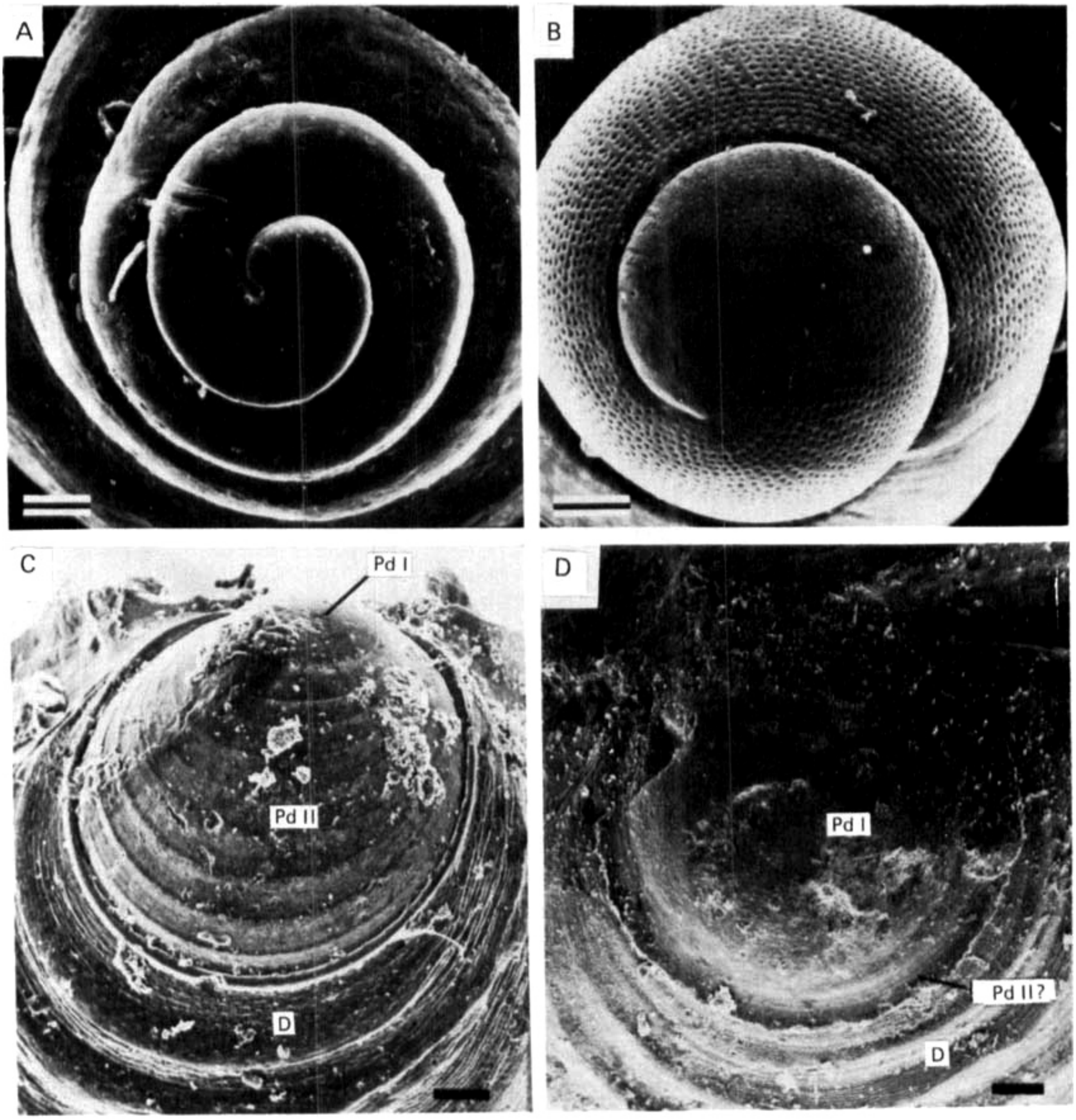

Fig. 2. Scanning electron micrographs illustrating differences in larval shell morphology of extant rissoid gastropods and Late Cretaceous crassatellid and carditid bivalves with different modes of development. A, *Rissoa guerini*, known to be planktotrophic; B, *Barleeia rubra*, known to be nonplanktotrophic; C, *Uddenia texana*, inferred to be planktotrophic; D, *Vetericardiella crenalirata*, inferred to be nonplanktotrophic. PdI, prodissoconch I; PdII, prodissoconch II; D, Dissoconch. Scale for A, B = 50 μm; Scale for C, D = 20 μm. (A, B, from Thiriot-Quiévreux & Rodriguez Babio, 1975; micrographs courtesy of Catherine Thiriot-Quiévreux; C, D, from Jablonski & Lutz, 1980.)

developed tubercules on the Protoconch I, such as have been suggested as aiding in the hatching process of *Littorina sitkana* (Buckland-Nicks *et al.*, 1973) might be a useful character for recognition of encapsulated gastropod larvae, which are generally nonplanktic (notable exceptions include *Coralliophila* spp. which have tuberculated protoconchs despite the fact that the planktotrophic larval stage is preceded by an encapsulated larval stage present during early development; Wells & Lalli, 1977). In some gastropods that emerge from the egg capsule as metamorphoses juveniles (*Buccinum undatum* and *Xancus angulatus*: Bandel, 1975*d*; *Cymbium pepo* and *Cymbium marmoratus*: Bratcher, 1978), the larva does not produce a calcified shell until just prior to hatching. This may account for the unusual appearance of these protoconchs.

Other clues to brooding behaviour may be found in the fossil record. The occurrence of large numbers of juvenile shells inside the shell of a conspecific adult has led to inferred ovoviviparity in at least six Neogene species of the gastropod *Turritella* (Burns, 1899; Sutton, 1935; Palmer, 1958; Marwick, 1971; Antill, 1974; unpublished data of the senior author). A similar phenomenon was reported in *Nassarius ficaratiensis* from the Pleistocene of Italy and in three related living species by Adam & Gilbert (1974, 1976; see also Kaicher, 1972; Cather, 1973). It is sobering to note that umbilical brooding in the Recent trochid gastropod *Margarites vortificerus* results in such marked sexual dimorphism that males and females were described as separate species (Lindberg & Dobberteen, 1981). In an occurrence seemingly analogous to the fossil brooding gastropods, D. R. Lindberg (pers. comm.) has found specimens of the Pliocene bivalve *Transennella* packed with young. Also in the Bivalvia, inferred sexual dimorphism in the form of shell convexity differences is attributed to a brooding habit in Cenozoic *Venericardia* and *Astarte*, by analogy with similar dimorphism in extant relatives (Heaslip, 1968, 1969; Kauffman & Buddenhagen, 1969; Kelley, 1980).

Shuto (1974) has made some empirical observations concerning correlations between gastropod protoconch morphology and mode of larval life. The ratio of the maximum diameter (D; in mm) to the number of whorls or volutions (Vol) was found to be greater than 1·0 for species with lecithotrophic larvae. Most protoconchs with D/Vol between 0·3 and 1·0 and less than 2·25 volutions also belong to species having lecithotrophic larvae, while larvae of species with D/Vol values less than 0·3 and with more than 3 volutions are generally planktotrophic. D/Vol values between 0·3 and 1·0 and with less than 3 volutions are found in species with planktotrophic larvae, as well as those with lecithotrophic larvae. These criteria, and the Protoconch I diameters cited above, were derived from observations on prosobranchs. Similar relationships prevail among opisthobranchs as well (Thompson, 1967; Rodriguez Babio & Thiriot-Quiévreux, 1975; Bonar, 1978; Clark & Goetzfried, 1978) with the exception of species within the Order Ascoglossa, which exhibit an unusual mode of embryonic nutrition involving albumen as a nutritional supplement (Clark & Goetzfried, 1978; Clark & Jensen, 1981).

Shuto (1974) also considered certain types of protoconch ornamentation, such as close brephic axials and fine cancellate and reticulate ornamentation, to be indicative of planktotrophy. Such ornamentation probably serves to strengthen the shell against the rigors of a more or less prolonged free-swimming interval (see also Bandel, 1975*b*, *c*). A sinusigera lip on the larval aperture (evident in later life as the protoconch–teleoconch boundary) accommodates the extended velar lobes of the larva and is best developed in teleplanic larvae (see also Robertson, 1974; Rex & Warén, 1982).

Finally, the most dependable method of distinguishing planktotrophic from non-planktotrophic developmental types (using protoconch morphologies) is the comparative approach advocated by Scheltema (1978, 1979; see also LaBarbera, 1974). In order to assess the mode of development, larval shells of a given species should be compared to those of a congeneric or confamilial species whose developmental characteristics are known. At these taxonomic levels, congruence of shell morphology probably indicates similarity of developmental history. Such comparative approaches are particularly important if egg size distributions tend to be skewed unimodal, rather than a more clear-cut bimodal distribution corresponding to developmental types (see Perron & Carrier, 1981). The comparative approach can yield other benefits as well. Perron (1981*b*) has recently made the intriguing suggestion, based on studies of Hawaiian *Conus*, that among related species Protoconch I size is inversely related to minimum planktic duration. For useful compilations of the taxonomic distribution of larval types in bivalves and gastropods, see Radwin & Chamberlin (1973), Taylor (1975), Beeman (1977), Webber (1977), Andrews (1979), Sastry (1979), Jablonski & Lutz (1980), and Spight (1981).

Use of a comparative approach for inferring larval ecology is complicated by the reported occurrence, in a few studies, of intraspecific variation in larval types or poecilogony (reviewed most recently by Robertson, 1974, Spight, 1975, and Bonar, 1978). The best-documented are among Hawaiian vermetid gastropods, in which the nonplanktotrophic larvae of certain species can be brooded until metamorphosis or can be released for a brief planktic interval. Such developmental variations within the major modes, which may be relatively insignificant for differences in dispersal capability, can be effected by simple changes in the timing of larval escape or release.

Many other supposed examples of poecilogony have, on closer scrutiny, proven to be due to unrecognized cryptic or sibling species, as with the polychaete *Capitella capitata* (see Grassle & Grassle, 1974, 1977) and the gastropods *Littorina saxatilis* (see Heller, 1975), *Rissoa membranacea* (see Rehfeldt, 1968; Robertson, 1974), and *Calyptraea dilitata* (see Gallardo, 1977, 1979*b*). Consequently, simple examples of apical polymorphism within gastropods within gastropod morphospecies (e.g. Verduin, 1977) are difficult to interpret. Other recently reported examples of possible poecilogony among the gastropods include: the prosobranchs *Littorina rudis* and *L. saxatilis* (ovoviviparous *vs.* oviparous nonplanktotrophic; Caugant & Bergerard, 1980; Roberts & Hughes, 1980; but see Hannaford-Ellis, 1979), *Modulus modulus* ('direct' *vs.* indirect development; Houbrick, 1980*a*), *Tonna galea* (planktic *vs.* nonplanktic development; Penchaszadeh, 1981), and *Alvania cimex* (planktic *vs.* nonplanktic; Thiriot-Quiévreux, 1980*b*); the nudibranchs *Tenellia pallida* (planktic, perhaps planktotrophic *vs.* nonplanktic, nonplanktotrophic; Eyster, 1979), *Spurilla neapolitana* (planktotrophic *vs.* nonplanktotrophic; Clark & Goetzfried, 1978), *Cuthona nana* (planktotrophic *vs.* nonplanktotrophic; Brown, 1980), *Aeolidia pagillosa* and *Hermissenda crassicornis* (planktotrophic *vs.* nonplanktotrophic; Williams, 1980); and the pyramidellid *Boonea impressa* (planktotrophic *vs.* nonplanktotrophic: Robertson & Mau-Lastovicka, 1979). Most of these variations in larval types are accompanied by differences in protoconch or egg sizes. Disheartening to the larval paleoecologist, however, is R. Robertson's report (pers. comm., 1979) that planktotrophic and lecithotrophic *Boonea* have identical protoconchs.

(*b*) *Cephalopods*

All modern-day cephalopods apparently undergo true direct development, in which a distinct larval stage is lacking (e.g. Boletzky, 1974; Arnold & Williams-Arnold, 1977; Wells & Wells, 1977; Bandel & Boletzky, 1979). The juvenile that hatches from the large, yolky egg (ca. 1 mm in diameter in most sepioids) may or may not pass through a planktic lecithotrophic existence before adopting the typical schooling or sedentary mode of life of the adults (e.g. Mangold & Fioroni, 1970; Boletzky, 1977; Fioroni, 1977). When present, this intermediate growth period has been called the 'larval' or 'pseudolarval' stage by various authors. In some groups a brief interval of accelerated growth involving some rapid changes in body proportions has been termed 'metamorphosis', but the application of such terms is imprecise and inadvisable. Recently, Fioroni (1977) and Nesis (1979), following a rather restricted definition of 'direct development', stated that because cephalopods develop and then lose organs for dealing with yolk, they should not be regarded as direct developers. Nevertheless, there is no doubt that cephalopods do not undergo the profound morphological reorganization known as metamorphosis that has been observed in other molluscan classes.

Little is known of the early development of the chambered *Nautilus*, which provides the living analogue for the shelled cephalopods that constitute such an important part of the marine fossil record. It is generally believed that development in *Nautilus* is direct, with hatching of a free-swimming, miniature adult at a size of about 25 mm. The effects of this event on shell deposition are somewhat controversial; hatching may be accompanied by a growth discontinuity, the nepionic constriction (Willey, 1896, 1897; Blind, 1976; Haven, 1977), or by a change in shell structure and crowding of septa (Eichler & Ristedt, 1966*a*, *b*). The latter authors present isotopic evidence that *Nautilus pompilius* hatches before the nepionic constriction is produced. They suggest that on hatching the juveniles live in warm, and by inference shallow, water (ca. 80–110 m), then migrate to cooler, deeper waters (200–300 m). Davis & Mohorter (1973) collected juvenile *Nautilus* (ca. 25 mm in diameter) living in even shallower water (less than 2 m), but the nepionic constriction was already present. In contrast, Ward & Martin (1980) argue that juvenile stages of *Nautilus* typically inhabit depths exceeding 300 m, also indicating that Eichler & Ristedt's data are actually consistent with hatching being coincident with the production of the nepionic constriction. They further argue that ambient temperatures are reflected by isotopic ratios in shell material deposited only after this stage. The same conclusions were reached by Cochran *et al.* (1981) in the course of their own isotopic studies of *Nautilus pompilius*.

While fossil nautiloid protoconchs may be interpreted along lines similar to those discussed above for their living relative, there exists considerable variation in the early ontogeny of the shells of numerous living and fossil specimens examined to date (Erben, 1964; Erben *et al.*, 1968, 1969), suggesting that there may be a greater diversity of life histories within the nautiloids than has generally been assumed. Kozłowski (1965), for example, has described chitinous vesicles from the Middle Ordovician closely resembling (although smaller than) egg capsules of certain Recent cephalopods.

As with other extinct groups of mollusks, there is considerable difficulty associated with interpreting the early ontogenetic stages of ammonites. The earliest growth stage of ammonites consists of a bulbous initial chamber composed of prismatic aragonite (Erben *et al.*, 1968, 1969; Kulicki, 1974, 1975, 1979; Tanabe *et al.*, 1980; Birkelund, 1981). This is separated from the first whorl by the proseptun, or first septum (discussed by Kulicki, 1975). A second important break in growth is the nepionic constriction of the shell which is produced by thickening of the shell wall ('nepionic swellings' of Kulicki, 1979), about 3/4 to 1 1/2 whorls after the proseptum, depending on the group (see Tanabe *et al.*, 1979, for a tabulation). This also marks the first appearance of nacreous shell structure. Together, the protoconch and first whorl, up to the nepionic constriction, have been termed the *ammonitella* by Drushchits & Khiami (1970).

The ammonitella has been interpreted in conflicting ways by various workers (see review by Kulicki, 1979). Some authors believe that the ammonites underwent indirect development, with a distinct trochophore or veliger stage, like many of the non-cephalopod mollusks (e.g. Erben, 1962, 1964; 1966; Erben *et al.*, 1968, 1969; Markowski, 1971; Kennedy & Cobban, 1976; Lehmann, 1976). In this view, the initial chamber corresponds to the Protoconch I or Prodissoconch I of gastropods or bivalves, respectively, with the pelagic larval life represented by shell growth between the initial chamber and the nepionic constriction. The ammonite initial chamber is relatively large, averaging about 300–600 μm (e.g. Druschchits *et al.*, 1977), suggesting that the larvae may have been nonplanktotrophic. In such an interpretation, the succeeding growth stage would be equivalent to the Protoconch II or Prodissoconch II of gastropods or bivalves, respectively. A shallow ventral sinus in growth lines has been interpreted by Erben (1964, 1966) as accommodating a velum-like larval swimming organ. According to Erben *et al.* (1968, 1969), the nepionic constriction reflects a brief interruption and reorganization of growth at the time of metamorphosis. At the nepionic constriction, there is an abrupt change (or initial appearance) of growth lines, as well as the first appearance of nacreous microstructure and, if present, shell ornamentation (Erben, 1962). Heteromorphic coiling begins at this point as well (Smith, 1901; Drushchits *et al.*, 1977; Birkelund, 1981; Tanabe *et al.*, 1981). Whatever the factors responsible for the nepionic constriction, it is clear that it reflects a significant event in the life history of the ammonite.

An alternative, perhaps more convincing, hypothesis of nonplanktotrophic (in this case, direct) development in ammonites, and one with a closer resemblance to nautiloid developmental patterns, has most recently been championed by Drushchits & Khiami (1970) and Kulicki (1974, 1979); see also Birkelund & Hansen (1974); Drushchits *et al.* (1977); Bandel & Boletzky (1979) and Tanabe *et al.* (1979). Morphological and ultrastructural change following the initial chamber is not as striking as that observed between the first and second stage of bivalve and gastropod larval shell growth; neither shell structure nor surface growth patterns show a discontinuity across this boundary (Kulicki, 1974, 1979; Drushchits *et al.*, 1977). In contrast, there is a distinct change in surface ornamentation at the nepionic constriction in at least some ammonites (Bandel *et al.*, 1982). Thus, it is conceivable that all shell growth prior to the nepionic constriction might have taken place within the egg, with hatching marked by all of the morphological changes associated with this shell feature. The ventral sinus in growth lines mentioned above might be interpreted as reflecting the position of the developing hyponome, rather than the presence of a unique larval organ (see Kulicki, 1979). Amonites, then, could have emerged from an egg capsule as miniature adults without passing through a distinct larval stage, and thus have paralleled the development of the other cephalopods. It is not clear if the Jurassic 'Ammoniten-Larven' reported by Wetzel (1959) had reached the free-living stage. Other intervals rich in ammonitellas with little or no growth after the nepionic constriction include the Oxfordian of Cuba (Kulicki, 1979), the Santonian of Montana (Landman, 1981), and the Maestrichtian of Denmark (Birkelund, 1979). Supposed egg cases of ammonites are also known (see Birkelund, 1981, p. 187), and these fall within size limits similar to those of ammonitellas.

In either of the above interpretations of larval ecology of ammonites, the relatively large diameter of the initial chamber suggests nonplanktotrophic development. It is not known if certain ammonites that might have been nektobenthic as adults (e.g. Kennedy & Cobban, 1976) had planktic or nonplanktic 'larvae,' but a systematic study of initial chamber morphometry might be useful in assessing distributions as reflections of larval dispersal, adult dispersion, or post-mortem transport. For example, the largest initial chambers reported by Drushchits *et al.* (1977) are in the Placenticeratidae (750–1000 μm), suggesting nonplanktic development in this family. In contrast, initial chambers at the small end of the scale, suggesting planktic lecithotrophic development, are present in the Phylloceratidae (220–280 μm), the Lytoceratidae (280–390 μm), and the Ammonitidae (200–350 μm) (see also Tanabe *et al.*, 1979).

(2) *Brachiopoda*

Because of the great paleoecological and biostratigraphic importance of brachiopods, particularly in the Paleozoic, it would be of great value to be able to infer the details of the developmental history of fossilized individuals. Unfortunately, the larvae of articulate brachiopods lack a shell; calcification does not begin until after settlement (see Chuang, 1977). All modern articulate brachiopods for which development is known are nonplanktotrophic, with the larval stage lasting from a few hours to a few days, and in many of these species the larvae are brooded (Senn, 1934; Percival, 1944, 1960; Long, 1964; Rickwood, 1968; Franzén, 1969; Rudwick, 1970; McCammon, 1973; Logan, 1975; Webb *et al.*, 1976; Thayer, 1975). Possible brood pouches have been reported in Devonian *Uncites* (Rudwick, 1964; see Jux & Strauch, 1966, for an alternative interpretation), *Pentagonia* (Dutro, 1971), Pennsylvanian *Cardiarina* (Cooper, 1956), Permian *Megousia* (Ferguson, 1969) and *Amphipella* (Grant, 1981) It is unknown if all Paleozoic articulate brachiopods possessed nonplanktotrophic larvae; in view of the highly cosmopolitan distributions attained by some taxa (e.g. Boucot, 1975), it may be that some did not. Valentine & Jablonski (in press *b*) have suggested that Paleozoic articulate brachiopods may have had planktotrophic larvae because the group exhibited latitudinal gradients resembling those of modern planktotrophs (with a distinct low-latitude maximum), rather than those of modern nonplanktotrophs including living articulates (with a much reduced or absent equatorial diversity maximum).

Noble & Logan (1981) recently suggested that the lack of a strong juvenile peak in the size-frequency distributions of many Paleozoic articulate brachiopod populations, and the dominance of a juvenile peak in many Recent populations, reflect a difference in reproductive behaviour rather than a taphonomic bias. They reasoned that many modern species brood their young, so that most larvae will settle in the immediate neighbourhood of the parent, with subsequent high juvenile mortality through crowding and competition resulting in a death assemblage dominated by juvenile shells. The lack of the juvenile peak in many Paleozoic species, then, would be a reflection of more widely dispersing larvae. However, we do not have sufficient data on Recent nonbrooding articulates to demonstrate that this type of development is indeed accompanied by a size-frequency distribution that resembles the Paleozoic pattern. Even with limited larval dispersal, local population densities may be more a function of settlement behaviour than dispersal powers. For example, although Recent *Terebratella inconspicua* reportedly has a free-swimming nonplanktotrophic larval stage lasting 20–30 hours (Percival, 1944), several of its populations have juvenile peaks (Stewart, 1981).

It is interesting that the soft-substratum death assemblage of *T. inconspicua*, seemingly analogous to many Paleozoic populations, like them does lack a juvenile mode in its size-frequency distribution; dissolution of juvenile shells may be occurring, however (Stewart, 1981). There are certainly not sufficient data to make definitive judgments, and we recommend further investigation of size–frequency distributions, both in living species, and in Paleozoic species inferred to have been brooders.

In contrast to the articulate forms, inarticulate brachiopods undergo planktotrophic development with a shelled larval stage (see Chuang, 1977, for review). These larval stages may be preserved in fossil material (e.g. Chuang, 1971) and Von Bitter & Ludvigsen (1979) have attempted to interpret the ultrastructure of the earliest growth stage, or *protegulum*, of Paleozoic acrotretid brachiopods in terms of larval ecology. The minute circular pits observed on the protegulum, as seen under the scanning electron microscope, may reflect a vesicular periostracum (Biernat & Williams, 1970), or they may be a result of progressive resorption of shell material during planktic larval development (a mechanism for slowing weight increase while increasing the size of the protective shell). Thus, Von Bitter & Ludvigsen (1979) suggest that species having a short planktic larval stage are those exhibiting simple, non-cross-cutting protegular pits, while complex cross-cutting or deep protegular pitting is an indication of a longer planktic larval stage. However, from what is known about reproductive energetics of other marine benthos, it would be suprising if these minute brachiopods (modal adult size approximately 1–2 mm; Rowell & Krause, 1973) could produce sufficient numbers of planktotrophic larvae to ensure successful recruitment. Perhaps the differences in protegular structure reflect brood duration or growth rates rather than duration of planktotrophic existence.

Recently, Lockley & Antia (1980) have reasoned that since numerous and well developed setae seem to aid in flotation in Recent *Discinisca* larvae (e.g. Chuang, 1973, 1977), high capillae densities in the protegulae of fossil inarticulate brachiopods might indicate a lengthy planktonic larval stage. This idea deserves testing in both Recent and fossil forms.

(3) *Bryozoa*

Few bryozoans undergo planktotrophic larval development; for example, Schopf (1977, p. 165) estimates that 95 % of modern cheilostome species have nonplanktotrophic larvae. Little attempt has been made to infer mode of development in fossil bryozoans, but because the planktotrophic form, the distinctive cyphonautes larva (e.g. Atkins, 1955) is generally much smaller than the nonplanktotrophic larvae, it may be possible to distinguish the two modes by measurements of the ancestrula, or initial zooid. One potential difficulty with this approach is mentioned by Cook (1973), who cites several species in which the large nonplanktotrophic larva differentiates into several small founding zooids almost simultaneously. The distribution of such ancestrular complexes needs to be assessed before ancestrular dimensions can confidently be used to infer mode of larval development.

Another means of inferring bryozoan larval ecology is from adult morphology. Polymorphic individuals that are reproductive in function have been identified in all bryozoan orders (Ström, 1977), and in most cases the larvae are brooded. Brood chambers are often calcified, as in the ooecia of cheilostomes and the gonozooids of cyclostomes (cf. Ryland, 1970; Hyman, 1959, pp. 331–345; Silén, 1977). Thus, acquisition of the ovoviviparous habit should be recognizable in at least some fossil lineages; see Stratton (1981) for a review of brood chambers recognized in fossil Bryozoa. It is not clear, however, if absence of skeletonized brood chambers can be reliably taken as evidence for planktotrophic larvae in fossil forms, as Taylor (1979*a*) did for Jurassic *Stomatopora* and McKinney (1979) did for Mississippian *Archimedes*. It is interesting to note that in both studies the species involved exhibited a number of other characteristics placing them near the 'r-selected', opportunistic end of the ecological spectrum. Nevertheless, we should mention that a few species of modern bryozoans are known in which larvae are brooded in noncalcified, external brood pouches (Cook, 1977). Furthermore, brood chambers arise through such a bewildering variety of developmental pathways that recognition of brooding zooids on the basis of morphology can sometimes be very difficult even in living representatives (e.g. Cook, 1979).

An ingenious inference of bryozoan larval type based on adult morphology was made by McKinney (1981), who found fused colonies of Permian fenestrate bryozoans. Both members of a fused pair were the same size, suggesting that they belonged to the same settlement episode. McKinney reasoned that such intercolony fusions could only take place between larvae that originated from a single fertilized egg (due to constraints of histological compatibility). Such proximity of sibling larvae after settlement seemed most likely if the larvae had very limited dispersal capability; McKinney thus concluded that such fused colonies suggest lecithotrophic development with a very brief planktic stage.

Vía Boada & Romero Díaz (1978) describe some interesting fossils from the Triassic of Spain that they consider to be related to cyphonautes larvae. However, the large size of the specimens (up to 238 mm across) and the lack of decisively diagnostic features make it difficult to accept the suggested affinities.

(4) *Echinodermata*

Although the larvae of certain echinoderms possess a calcified skeleton, most notably in the Echinoidea (cf. Raup, 1966), enchinoderm larvae have not yet been recognized in the fossil record. Skeletal morphology has been shown to be diagnostic in Recent larval forms, however (e.g. Mortenson, 1921; Strathmann, 1979). Interpretation of early growth stages in adult material is hindered by the lack of calcification in some groups (e.g. the Asteroidea), and by the nature of the process of metamorphosis in echinoderms in which the larval skeleton in part forms the nucleus for some of the adult plates and, in part, is resorbed (see Hyman, 1955, for review). As in mollusks, however, it is sometimes possible to infer developmental history in echinoderms through careful examination of adult morphology. Kier (1969) points out that sexual dimorphism is present in modern echinoids only in species in which there is not a free-swimming larval stage. Brooding behaviour is often accompanied by a skeletal modification of the parent (see Boolootian, 1966, for a survey of brooding in the Echinodermata), so that nonplanktic development can be inferred in specimens having a marsupium, a more or less deep depression in the adult test in which juveniles are brooded. To date, a marsupium of one kind or another has been reported from 28 living species of echinoids, including 23 from Antarctic waters and two from Arctic waters (see Philip & Foster, 1971), from five Cretaceous species (reviewed by Kier, 1969) and from twelve Tertiary species (ten from Australia: Philip & Foster, 1971; one from North America: see Kier, 1969; and one from China: Liao & Lin, 1981) we note here that the much-cited '*Brissopneustes danicus*' is considered by Asgaard (1976) to be a *Cyclaster* and non-marsupiate. Marsupia have also been reported in a few living crinoid genera at the junction of the arms and pinnules (see Boolootian, 1966), but such structures have not been convincingly demonstrated for fossil species (Ubaghs, 1978); the Crinoidea are entirely nonplanktotrophic today (Breimer, 1978). Evidence for brooding in the extinct class Blastoidea is presented by Katz & Sprinkle (1976), who found fossilized eggs in the anal hydrospires of the Pennsylvanian blastoid *Penetremites rusticus*. It is not known if the hydrospires, unique and characteristic features of the blastoids, functioned solely as brood chambers, or if their role was primarily, or even solely, respiratory in this group (Paul, 1977).

Müller (1970) has stated that in Recent echinoids, the genital pore diameter reflects egg size and thus mode of larval development, with the dividing line between planktotrophic and nonplanktotrophic larval development being a genital pore diameter of about 1 mm. On this basis, he concludes that Late Cretaceous *Stereocidaris* spp. had planktotrophic larvae (echinopleutei). If Müller is correct in his assertion, this would provide a widely applicable means for distinguishing larval types in another group of marine benthic invertebrates. Clearly this idea deserves further testing, and a survey of genital pore diameter versus developmental mode in Recent echinoids (and other echinoderms?) would be extremely worthwhile.

(5) *Arthropoda*

Although adult arthropods are a significant component of the fossil record, only a few fossilized larval forms have been reported. In part this is because the arthropod skeleton grows through a series of moults, accompanied by postlarval metamorphosis in most cases, so that it is extremely difficult to link larval material with taxa described from adult specimens. Polz (1975 and references therein) describes exuviae (cast off skins) of phyllosoma larvae of decapod crustaceans from the Middle Jurassic Solnhofen limestones of Bavaria; this interpretation, however, has been questioned (Hedgpeth, 1978; but see Bergström *et al.*, 1980). Fortey & Morris 1978) describe phosphatized trilobite larvae, which they term the *phaselus*, from the Early Ordovician of Spitsbergen. The phaselus stage apparently preceded the more familiar protaspid phase (e.g. Whittington, 1957) in ontogeny, and Fortey & Morris (1978) argue that the former is homologous with the crustacean nauplius stage. Other authors have regarded the protaspid and/or early meraspid growth stages of trilobites as planktotrophic larvae (e.g. Cisne, 1973). Neither the phyllosoma nor phaselus larvae have been placed in an ontogenetic series linking them with described fossil species.

IV. DISTRIBUTION OF DEVELOPMENTAL TYPES

The distribution of developmental types found within benthic organisms is clearly not random in modern seas, although we have yet to approach a complete understanding of controlling factors. As data have accumulated on the development of a wide variety of species, some patterns have emerged, and the apparent relationships between larval type and such factors as latitude, water depth, and the ecology of the individual species are briefly discussed in this section. Such distributional patterns are of great significance to the paleobiologist, both as modern models for comparison against ancient distributions and as evolutionary patterns to be explained and perhaps documented during their emergence.

(1) *Relationship to adaptive strategies*

Developmental type appears to be only secondarily determined by phylogenetic relationships. At first glance, the distribution of larval types seems to conform to the predictions of the r–K model for reproductive strategies (MacArthur & Wilson, 1967; Pianka, 1970; Gadgil & Solbrig, 1972; Southwood, 1976; and see Stearns, 1976, 1977, for a discussion and critique). In shallow marine waters, many of the more generalized 'opportunistic' species (supposed 'r-strategists') have a high rate of gamete production, and produce small planktotrophic larvae which receive little or no parental care; populations may show wide annual fluctuations (Thorson, 1950, 1966; Coe, 1953, 1956). Such fluctuations may be due to physical factors (Coe, 1956) and/or biotic factors, including larviphagy and competitive exclusion by adults (Woodin, 1976, 1979; Timko, 1979). The more narrowly adapted 'equilibrium' species (supposed 'K-strategists') tend to produce fewer, larger eggs, invest more energy reserves per offspring and have nonplanktotrophic larvae; Mileikovsky (1971) cites evidence that these species tend to have more stable populations (see also Holland & Polgar, 1976, for an intertidal exmple). This reasoning could be invoked, for example, a an explanation for the presence of planktotrophic larvae in the opportunistic bivalve *Mulinia lateralis* (Levinton, 1970; Calabrese & Rhodes, 1974), and planktic lecithotrophic or nonplanktic larvae in *Nucula* and other protobranchs that are seemingly more K-selected (Rhoads *et al.*, 1978; Cerrato, 1980). Similar reasoning could be followed in explaining the prevalence of nonplanktotrophic larvae in the carnivorous neogastropods, which are at a high trophic level and may be more specialized than many of the mesogastropod groups that have planktotrophic larvae (cf. Radwin & Chamberlin, 1973; Shuto, 1974).

When habitats or trophic resources are predictable, or species are adapted to life within rather narrow environmental limits, survival of offspring is likely to be high if larvae do not disperse any great distance from the parent (see Vermeij, 1972, 1978, on tropical high intertidal gastropods; Hadfield, 1963, on nudibranch development related to prey population structure; Clark & Goetzfried, 1978, on Florida ascoglossan and nudibranch opistobranchs). Selection will also favour low dispersal if suitable habitats are highly restricted geographically, as has been suggested for dominantly nonplanktotrophic gastropod faunas of certain oceanic islands (e.g. Radwin & Chamberlin, 1973; Moore, 1977) and of continental slopes (Red & Warén, 1982; see also Gage & Tyler, 1981, who describe massive non-viable settlement in the abyssal zone by the planktotrophic larvae of the slope ophiuroid *Ophiocten grandis*). On the other hand, if habitats are patchy, or if the parent cannot 'predict' whether its present location is likely to provide a better setting for survival and reproduction of its offspring than some other location, high dispersal is the best strategy (Strathmann, 1974*b*, 1975*a*, but see Palmer & Strathmann, 1981, for a different view; Horn & MacArthur, 1972; Roff, 1975; Obrebski, 1979). Species inhabiting patchy but widespread habitats are thus more likely to have planktotrophic larvae, regardless of 'adaptive strategy' in the classic ecological sense. Strikingly similar arguments were developed independently by Barlow (1981) in

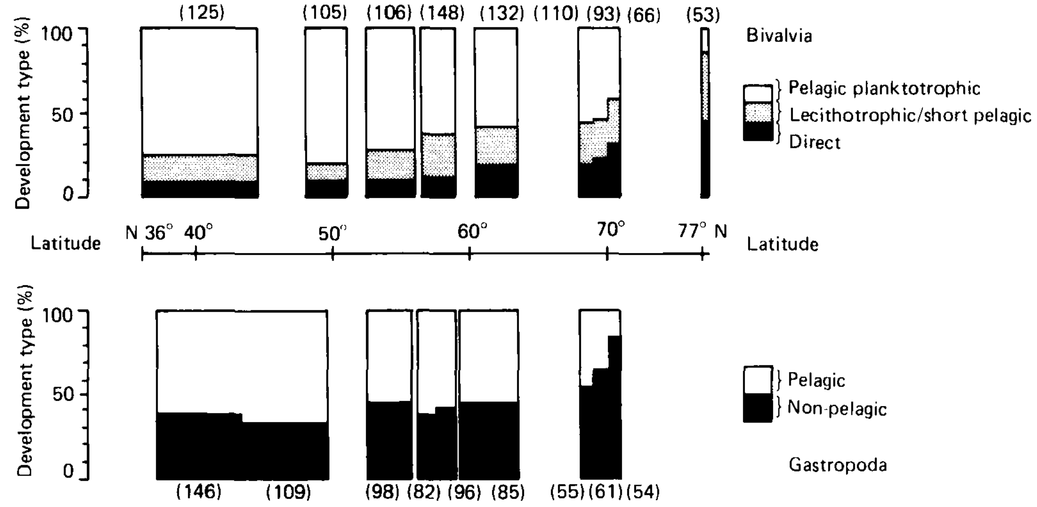

Fig. 3. Molluscan developmental types as a function of latitude on the eastern North Atlantic shelf. Figures in parentheses indicate number of species; bar widths delimit approximate latitudinal coverage of samples, with subdivisions within bars indicating samples with overlapping latitudinal ranges. (From Jablonski & Lutz, 1980; bivalve data modified after Ockelmann, 1965, and gastropod data modified after Thorson, 1965.)

his excellent review of dispersal in coral-reef fishes, and by several authors studying the significance of dispersal in insects (e.g. Davis, 1980; Harrison, 1980).

Another interesting trend in modes of larval development, which seems to conflict with an r–K strategy model, is seen in the latitudinal distribution of developmental types shown in Fig. 3. According to Thorson (1950, 1965), larvae of approximately 57–68 % of the marine prosobranchs from Gibralter to Trondheim on the Norwegian coast are 'pelagic' (planktotrophic or lecithotrophic with a brief planktic stage), while north of this point the proportion of species with pelagic larvae declines until it reaches about 17 % near Murmansk (see also Spight, 1977, on the Muricacea). Ockelmann 1965) reports a similar trend (sometimes called 'Thorson's Rule'; Mileikovsky, 1971) in the eastern Atlantic shelf Bivalvia, with about 75 % of the Gibraltar bivalves having planktotrophic larvae (about 17 % lecithotrophic with a short pelagic stage, and about 8 % nonpelagic), while only 15 % of the Spitsbergen bivalves have planktotrophic larvae (about 37 % pelagic lecithotrophic, and 48 % nonpelagic). Dell (1972) reports a high incidence of viviparity and ovoviviparity in Antarctic benthos as well. Of the 13 Antarctic prosobranchs for which development is known (Picken, 1979, 1980), only one has free-swimming larvae; a similar trend is apparent for the few Antarctic opisthobranchs studied to date (Seager, 1979; see also Richardson, 1979, for a tabulation of Antarctic bivalves that brood).

In his discussion of Antarctic faunas, Dell (1972) points out that brevity or absence of a pelagic stage need not invariably lead to a limited geographic distribution. In Antarctic waters, at least some ovoviviparous species have achieved wide geographic distributions, and he attributes this to passive dispersal by attachment to floating algae (see also Arnaud, 1974; Arnaud *et al.*, 1976; Simpson, 1977; Pearse, 1979). Dell (1972,

p. 163) stresses that the "significance of such a bivalve arriving in a new area with several hundred well developed young ready for release is obvious enough." However, it seems unlikely that this could serve as a general mechanism for widespread dispersal of subtidal benthos, and Picken (1979) states that many subtidal Antarctic invertebrates have restricted ranges and that species endemism is high.

One globally distributed group in which adult, rather than larval, dispersal plays an important role is that of the wood-boring teredinid bivalves. Hoagland & Turner (1980) state that in the Teredinidae, the most successful invading species are those having long brooding stages and short free-swimming stages. Adults are transported within floating wood, and, on release, their brooded larvae can quickly colonize nearby substrata at high densities.

The above observations stand in contrast to our first-approximation assignment of species with planktotrophic larvae to the r-selected end of the adaptive strategy spectrum, and species with nonplanktrotrophic larvae to the K-selected end of the spectrum (see also Valentine & Ayala, 1978; Christiansen & Fenchel, 1979). The latitudinal pattern may be more consistent with the predictions of a stochastic model for the evolution of life history strategies (e.g. Murphy, 1968; Schaffer, 1974; Stearns, 1976 (the 'bet-hedging model'), 1977; Barclay & Gregory, 1981). Such a model suggests that where juvenile mortality is more variable and greater than adult mortality, organisms with delayed reproduction, low reproductive efforts, and a few young are favoured. Thus, for species or situations in which fluctuations in population densities result primarily from fluctuations in survival of early growth stages, evolution will lead to a complex of characteristics more typical of K-selection than of r-selection regimes. This may be the case in high-latitude mollusks, where harsh conditions in surface waters (salinity fluctuations; short, intense bursts of phytoplankton production; low temperatures, etc.) might lead to unusually high planktic larval mortality. Conversely, in situations where adult mortality fluctuates more than juvenile mortality, so-called r-selected traits would be expected. Although such stochastic models do afford some predictive capabilities, patterns associated with marine invertebrate reproductive strategies are often exceedingly complex and considerably more work is required before these complexities can be adequately characterized in a unifying model. Thorson (1950) actually attributed the latitudinal pattern in marine invertebrate larval types to the timing of primary production (for critique, see Menge, 1975, and Clark & Goetzfried, 1978); phytoplankton blooms become progressively shorter in duration at high latitudes and thus time available to planktotrophic larvae for completion of growth and metamorphosis is progressively restricted. This problem is compounded by the slower metabolic and developmental rates brought about by the colder water temperatures of high latitudes (e.g. Strathmann, 1975*a*; Vermeij, 1978), which might also indirectly contribute to increased larval mortality by depressing developmental rates and thus prolonging the duration of exposure to predation while in the plankton (Vance, 1973*a*; Picken, 1980; Christiansen & Fenchel, 1979). Strathmann (1975*a*) has also suggested that selection for larger size at the beginning of benthic life could result in a shift from planktotrophy to nonplanktotrophy.

Clark & Goetzfried (1978) report that ascoglossan and nudibranch opisthobranchs in Florida show a higher incidence of nonplanktotrophy than those of Great Britain or southern New England – the opposite to the general trend observed by Thorson (1950).

They believe that this is due to the trophic stability of Florida waters, which relaxes selection pressure for high, opportunistic dispersal capability and thus favours the energetically more efficient nonplanktotrophic mode of development.

Thorson's (1950) observation of an increase in the proportion of pelagic to nonpelagic larvae from temperate to equatorial waters could, in part, have been an artifact of the faunas studied to that date (Radwin & Chamberlin, 1973). Thorson's original data were obtained from the Persian Gulf (the waters of which are subject to unusually high temperatures and salinities) and oceanic islands (Bermuda, and the Canary Islands, in which initial colonization would likely have been limited to planktotrophic species). Unless mainland species were fortuitously transported to the isolated islands, say by rafting or human activities, the only nonplanktic developmental histories present would have to evolve *in situ*. The fact that any species with nonplanktic development are found on oceanic islands probably testifies to the intensity of selection favouring this developmental type. Curtailment of the planktic phase could be an adaptation to avoid mass loss of larvae which might otherwise be carried by prevailing currents away from the islands and into the open ocean. This may explain why young oceanic islands, such as Ascension Island, tend to have a benthic fauna with predominantly planktic larvae (Rosewater, 1975; Pawson, 1978) while older islands have a higher proportion of species with nonplanktic larvae (cf. compilations of Thorson, 1965; Radwin & Chamberlin, 1973); suppression of a pelagic naupliar stage in certain insular balanomorph barnacles may also have a similar basis (cf. Newman & Ross, 1977). The landward component of near-bottom coastal water movement may also play a role in preventing larvae from being lost to the open ocean (see Scheltema, 1975*a*).

The doubts concerning the applicability of 'Thorson's Rule' are partially alleviated by Spight (1981), who presents some preliminary results of what will be the most thorough survey of latitudinal distribution of developmental types for marine invertebrates. His compilation of data for over 1100 species of gastropods supports Thorson's original observations, although a steep decline in planktic development is detectable only above latitudes of 40°N or 40°S; evidence for latitudinal gradients at lower latitudes is ambiguous. Of the 59 prosobranch families, only seven showed a pronounced change from planktic to nonplanktic larval development with increasing latitude. However, these families (e.g. Buccinidae), together with families that contain both larval types throughout their latitudinal ranges (e.g. Turridae), are the most important constituents of high-latitude faunas (Taylor & Taylor, 1977; Spight, 1981). It is perhaps surprising that exclusively nonplanktic groups are restricted to low latitudes, as are many families characterized by exclusively planktic larval development. It is unfortunate, however, that Spright's literature survey was not able to distinguish between planktotrophic and nonplanktotrophic modes of development, as opposed to a simple planktic/nonplanktic dichotomy.

Much further work is needed on latitudinal patterns in modes of larval development, both in the form of data accumulation, and with regard to possible sampling biases. For example, Clark & Goetzfried (1978), in discussing the anomalous latitudinal pattern in development in the Ascoglossa and Nudibranchia, suggest that there may actually be a general tendency toward nonplanktotrophy in other groups of opisthobranchs as well, but that because species with nonplanktotrophic larvae have lower fecundities, their reproduction may tend to be overlooked (particularly if surveys emphasize plankton tows).

(2) *Relationship to depth*

Among the mollusks, a trend from planktotrophy to nonplanktotrophy is also seen along intertidal–outer shelf transects (Jackson, 1974; Bandel, 1975*b*; Jablonski, 1980*a*; Jablonski & Valentine, 1981; Rex & Warén, 1982; Valentine & Jablonski, in press, *a*), as well as along transects from the subtidal shelf to the deep sea. Thorson (1950) predicted that deep-sea mollusks would dominantly show 'nonpelagic' nonplanktotrophic development, with planktotrophic development being least common. More recent studies have shown that lecithotrophy (with a brief, free-swimming, but nonfeeding, stage) is the most common mode of development among deep-sea bivalves (Ockelmann, 1965; Knudsen, 1970, 1979; Scheltema, 1972; Sanders & Allen, 1973, 1977; Lightfoot *et al.*, 1979; Rokop, 1979; Oliver & Allen, 1980). Despite this low dispersal capability, the relatively broad distribution of deep-sea bivalve species (Scheltema, 1972; Allen, 1978, 1979) suggests that this mode of development is sufficient for maintenance of gene flow and recruitment over wide areas of the deep sea; dispersal in homogeneous and rarely disturbed environments could proceed in a step-wise fashion over long periods of time. It is interesting to note that no brooding molluscan species have been reported from the deep sea.

In contrast to the bivalves, incidence of planktotrophy apparently increases in prosobranch gastropods beyond the continental slope. Bouchet (1976), Bouchet & Warén (1979) and Rex & Warén (1982) have used the criteria discussed here to infer planktotrophic development from shell morphology for a large number of deep-sea North Atlantic prosobranchs (see also Fechter, 1979; Houbrick, 1980*b*). Bouchet & Warén (1979) estimated that about 30 % of northeast Atlantic gastropods living at depths greater than 1000m have larval shells indicating planktotrophic development. Furthermore, Rex & Warén (1982) found that the percentages of prosobranch species and individuals having planktotrophic development both increase dramatically with depth (beginning at the continental rise) in the northwest Atlantic. They suggest that selective pressures favouring high dispersal in deep-sea prosobranchs might include their relatively low population density compared to other deep-sea taxa and their role as predators in vast habitat areas in which food may be temporarily and spatially patchy (though some deposit-feeding species are also planktotrophic; see also Rex *et al.*, 1979). Bouchet (1976) believes that the larvae of these species rise to feed in the photic zone, allowing gene flow among populations separated by major bathymetric features such as the mid-Atlantic ridge. It is not obvious how the larval shells of planktotrophic planktic species and demersal species might be distinguished if both types of larvae are capable of feeding during development (both types would be expected to possess similar protoconchs). In an ingenious response to this problem, Bouchet & Fontes (1981) studied stable isotopes in the shells of four deep-sea species and found evidence that the larval shells of three of them grew at different temperatures and in different water masses from the adult shells, suggesting that at least some vertical migration had taken place. Feeding planktic or demersal larvae are also found in deep-sea mollusks that inhabit rare or transient environments, such as decomposing wood (Turner, 1973), seagrasses (Wolff, 1979), and hydrothermal vents (Lutz *et al.*, 1980). However, seagrass-exploiting cocculinacean gastropods, regarded by Wolff (1979) as opportunists, are archaeogastropods and thus unlikely to possess feeding larvae (as also suggested by their protoconch morphology); the same is true of the deep-sea limpet *Pectinodonta*

(D. R. Lindberg, personal communication, 1982). Much less is known about life histories in other deep-sea groups. Some arthropod taxa brood their young (e.g. peracarid crustaceans) (Hessler, 1970; Gardiner, 1975; Sanders, 1977), while at least some ophiuroids apparently undergo planktotrophic development (Schoener, 1972; Tyler, 1980; Tyler & Gage, 1980; but see Hendler, 1975, who argues that they may be planktic lecithotrophic). Much more work needs to be done before generalizations can be made constructively and, as Rex *et al.* (1979, p. 187) conclude, "It may be no more meaningful to speak of a typical deep-sea reproductive strategy than it would be to typify a single shallow water or terrestrial strategy."

(3) *Relationship to body size*

Also underlying the distribution of larval types in marine organisms is the relationship between body size and mode of development (which, of course, need not be mutually exclusive with the relationship between life history traits and development). Because of the great larval mortality associated with planktotrophy, species following this developmental mode must release immense numbers of larvae. As body size becomes small, so does the absolute amount of energy available for reproduction (Giesel, 1976). Thus, below a certain size, species may be unable to produce enough planktotrophic larvae to ensure recruitment to (and, hence, maintenance of) the population(s). Here, the most efficient strategy is to invest a greater proportion of energy per offspring in a few eggs that have a relatively good chance of surviving to complete their development (Mileikovsky, 1971; Arnaud, 1974; Chia, 1974; Menge, 1974, 1975; Gould, 1977; Hoagland, 1977; McCall, 1977; Simpson, 1977; Nott, 1980). For example, Sellmer (1967) presents a partial tabulation of known cases of brooding in bivalves (see also Sastry, 1979), and, except for the oysters, all species have a very small body size; minute gastropods also appear to follow this pattern (e.g. Fretter, 1948; see Underwood, 1979, for a more extensive discussion, and Lindberg & Dobberteen, 1981, for an interesting exception – the relatively large and fecund trochid gastropod *Margarites vortificerus*). Hendler (1979) recently presented a similar account regarding brooding in some small, possibly progenetic, Caribbean ophiuroids. It is significant that Barlow (1981) draws similar conclusions on the relationships among body size, fecundity, mode of development, and dispersal capability in coral reef fishes.

The importance of body size as a constraint on larval type suggests that the diminutive size of most deep-sea (Thiel, 1975; Allen, 1978) and high-latitude (Nicol, 1964, 1966, 1978; Arnaud, 1974) mollusks may govern their developmental histories. These species are 'forced' to adopt a nonplanktotrophic strategy because they are unable to produce enough planktotrophic larvae per breeding episode to ensure adequate recruitment. Lack of a planktic food source has been invoked to explain the rarity of planktotrophic larvae in the deep sea (just as Thorson, 1950, cited brief productivity episodes in high latitudes), but the ability of larvae to utilize detritus and dissolved nutrients cannot be ruled out (e.g. Pilkington & Fretter, 1970). Even within communities, it appears that competition (Menge, 1974, 1975) and selective predation on larger-sized individuals (Brooks & Dodson, 1965; Menge, 1973; Zaret, 1980) can also lead to an optimal reproductive size that requires nonplanktotrophy, or even nonplanktic development.

A much less explored aspect of the relationship between body size and reproduction concerns possible advantages of large size for newly hatched or newly settled individuals.

For example, Spight (1976*b*, 1979) notes that large hatching size may reduce vulnerability to physiological stress and predation in juveniles of the 'direct' developing muricid gastropod *Thais emarginata*. Similarly, Woodin (1976) has suggested that the nonplanktotrophic, brooded offspring of the small bivalve *Gemma gemma* are released at a size large enough to survive among deposit-feeding polychaetes. Because hatching size is closely correlated with egg size, at least in certain gastropods (Amio, 1963; Fioroni, 1966; Spight, 1976*b*; Perron, 1981*a*), barnacles (Barnes & Barnes, 1965), and stomatopods (Reaka, 1979), selection favouring large hatchlings could ultimately affect modes of larval development as well. However, Perron (1981*a*) did not detect a correlation between egg size (or hatching size) and settling size in six Hawaiian species of *Conus*; it is possible that in these species settling size is related to species-specific prey preferences of post-metamorphic individuals.

The role of adult body size in constraining certain modes of larval development is complex and not completely understood (e.g. Lindberg & Dobberteen, 1981; Strathmann & Strathmann, 1982). Underwood (1979, pp. 116–117) has suggested that there are two important size thresholds in gastropod developmental patterns. First is a smaller size below which nonplanktic larvae must be produced, as discussed above. A second, larger size limit may be envisioned, below which sufficient large, planktic lecithotrophic larvae cannot be produced, and below which organisms must rely on the production of smaller, planktotrophic larvae (or a few, nonplanktic larvae) to ensure successful recruitment. Above this second size threshold, any mode of reproduction is possible. There may be, however, an upper size limit for efficiency in brooding organisms. M. Strathmann (in Strathmann, 1975*a*, p. 11) has suggested that if fecundity is volume-dependent and brooding capacity more dependent upon surface area, larger animals can brood a smaller fraction of what they could potentially produce. Thus, with increasing adult size, the ability to produce offspring might outstrip the ability to afford them brooding protection.

This adaptive link between body size and mode of reproduction is probably also a primary factor in the discordance between reproductive strategies in marine benthos and the r–K model. Many of the most strongly opportunistic species in the marine realm have nonplanktotrophic larvae (Grassle & Grassle, 1974, 1977). Small adult size, and attendant rapid onset of reproductive age, are characteristics of these species, which in many cases compensate for low adult yield per reproductive episode by reproducing several times, with only brief intervening pauses (e.g. Grassle & Grassle, 1974, 1977). This is in contrast to Pianka's (1970) generalization that r-selected species have a single reproductive episode per generation. Menge (1974, 1975) has suggested that this strategy occurs in the brooding starfish *Leptasterias hexactis*. Small body size is maintained by interactions with a superior competitor (*Pisaster ochraceus*, which is thus ostensibly the K-strategist of the pair) which releases large numbers of planktotrophic larvae. Grahame (1977) has attempted to reconcile these results with the r–K model by stressing the prediction (Gadgil & Solbrig, 1972) that r-selected species will allocate a greater proportion of their energy reserves to reproduction. *L. hexactis* does invest more energy in reproduction than *P. ochraceus*, and by this criterion could be regarded as more r-selected, despite its low gamete production per reproductive episode. In two species of the littorinid snail *Lacuna*, Grahame (1977) found that the species exhibiting greater reproductive effort, and showing other r-selected characteristics as well, had long-lived planktotrophic larvae. Similarly, the supposedly K-selected, nonplanktotrophic Antarctic opisthobranch *Philine gibba* exhibits a relatively low gametic to somatic biomass ratio (Seager, 1979; see also Todd, 1979, on nudibranchs), as do the two species of Antarctic shrimp studied by Clarke (1979). However, it is premature to generalize on the relationship between mode of development and energy expenditure of the parent in marine organisms; no universal correlation emerges from the sparse literature. For example, Lassen (1979) states that *Hydrobia ulvae* has planktotrophic larvae but exhibits lower reproductive effort and is less 'r-selected' than the nonplanktotrophic *H. neglecta* (see also Christiansen & Fenchel, 1979; Hughes & Roberts, 1980; Hart & Begon, 1982). Taken together, then, the data do not indicate any close relationship between larval type and the concepts of r and K selection.

In an evolutionary context, small body size might be readily attained by progenesis (acceleration of gonad maturation relative to somatic growth), a mechanism Gould (1977) links to an 'r-selected' regime (i.e. unstable or frequently disturbed habitats). This, in turn, would rule out planktotrophic larvae in the life histories of these species if a critical threshold was crossed, below which insufficient numbers of planktotrophic larvae could be produced. For example, Gould (1977, pp. 327–328) has suggested progenesis for the origin of the assemblage of minute bivalves described by Soot-Ryen (1960) from Tristan de Cunha; Gould envisions this as a response to superabundant resources by a number of normal-size species that drifted in as planktotrophic larvae. Seven or eight of the tiny, progenetic descendents of the initial colonizers are brooders. Gould (1977) presents a number of other marine examples, along with a discussion of the ecological situations mot conducive to progenesis, such as unstable environments, colonization, parasitism, and a variety of habitats favouring small size *per se*.

(4) *Ecological and evolutionary implications*

Consideration of the selective forces and adaptive responses operating here can lead to a chicken–egg paradox. It is clear that the interrelationships among body size, adaptive strategy, energetic limitations, dispersal capability, environmental tolerance, and speciation and extinction rates are as complex as they are fundamental. The coadaptational nature of these traits is well exemplified in Sanders's (1977) review of life histories in deep-sea organisms. Many deep-sea ophiuroids apparently have planktotrophic larvae, are geographically widespread, are highly eurybathic, and exhibit low levels of species richness. Deep-sea peracarid crustaceans brood their young, are often endemic, are highly stenobathic, and are among the most diverse groups in the deep sea. Deep-sea protobranch bivalves, which tend to have lecithotrophic larvae, are intermediate in the other respects as well. Similar assortments of traits co-occur in shallow-water invertebrates as well (e.g. Jackson, 1974; Jablonski, 1980*a*). It is difficult, and perhaps inappropriate, to single out any one factor in an attempt to explain the constellation of traits displayed by an assemblage of more or less disparate organisms.

As emphasized by Valentine & Ayala (1978) and Christiansen & Fenchel (1979), classic life-history theory does not adequately explain the distribution of developmental modes in marine organisms. While numerous organisms that could be called 'r-selected' do have planktotrophic larvae, some of the ocean's most prolific opportunists have nonplanktotrophic larvae. The heterogeneous and unpredictable environments of high latitude shelves are also dominated by species having nonplanktotrophic larvae, but so are vast expanses of abyssal plains; and yet some of the most abundant and widespread inhabitants of these environments have planktotrophic development. Furthermore, constraints imposed by body size, and perhaps additional energetic limitations reviewed above (along with phylogenetic affinities), may overrule other ecological factors.

Differences in modes of development have significance not only on ecological time scales, but also on evolutionary ones. On either temporal scale, selection for larval developmental modes and interactions with other aspects of the organisms' biology can be expected to affect the distribution of larval ecologies. Most current models concerning the advantages of different developmental types concentrate solely on short-term processes (cf. Strathmann, 1980). For example, the theoretical analyses of Palmer & Strathmann (1981) suggest that there are few short-term advantages to wide dispersal in benthic invertebrates, implying that advantages of planktotrophy *vs.* nonplanktotrophy must lie with other aspects of life history, such as the ability to produce the requisite number of eggs (see also Vance, 1973*a*, *b*; Christiansen & Fenchel, 1979).

While we do not challenge the potential role of selection for mode of development on ecological time scales, we urge neontologists to consider effects on evolutionary time scales as well. As will be discussed later in this paper, dispersal capabilities associated with different developmental modes can result in very different rates of extinction and speciation, and ultimately in very different clade shapes. Selection among species for one mode or another as environmental conditions change might be a more pervasive influence than generally recognized; though, as mentioned above, evolutionary and ecological traits will often be coadapted, and cause and effect difficult to separate. At the same time, selection on ecological time scales for a given larval type could also have far-reaching evolutionary consequences or side-effects. Of all the factors discussed here, we suspect that a combined dispersal–fecundity model might be more useful in understanding the significance of larval ecology on both evolutionary and ecological time scales. However, it is obvious that the links between these hierarchical levels in evolutionary biology are not very well understood, perhaps in part because we lack a well developed theory of extinction – on either time scale.

V. PALEOBIOLOGICAL IMPLICATIONS

Fossil shells sufficiently well preserved to be assigned with some confidence to the planktotrophic or nonplanktotrophic categories have been reported from Late Tertiary (e.g. Sorgenfrei, 1958; LaBarbera, 1974; Scheltema, 1978, 1979; Fatton & Bongrain, 1980), early Tertiary (Hansen, 1978*a*, *b*, 1980*a*, *b*, 1981), Late Cretaceous (Jablonski, 1979*a*, *b*, 1982; Jablonski & Lutz, 1980; Lutz & Jablonski, 1978*a*, *b*), and even some Paleozoic deposits (e.g. Runnegar & Jell, 1976, – although this may be post-settlement calcification: Morris, 1979 – Harrison, 1978; Hoare & Sturgeon, 1978; J. Kříž, 1979, and personal communication). Protoconchs have also been described and interpreted for an extinct class of Paleozoic mollusks, the Hyolitha (Dzik, 1978, 1980; see also Jablonski & Lutz, 1979*b*). Application of the criteria outlined in this chapter to well preserved fossil larval and early juvenile shells enables us to assess the effects of different developmental types from the unique time perspective of paleontology.

(1) *Evolutionary rates and patterns*

(*a*) *Speciation and extinction*

The role of larval ecology in species-level evolutionary processes seems well established in the paleobiological literature, thanks especially to the models developed by Shuto (1974) and Scheltema (1977, 1978, 1979) (see also Crisp, 1976*b*, 1978, 1979, for an extremely compatible neontological approach). Planktotrophic species having a relatively long planktic stage will have the ability to disperse over wide geographic areas in a single generation. Local catastrophes are unlikely to eliminate a species over its entire geographic range, and larvae from other, persistent populations will replenish populations reduced by local extinction.* These effects will combine to produce a geologically long-lived species, and lineages characterized by low extinction rates. In contrast, species having nonplanktotrophic larvae will tend to have smaller, necessarily more continuous geographic ranges. As a result of the more restricted geographic (and, often, ecological) range of such species, local catastrophes and random population fluctuations are more likely to result in extinction. Consequently, nonplanktotrophic species will tend to be geologically short lived, and lineages will be characterized by high extinction rates.

Dispersal capability should also affect speciation rates. Wide dispersal of planktotrophic larvae will maintain gene flow among disjunct populations of sedentary adults and thus suppress genetic divergence required for most modes of speciation. Planktotrophic lineages, then, should have relatively low speciation rates. On the other hand, for species having more restricted dispersal capabilities, local populations will tend to remain isolated after initial colonization or separation from the parent population, and thus speciation will be more common among nonplanktotrophs. Consistent with these predictions are a number of electrophoretic and biochemical studies in living populations, in which benthic species having planktic (usually planktotrophic) larvae were found to have low levels of genetic differentiation relative to species having nonplanktic or planktic nonplanktotrophic larvae (Wium-Andersen, 1970; Gooch *et al.*, 1972; Berger, 1973; Snyder & Gooch, 1973; Gooch, 1975; Campbell, 1978; Crisp, 1978; Grassle & Grassle, 1978; Siebnaller, 1978; Wilkins *et al.*, 1978; Black & Johnson, 1979; Buroker *et al.*, 1979*a*, *b*; Ward & Warwick, 1980). Low dispersal capability is often reflected by geographic differentiation into morphological variants or subspecies as well (e.g. Clench & Turner, 1956; Scheltema, 1971*a*, *b*, 1977; Shuto, 1974; Gerrodette, 1981), and Ament (1979) presents experimental evidence for physiological patterns in the gastropod genus *Crepidula* among species having different dispersal capabilities.

The patterns of genetic (and morphological) differentiation as inversely related to dispersal capability is not always a simple one. While nonplanktotrophic species do generally exhibit geographic differentiation, planktotrophic species also sometimes exhibit clinal or other geographic differentiation on a variety of scales. Most authors have attributed this to differential post-settlement mortality (or habitat selection) rather than a lack of larval dispersal (Struhsaker, 1968; Boyer, 1974; Koehn *et al.*, 1976; Marcus, 1977; Milkman & Koehn, 1977; Levinton & Lassen, 1978*a*, *b*; Theisen, 1978; Ament, 1979; Buroker, 1979). For example, Black & Johnson (1981) found that newly settled postlarvae of the planktotrophic limpet *Siphonaria kurracheensis* were

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* Because conditions may vary from parents' location to settlement site, selection for flexibility or eurytopy may be significant in species with planktotrophic larvae (e.g. McKillup & Butler, 1979).

electrophoretically homogeneous over the area studied, although the adult populations were not (unfortunately, they did not follow a single generation through a time series, enabling them to rule out the effects of successive spatfalls of differing genetic composition). In one of the most extensively studied planktotrophic mollusks, the bivalve *Mytilus edulis*, allele frequencies at most polymorphic loci exhibit only small differences among populations, as predicted (Levinton & Koehn, 1976). However, strong geographic variations in allele frequencies at the *Lap* locus have been reported, apparently correlated with salinity variations and maintained by natural selection on post-settlement juveniles (Koehn, Bayne, Moore & Siebnaller, 1980; Koehn, Newell & Immerman, 1980; see also Levinton & Lassen, 1978*a*, *b*). As several authors have pointed out, dispersal is just one component of gene flow (e.g. Grant, 1980). Local intense natural selection could cause populations to diverge despite larval dispersal if propagules from distant populations do not survive to reproductive age – *and* locally produced larvae are retained in the area and do survive.

The models of Shuto and Scheltema, and their supporting data, were made for situations in which major oceanic barriers are present. However, there is some evidence that the effects of differential dispersal capabilities are significant even along a single continental shelf or within an epicontinental sea. Hansen (1978*a*, *b*, 1980*a*) found in the Lower Tertiary volutid gastropods of the Gulf Coast that species having 'planktonic' larvae had a mean species duration of 4·4 m.y., while those with 'nonplanktonic' larvae had a mean duration of 2·2 m.y.; in addition, geographic range of 'planktonic' species averaged about twice that of 'nonplanktonics). Similarly, in a survey of Gulf and Atlantic Coastal Plain gastropods from the Late Cretaceous, Jablonski (1979*a*, 1980, 1982) found that species having planktotrophic larvae had a mean duration of about 6 m.y. and a mean geographic range of 1500 km, while nonplanktotrophic species had a mean duration of only about 3 m.y. and a mean geographic range of 610 km (Fig. 4). In both studies, degree of environmental tolerance also played an important role in determining species durations and geographic ranges (cf. Jackson, 1974, 1977; Jablonski & Valentine, 1981). This factor may be responsible for the lack of a simple direct relationship between planktotrophy and species durations in Late Cretaceous bivalves (Jablonski, 1979*a*).

Scheltema (1978) has elaborated on his earlier (1977) conceptual model by suggesting that lineages or clades having planktotrophic larvae will produce new species via 'punctuated equilibria' (Eldredge & Gould, 1972, 1977; Stanley, 1975, 1978; Gould & Eldredge, 1977), by occasional isolation of small outlying populations which, once isolated, would tend to evolve rapidly into new species. Barriers that might disrupt the flow of larvae among marine populations are not easily envisioned. Nonetheless, Murphy (1978) has suggested a climatic isolating mechanism for allopatric speciation in the acmaeid limpet *Collisella*. During warming trends planktic larvae of a warm-water species will successfully settle at higher latitudes, thus extending the species' range. Subsequent cooling intervals will cause geographic ranges to contract equatorward again, but some populations might become isolated in suitably warm, higher latitude embayments. Should this isolation last long, speciation might occur (Murphy, 1978). Dando & Southward (1981) have also hypothesized Pleistocene hydrographic fluctuations for separation and divergence of benthic populations in the western Mediterranean, relative to Atlantic ancestors.

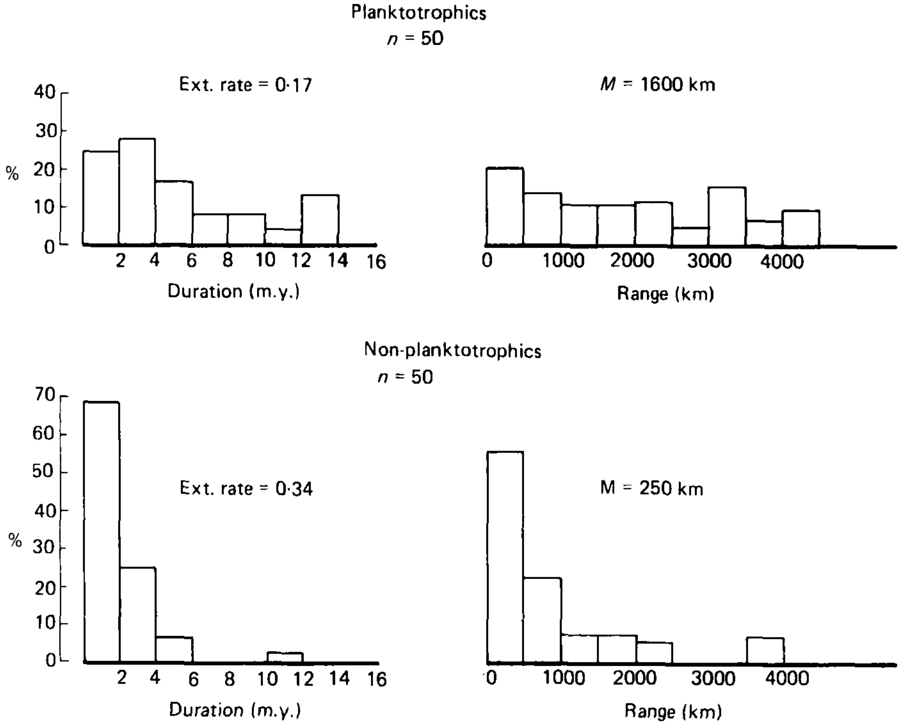

Fig. 4. Geological durations and geographic ranges of Late Cretaceous gastropods of the Gulf and Atlantic Coastal Plain, North America. Planktotrophic species have significantly greater durations and geographic ranges than nonplanktotrophic species. *n* = number of species; ext. rate = extinction rate in species per lineage-million years (as defined by Raup, 1978); M = median; m.y. = million years. (From Jablonski, 1982.)

Within species' ranges, isolation and selection of populations in estuaries or other basins in which hydrography restricts influx of larvae from open-marine areas might permit differentiation of rather large populations of shallow-water species (Levinton & Lassen, 1978*b*; Levinton, 1980). Once established, such patterns can be maintained by behavioural adaptations of the larvae themselves (e.g. Wood & Hargis, 1971; de Wolf, 1974; Scheltema, 1975*a*; Forward & Cronin, 1980; Sulkin *et al.*, 1980). Of course, sympatric and parapatric speciation processes (e.g. Endler, 1977; Rosenzweig, 1978; White, 1978; Hammond, 1981) would not require physical barrier formation and may play an important part in the multiplication of species. For example, genetically determined habitat preferences during settlement of planktic larvae may offer a mechanism of rapid, essentially sympatric speciation (e.g. Doyle, 1976; Crisp, 1979). Such ecological isolation has been invoked for the origin of sibling species pairs of spirorbid polychaetes (Knight-Jones *et al.*, 1975) and of nine sympatric species of Late Cretaceous limopsid bivalves (Heinberg, 1979). These processes might actually be most likely to culminate in speciation for those groups possessing internal fertilization mechanisms (thus fulfilling the requirements of 'habitat selection' in the sense of Smith's (1966) classic paper on sympatric speciation).

Scheltema (1978) has suggested that species with nonplanktotrophic larvae would be expected to undergo a gradual transformation into new species because populations are more localized and genetically more homogeneous; thus, they will be particularly susceptible to selection pressures generated by local environmental changes. However, good cases of gradualism may be rare even among species with nonplanktotrophic larvae; species are more likely to become extinct or migrate along with their shifting habitat or temperature regime than evolve *in situ* along with changing environmental conditions. Furthermore, if morphological change is concentrated at speciation events (Eldredge & Gould, 1972; Stanley, 1975, 1979; Gould & Eldredge, 1977), the predicted high speciation and extinction rates associated with nonplanktotrophy should lend these lineages a particularly punctuated aspect. Finally, the genetic population structure engendered by low larval dispersal capability may favour 'shifting balance' modes of evolution (see Wright, 1949, 1977, 1978) or processes of group selection (*sensu* Wade, 1978; Wade & McCauley, 1980). Ultimately, evolutionary change in such circumstances could well be indistinguishable from punctuated equilibria on geological time scales (Lande, 1980). Schopf & Dutton (1976) present possible evidence in favour of phyletic gradualism in bryozoans having low dispersal capability, in the form of data on morphological and genetic differentiation over short distances in the extant species *Schizoporella errata*; the link between clinal geographic variation and speciation, however, is still unclear (Gould & Johnston, 1972; Endler, 1977; Futuyma & Mayer, 1980).

Evolutionary patterns in the fossil record will be affected by the bathymetric gradient in adaptive types discussed by Jackson (1974, 1977) (see earlier discussion above). Jablonski (1979*a*, 1980) found evidence in Late Cretaceous coastal plain sediments that very near-shore fossil assemblages tend to be composed of species with greater geologic and geographic ranges (the latter presumably a reflection of greater environmental tolerance), and have a greater proportion of species with planktotrophic larvae, than deeper-water assemblages. Thus, although the more offshore assemblages inhabit a somewhat less heterogeneous habitat, low dispersal and relative stenotopy may combine to make speciation more likely in these mollusks than in those inhabiting very shallow water. This may be a more satisfying reconciliation between an allopatric model for speciation (Mayr, 1963, 1970; Bush, 1975; White, 1978) and the observation that offshore assemblages are more diverse and less persistent than very near-shore ones (Bretsky & Lorenz, 1970; Bambach, 1977) than Eldredge's (1974) suggestion that new species arise on shore and migrate to the offshore areas. Jablonski & Bottjer (1982) have recently suggested that these bathymetric gradients in larval ecology may also affect large-scale patterns of community change.

The general scarcity of well documented instances of intraspecific variation in developmental modes, at least among Recent bivalves and prosobranch gastropods (see discussion above), suggests that there are strong constraints on developmental pathways within most molluscan species.* This is hardly surprising in the light of the complex relationships among larval and adult morphology, energetics, and ecology outlined previously. Therefore, when switching among modes does occur it also may be concentrated at speciation events, where developmental constraints may be relaxed or

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• Certain other groups are apparently much more variable, even at the level of the individual. For example, Blake & Kudenov (1981) cite several polychaete species in which both modes of development co-occur in a single egg capsule.

disrupted (see Mayr, 1963, 1970; Williamson, 1981). Patterns of evolution related to life history thus deserve special attention at the species level and above, as Stearns (1980) has suggested in a more general context. The concentration of changes in developmental mode at speciation events underscores the potentially far-reaching effects such alterations might have on evolutionary rates and patterns at higher taxonomic levels. For example, a speciation event that includes a change from planktotrophy to nonplanktotrophy (engendered, perhaps, by a progenetic diminution in adult size: Gould, 1977, and discussion above) should give rise to a clade with significantly higher speciation and extinction rates than its ancestral clade (see also Jablonski, 1982).

With larval shell morphology giving an indication of dispersal capability, it will be possible to separate the processes underlying extinction and speciation better (Scheltema, 1978; Jablonski, 1979*a*, 1982). Numerous authors (e.g. Moore, 1954, 1955; Kauffman, 1972, 1977*a*, 1978) have considered environmental stress to be responsible for both the extinction and origination components of species' turnover rates. However, as Eldredge & Gould (1977, p. 36; see also Eldredge, 1974; Bush, 1975) point out, "directions and intensities of selection regimes have never been directly correlated with speciation rates". If speciation in marine organisms proceeds primarily via the formation of peripheral isolates or subdivision of ancestral ranges (allopatry by founder events or vicariance events; see Valentine & Jablonski, in press, *b*), rates through time will depend on species' ability to maintain genetic continuity among populations (i.e. on their dispersal capability). Thus, lineages having planktotrophic larvae should have lower speciation rates than taxa having nonplanktotrophic larvae.* A symmetrical pattern of speciation rates through a transgressive–regressive cycle (e.g. Kauffman, 1972, 1977*a*) can be expected only if transgressive–regressive cycles are symmetrical with regard to degree of spatial heterogeneity on the affected shelf. This may not, however, be the case. We agree with Kauffman (1977*a*) and others (e.g. Moore, 1954, 1955) that increasing environmental stress during regression will result in increasing extinction rates. Here, too, this effect will be ameliorated for species having planktotrophic larvae (see Jablonski, 1979*a*; 1982; Hansen, 1980*a*). While extinctions within a single basin may be most closely correlated with degree of environmental tolerance as modelled by Kauffman (1977*a*), planktotrophic taxa will be more widespread and undergo a high proportion of local, rather than complete, exterminations. With the subsequent transgression, the same species (or a closely related descendent) can return to colonize the area. Species with nonplanktotrophic larvae will tend to be driven into extinction during regression (or any other major environmental perturbation), and lineages will often terminate. With the return of suitable habitats, recolonizing species will be derived from more distantly related stocks.

In an interesting hypothesis of 'stabilizing species selection', Gilinsky (1981) attributes reduction in the variety of archaeogastropod shell shapes through time to extinction of the superfamilies with outlying morphologies and to proliferation of the superfamilies Trochacea and Neritacea, which are morphologically conservative. He attributes this pattern to differential origination rates, with the Trochacea and Neritacea having highest speciation rates as a consequence of their supposed nonplanktic

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* Again, this will not be completely exclusive of a eurytopy–stenotopy effect, as eurytopy and planktotrophy often co-occur in the same species.

development. However, this is completely contradicted by the available data on modern species. The Neritacea are actually dominantly planktic in mode of development; the most recent compilation (Spight, 1981) cites 22 species for which development is known, and only two are nonplanktic. Furthermore, among the Trochacea, only 18 of the 51 species listed by Spight (1981) are nonplanktic. Perhaps most troublesome is the fact that the Neritacea, which Gilinsky (1981) claims should have high speciation rates due to their supposed nonplanktic development, are actually the only archaeogastropods with planktotrophic larvae (Strathmann, 1978*a*, *b*; also Lebour, 1945; Robertson, 1971; Scheltema, 1971*a*; Taylor, 1975; Webber, 1977). Thus, they should have the lowest, not the highest, speciation rates within the order Archaeogastropoda – and the lowest extinction rates. On the basis of these data, Gilinsky's hypothesized mechanism (which may be useful for other groups) should be discarded for the archaeogastropods; the available larval data even suggest that differential extinction, not origination, was the mechanism involved, if larval ecology played a direct role in shaping his observed pattern at all. This is questionable as well, because in making evolutionary rate distinctions among the non-neritacean archaeogastropods, Gilinsky is forced to claim that planktic, lecithotrophic lineages will have significantly lower speciation rates than nonplanktic lineages. However, as we discuss earlier in this paper, most authors group these two modes of development together and contrast them with evolutionary rates among planktotrophic lineages.

(*b*) *Evolution of developmental types in higher categories*

Larval traits have been regarded by many authors as highly conservative, and thus have played an important role in phylogenetic hypotheses at high taxonomic levels (e.g. deBeer, 1958; Jägersten, 1972), as well as at intermediate and low taxonomic levels (e.g. Iredale, 1911; Grabau, 1912). However, as evolutionary patterns in marine invertebrates become better understood, it has become clear that developmental histories have undergone considerable evolutionary change both within and between major taxonomic groups. Rather than passively documenting phylogenetic history (cf. historical discussion in Gould, 1977), larval stages of marine invertebrates have been as subject to natural selection as adult stages and have proven as capable of a wide range of adaptive responses. Furthermore, since different selective forces would be expected to operate on minute, planktic larvae and on relatively large, benthic adults, it could be argued that adult and larval traits are, in most instances, unlikely to evolve in concert or at the same rates. Life-history theory does suggest, however, that truly profound alterations in adaptations and mortality patterns in one stage of the life cycle should affect other stages as well.

Jägersten (1972) argues that planktotrophy is the primitive condition in many marine invertebrate groups (including Coelenterata, Phoronida, Bryozoa, Brachiopoda, Platyhelminthes, Sipunculida, Mollusca, Annelida, Echinodermata, and Enteropneusta) (see also Strathmann, 1978*a*, *b*) and further suggests that planktotrophy was present in the common ancestor(s) of these phyla. However, numerous groups within these phyla have independently adopted nonplanktotrophic life histories, and the evolutionary history of the larval stages of marine benthos has probably been one of repeated loss of planktotrophy, with very few subsequent reversions to the apparent primitive condition (cf. Strathmann, 1978*a*, *b*). Thus, there appears to have been an evolutionary tendency towards fewer, larger larvae with higher probability of survival and lower dispersal capability. Hermans (1979) has suggested that the 'founding species' of the supposedly primitively planktotrophic phyla listed above might have been either planktotrophic or nonplanktotrophic, but that there would be low selective pressure for the succeeding 'pioneer species' of the adaptive radiation to evolve planktotrophy as a response to population instability and selection for rapid population growth. This seems a dangerously simplistic approach to applying such concepts as opportunistic species to macroevolutionary phenomena (for an introduction to the problem, see Gould & Eldredge, 1977), and, in fact, in the case of the Neogastropoda, Jablonski (1979*a*, *b*) has argued for selection for nonplanktotrophy among lineages as a means for increasing speciation rates during their adaptive radiation.

Farmer (1977, pp. 504–505) makes the interesting argument that the ancestral developmental type of a group may actually be a function of the position in the latitudinal gradient of larval ecologies in which its root stock originated, rather than the straightforward reflection of phylogenetic relationships or evolutionary requirements for the origin of higher taxa. From Thorson's observations on modern taxa (see preceding discussion on relation of larval type to latitude), we would expect the presence of planktotrophic larvae to be a primitive character for most groups originating in low latitudes; perhaps the predominance of planktotrophy as a primitive character in so many metazoan groups is an indication that most of them originated in low latitudes. However, Thorson's Rule may only prevail when steep latitudinal gradients are present; for example, Jablonski (1979*a*) was unable to detect gradients or discontinuities in developmental type in Late Cretaceous molluscan assemblages from New Jersey to Texas. Thus, taxa having planktotrophic larvae as the primitive state might arise at almost any latitude in certain geological periods.

(i) *Echinoderms*. The evolutionary picture that emerges from study of the Echinodermata is one of repetitive, unidirectional evolution away from planktotrophy. According to Strathmann (1974*a*), nonplanktotrophy has evolved at least 17 to 24 times in the Echinodermata, three times in the Ophiuroidea, six to nine times in the Asteroidea, six to nine times in the Echinoidea, at least twice in the Holothuroidea, and, if the common ancestor of the Crinoidea and other existing echinoderms had planktotrophic larvae, at least once in the Crinoidea. Unlike the Mollusca and Polycheata, there are very striking differences in functional morphology in planktotrophic and nonplanktotrophic echinoderm larvae, and Strathmann (1974*a*, 1975*b*, 1978*a*, *b*) has suggested that it may be impossible for an echinoderm lineage to regain complex larval feeding adaptations once they have been lost. Thus, lineages will be locked into a nonplanktotrophic larval state once they have lost feeding adaptations; this, in turn, may perhaps lead to a progressive loss of planktotrophic development in higher taxa through time. A case in point may be the Crinoidea, which today are exclusively nonplanktotrophic (see Breimer, 1978). This is particularly striking because most crinoids today inhabit shallow waters in the temperate and tropical regions, where many benthic organisms are characterized by planktotrophic larvae. Strathmann (1978*a*) suggests that this seemingly anomalous developmental pattern might be an artifact of the Permo–Triassic extinctions, which selectively or by chance could have included those lineages having planktotrophic larvae. This suggestion is made all the more plausible by Raup's (1979) computation that the Permo–Triassic boundary event could have eliminated well over 90% of the invertebrate benthic species.

(ii) *Lophophorate phyla.* The Bryozoa are dominated by nonplanktotrophic development, with an estimated 95 % of modern cheilostome species having nonplanktotrophic larvae (Schopf, 1977, p. 165; see also Nielson, 1971; Ryland, 1974; Ström, 1977). However, it has been argued that planktotrophic development is the primitive condition in the Bryozoa on the basis of embryological studies (e.g. Jägersten, 1972), as well as its presence both in certain Ctenostomata and in malacostegoid genera believed to be primitive within the Cheilostomata (e.g. Farmer, 1977; Zimmer & Woollacott, 1977*a*, *b*). It is interesting, although hardly conclusive, to note (Ross, 1979) that the oldest known cheilostome, from the Late Jurassic of England (Pohowsky, 1973), has been considered ancestral to the extant *Pyripora*, which is believed to have a planktotrophic, cyphonautes larva. It is probable that there has been considerable evolution in larval forms of the Bryozoa, with planktotrophic adaptations (including the distinctive shelled cyphonautes morphology and the presence of a functional gut) having been lost at least three to six times (Strathmann, 1978*a*; see Farmer, 1977, for review.) Almost nothing is known of the evolutionary pathways by which Bryozoa became dominated by lineages having nonplanktotrophic development, but as mentioned previously, it might be possible to trace this process in the fossil record if the far smaller dimensions of planktotrophic, cyphonautes larvae, relative to nonplanktotrophic larval forms, are reflected in the skeletons of the earliest growth stages of Bryozoan colonies.

In the Brachiopoda, the inarticulates are primarily planktotrophic, while the articulates are apparently exclusively nonplanktotrophic. Jägersten (1972) argues that the planktotrophic inarticulate brachiopod larvae retain some of the primitive characters of the ancestral lophophorates and there is fossil evidence for planktotrophy in Ordovician articulate brachipods (Chuang, 1971). Thus, planktotrophy might represent the primitive state in the Brachiopoda; it is not clear if the similarities between articulate brachiopod larvae are a consequence of convergence and repetitive derivation from ancestors with similar planktotrophic larvae, or if planktotrophy was lost only once, and the inarticulates have been nonplanktotrophic since their separation from the inarticulates (Strathmann, 1978*a*). However, unlike the mollusks, the inarticulate brachiopods do not possess unique larval organs for feeding and locomotion – this role is fulfilled by the lophophore, which is retained throughout brachiopod ontogeny. Thus, it is possible that brachiopods were primitively nonplanktotrophic, but in the inarticulates, development of the lophophore was accelerated so that it was functional during the larval stage (see Strathmann, 1978*a*). Steele-Petrović (1979) has suggested that one factor leading to the domination of benthic assemblages by bivalves rather than brachiopods in the post-Paleozoic is the low larval dispersal capability of articulate brachiopods. Valentine & Jablonski (in press, *b*) have suggested that the articulate brachiopods declined while the bivalves flourished in the post-Paleozoic world because the articulates were locked into a nonplanktotrophic larval type, and thus have only persisted in habitats and latitudes in which this mode of development is not a disadvantage.

(iii) *Mollusks.* The Neogastropoda are another group in which planktotrophy is probably the primitive condition, although many, if not most, modern members of the group are nonplanktotrophic even in shallow tropical seas (Radwin & Chamberlin, 1973; Jablonski & Lutz, 1980; Spight, 1981). There is fossil evidence for a progressive increase in the proportion of nonplanktotrophic species in the Neogastropoda through the Late Cretaceous and Tertiary (Hansen, 1978*c*; Jablonski, 1979*a*, *b*; see also Vokes, 1971). This is all the more intriguing because, as Strathmann (1978*a*) points out (see also Fioroni & Schmekel, 1976; Christiansen & Fenchel, 1979), many neogastropods retain larval feeding organs during lecithotrophic or nonplanktic development (as do many opisthobranchs: Bridges, 1975). Thus, gastropod lineages might not be locked into a nonplanktotrophic mode of development once it had been adopted. Furthermore, an extinction filter, such as might have resulted in the now exclusively nonplanktotrophic crinoids, would be far less likely to restrict developmental types in gastropods permanently should one mode or another be selectively (or stochastically) eliminated. A case in point may be Marshall's (1978) suggestion that the living cerithiopsid gastropod species *Euseila nucleoproducta* and *Seila* (*Notoseila*) *terebelloides* have secondarily acquired planktotrophic development.

Since it appears that the high frequency of nonplanktotrophic development in the Neogastropoda is not simply an artifact of unidirectionality of change in developmental type, a more complex evolutionary explanation is needed. Jablonski (1979*a*, *b*) has suggested a twofold combination of selective pressures which, in concert, might have produced the distribution of developmental types seen today in the Neogastropoda. Firstly, during the Cretaceous, when the neogastropods originated (Ponder, 1973; Taylor, 1981), shelf seas presented far more continuous and widespread habitats than do the modern seas, which have steep latitudinal gradients and lack vast, shallow, epicontinental extensions. Thus, in the Cretaceous, even relatively stenotopic, predatory species, such as typify the neogastropods, could have released planktotrophic larvae which would have had a high probability of encountering suitable sites for settlement and growth. However, with an increasingly heterogeneous world, the possibility of finding favourable settlement sites would be greatest in the immediate vicinity of adults that had survived to reproductive age (cf. Strathmann, 1974*a*), and due to steepening thermal gradients larvae would be more likely to be transported outside of the reproductive range, even if they did find suitable substratum types. The result of these environmental changes could be progressive selection for nonplanktotrophy in neogastropods since the mid Cretaceous. (Note that this explanation implies that selection operated directly on dispersal, rather than indirectly affecting dispersal capability by selecting for number of offspring or size of egg or larva at time of settlement.)

A second, not mutually exclusive, factor that might favour nonplanktotrophy in neogastropods might be found in the concept of species selection (Stanley, 1975, 1979; Gould & Eldredge, 1977). Nonplanktotrophic neogastropod lineages tend to be relatively stenotopic and to have high extinction and speciation rates (Hansen, 1978*a*, *b*, *c*, 1980*a*; Jablonski, 1979*a*, *b*, 1982). Conversely, the more eurytopic, extinction-resistant planktotrophic lineages would generate fewer species per unit time. Even at a species-level diversity equilibrium (in the absence of which nonplanktotrophic clades would probably quickly far outspeciate planktotrophic clades), long-term selection might favour the nonplanktotrophic clades. This is because episodes of environmental change or random events will occasionally eliminate species belonging to the much less species-rich planktotrophic clades and thus be more likely to cause a terminal extinction event than in nonplanktotrophic clades, in which rapid taxonomic turnover in large groups of species is the rule (Hansen, 1980*a*; Jablonski, 1979*a*, *b*, 1982). Furthermore, nonplanktotrophs, although more stenotopic, will have shorter durations and more rapid speciation rates, and thus a better chance of tracking environmental changes through a series of speciation events than would the less species-rich survivor clades. The neogastropods may exhibit this evolutionary pattern so clearly because of the timing of their adaptive radiation (Jablonski, 1979*b*, 1980*b*). The evolution of the neogastropods took place in marine ecosystems that were near saturation – a distinct contrast to the marine adaptive radiations of the relatively empty seas of the early Paleozoic (cf. Sepkoski, 1981). Neogastropod species richness rapidly reached modern-day levels, but familial origination was a more gradual process, not reaching modern levels until over 60 million years after the initial appearance of the group. Jablonski (1979*b*) attributes this to the near-saturation levels of the Late Cretaceous–Cenozoic ecosystems, and suggests that prolific speciation among lineages having nonplanktotrophic larvae would have increased the probability of successfully invading a new adaptive subzone (familial origination) under such conditions.

The directions of evolutionary change of larval development within the Class Bivalvia are less clear than those described above for other groups. Most bivalves are characterized by planktotrophic larvae (e.g. Thorson, 1961; Sastry, 1979), but nonplanktotrophic development is present in almost every family, most often in species having small adult size (e.g. Turner, 1975). However, some interesting taxonomic patterns emerge from a consideration of those groups that are exclusively nonplanktotrophic in their development.

The protobranch bivalves (Palaeotaxodonta) all exhibit an unusual mode of lecithotrophic development, possessing a stage that has been termed a 'Pericalymma' larva, characterized by the presence of a ciliated, barrel-shaped epithelial test which is discarded at metamorphosis (cf. Drew, 1899, 1901; Salvini-Plawen, 1972, 1980). Since the protobranchs have been regarded by many biologists as the closest living group to the ancestral bivalve condition (e.g. Yonge, 1959), Chanley (1968) and others have suggested that the primitive larval condition of the Bivalvia was one of nonplanktotrophy, and that subsequent evolution, in contrast to many other benthic groups (Strathmann, 1978*a*, *b*) has been towards planktotrophy and increased dispersal capability. That protobranch larval morphology may be primitive to the Mollusca is further suggested by the presence of similar epitheliated larvae in certain neomenioid Aplacophora (e.g. Thompson, 1960; Salvini-Plawen, 1969; Hadfield, 1979). The Aplacophora are considered to have diverged very early from the molluscan line and may be closest in overall morphology to the molluscan stem group (Salvini-Plawen, 1969, 1972; Stasek, 1972; but see Yochelson, 1979). In cladistic terms, the Aplacophora are the sister group for the rest of the Mollusca, and thus if the common ancestor of the aplacophorans and the protobranchs possessed nonplanktotrophic 'barrel' or 'Pericalymma' larvae as well, it could be argued that this would represent the primitive condition for the entire phylum. However, evolutionary modification of the Aplacophora in response to small body size and a primarily deep-sea existence (cf. A. H. Scheltema, 1978) might have obscured ancestral character states (although, of course, the oldest fossilized molluscs are also minute: Runnegar & Jell, 1976, and references therein). Perhaps more significantly, if the epitheliated test could be derived by hypertrophy of the velum, repetitive derivation of such a feature might be more probable than independent derivation of the opposed band feeding mechanism in the trochophores of more 'advanced' bivalves and gastropods (see Strathmann, 1978*a*), as would be required if their common ancestor had larvae resembling those of the protobranchs and the Aplacophora. Salvini-Plawen (1980), however, has argued that the Pericalymma larva is primitive in these groups, as well as in a number of other protostome phyla.

The Scaphopoda (Lacaze-Duthiers, 1856–1857; see review by McFadien-Carter, 1979), Polyphacophora (e.g. Smith, 1966; Pearse, 1979), and the archaeogastropods (except the Neritacea*; see Weber, 1977; Strathmann, 1978*a*, *b*; Heslinga, 1981) are also exclusively nonplanktotrophic. However, the diversity of larval forms apparent among these groups weakens an argument for nonplanktotrophy of the common ancestor of these groups (as well as of the protobranchs and aplacophorans; e.g. Scarlato & Starobogatov, 1978). Even the hyolithids reportedly exhibit apical morphologies suggesting the presence of both kinds of development in different families (Dzik, 1980). Nonplanktotrophy has also been inferred for the septibranch bivalves (e.g. Knudsen, 1970; Bernard, 1974), a group considered to have close affinities with the protobranchs (e.g. Yonge, 1959; Purchon, 1963), and for the modern monoplacophorans (see Gonor, 1979). However, the same selective pressures for nonplanktotrophy that may affect developmental types in the Aplacophora, namely a predominantly deep-sea distribution and small body size, may be operating in these groups as well.

Nonplanktotrophic development is also the rule in the supposedly most primitive living eulamellibranchs, the Carditidae and the Astartidae (combined by Yonge, 1978, and other authors into the single superfamily, the Crassatellacea; see also Boyd & Newell, 1968, and Yonge, 1969). However, evidence for planktotrophic development in Cretaceous Crassatellacea is presented in Fig. 2; while the Cretaceous carditid *Vetericardiella crenalirata* is indeed nonplanktotrophic (Fig. 2D), the crassatellid *Uddenia texana* possesses a prodissoconch morphology strongly indicative of planktotrophic development (Fig. 2C). Thus, exclusive nonplanktotrophy in this superfamily might be a consequence of replacement of larval types or extinction of planktotrophic lineages rather than a reflection of a primitive condition.

The Lucinacea, which supposedly diverged from the bivalve line of evolution early in their history (e.g. Pojeta, 1978), are also known to have nonplanktotrophic larvae in the Thyasiridae (e.g. Blacknell & Ansell, 1974); again, this may reflect the predominantly high-latitude and deep-sea occurrence of the group, rather than the ancestral condition.

Finally, nonplanktotrophic development is the rule in the Pandoracea (Chanley & Castagna, 1966; Chanley, 1968). This anomalodesmatan group has no claims to great antiquity or primitive morphology; they first appear in the Cretaceous and are morphologically distinct from the more ancient members of the subclass (cf. Runnegar, 1974).

Thus, we remain with an equivocal phylogeny of bivalve developmental types. If we can regard larval types as being evolutionarily static, there is considerable circumstantial evidence for nonplanktotrophy being the primitive state in this group – the protobranchs, septibranchs, thyasirid lucinaceans, carditaceans, and crassatellaceans, all located near

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* Facultative planktotrophy may be present in at lest some archaeogastropods (e.g. *Haliotis*, Crofts, 1937; *Patella*, Dodd, 1957; *Notoacmaea*, Kessel, 1964; although Simpson, 1982, is sceptical) and larval ecology in this group needs further study. Other nonplanktotrophic mollusks for which facultative planktotrophy is reported include the gastropod *Conus pennaceus* (Perron, 1981*b*) and the bivalve *Pandora inaequivalvis* (Allen, 1961). Despite this apparent additional food source, both of these species normally have only brief planktic durations (less than 24 hours).

the base of the bivalve or eulamellibranch phylogeny are today nonplanktotrophic (as are the aplacophorans, most archaeogastropods, the chitons, and the scaphopods). However, the testimony of other marine benthic groups, and of the fossil record, is one of plasticity of developmental types. Here, immediate ecological demands, such as those presented by high latitude, the deep sea, and small body size (and thus limited resources for gamete production), are all seemingly capable of overriding phylogenetic affinity to produce a nonplanktotrophic life cycle. This, however, is still not a truly convincing argument. For example, given the diversity of developmental types known in deep-sea benthos (cf. Rex *et al.*, 1979), can we be sure that the dominantly nonplanktotrophic bivalves reported by Knudsen (1970) are not a reflection of the dominance of deep-sea bivalve assemblages by developmentally primitive protobranchs and septibranchs? Clearly, more work is needed on the distribution of larval types in the Bivalvia before a satisfactory developmental phylogeny will be available, and the fossil record has much to offer in this regard.

(2) *Biostratigraphy and paleobiogeography*

Several authors have emphasized the biostratigraphic potential of benthic species having planktic larvae: despite the sedentary habits of the adults, such species can disperse over wide geographic ranges within geologically instantaneous time intervals (see Shuto, 1974; Kauffman, 1975, 1977*b*; Scheltema, 1977; Hansen, 1980*b*, 1981). Application of the criteria discussed above will enable a biostratigrapher to recognize those groups within a fauna most suited for the biostratigraphic problem at hand. Taxa with planktotrophic, teleplanic larvae should be most useful for intercontinental correlations, while nonplanktotrophic taxa should be most useful for local, finely subdivided correlation schemes. For the paleobiologist, larval ecologic studies can shed light on the processes underlying the different stratigraphic and geographic distributions already abundantly documented by biostratigraphers. As we gain understanding of the biological factors that affect rates of evolution, index species raise interesting problems, as commented upon by Scheltema (1977), Jackson (1977), and Kauffman (1977*b*). These authors note that biostratigraphic index species, including many lineages of benthic organisms, are useful because they are widespread and geologically short lived. However, benthic species tolerant enough, and having larvae with a sufficient planktic duration, to maintain a broad geographic distribution would not be expected to evolve very rapidly, in terms of either speciation or extinction rates (see preceding section). Some other aspect of the organisms' biology, for example trophic level and/or adult ecology (Levinton, 1974; Alexander, 1977; Kauffman, 1978; and many others) must play a key role in keeping certain widespread lineages subject to high extinction rates.

Larval shells themselves are potentially useful as index fossils, particularly if they can be definitively assigned to known species by means of growth series, or by comparison to adult specimens having well preserved juvenile stages. Several authors have pointed out that larvae may settle in a broader range of environments than are occupied by adults; this would tend to increase a species' geographic range and reduce facies dependence (e.g. Harrison, 1978, 1979; Hansen, 1980*b*, 1981). This has been documented in Recent faunas by several workers. For example, Kiørboe (1979) found that species in Hoback Fjord, Denmark, exhibit widest distributions immediately after larval settlement.

When viewed in the light of larval dispersal, analysis of paleobiogeographic patterns can provide many interesting insights. As Zinsmeister & Emerson (1979) point out, oceanic currents may be viewed as distinct one-way corridors of passive larval dispersal. Consequently, distributions of fossil organisms can be useful in reconstructing ancient current systems, or in testing hypotheses concerning paleocurrents derived from geophysical considerations. The situation may be very complex in shallow shelf areas (cf. Zinsmeister, 1974; Scheltema, 1975*a*, *b*), but planktotrophic and, especially, teleplanic larvae should, nonetheless, be extremely useful in reconstructing ancient currents. The dependency of larval dispersal on current direction should also be kept in mind when considering physical controls on biogeographic patterns. A low (or high) degree of faunal similarity between regions in which similar environments are present need not be a simple indication of large (or small) geographic disjunctions, but rather it may be a reflection of the prevailing current system. For example, Zinsmeister & Emerson (1979) reject Kay's (1967) derivation of the Hawaiian molluscan fauna from the islands to the southwest in favour of a western Indo–Pacific source area via the Kuroshio Southern Extension Current. Similarly, Knudsen (1973) attributes similarities between the West African and Mediterranean–Lusitanian molluscan faunas to transport of planktic larvae by the Canary current, while the low degree of similarity between South African and West African faunas may be due to the intervention of the cold Benguela current (and perhaps the turbid freshwater input of the Congo River). Mathematical models of the Suez Canal by Agur & Safriel (1981) suggest that the disparity in frequency of colonization events between the Red Sea and the eastern Mediterranean may also be influenced by the effect of current regimes on the dispersal of free-swimming larvae. Through their computer simulations they found that the completion of a Red Sea-to-Mediterranean passage is far faster and more likely than completion of a Mediterranean-to-Red Sea passage, which may in part explain why more than 120 Red Sea species have colonized the eastern Mediterranean, while fewer than 10 Mediterranean species have colonized the Red Sea (although, as these authors recognize, successful dispersal is not the sole requirement for successful colonization; see Por, 1978; Safriel & Ritte, 1980).

A final example of the interaction between larval ecology and hydrography in determining geographic distribution may be found in Yamada's (1977) study of the intertidal gastropods *Littorina sitkana* and *L. planaxis*, whose ranges abut near Charleston, Oregon. The planktotrophic species *L. planaxis* is apparently unable to expand further northward due to southerly coastal currents during the summer period rather than physiological limiting factors, while the 'direct' developing *L. sitkana* is prevented from spreading south by the rarity of suitable habitats along this portion of the coast (and, perhaps, the presence of the predatory crab *Pachygrapsus*).

Species with planktotrophic larvae can also confound the paleobiogeographer by occasionally dispersing well outside their home ranges, resulting in biogeographically or climatically anomalous occurrences of rare or unique specimens, which may not actually represent breeding populations (e.g. Zinsmeister, 1974; Robertson, 1979). This process has been described in terms of 'vegetative' and 'reproductive' ranges of environmental temperature, for example, by Kinne (1970). This is an important and sometimes difficult distinction to make in Recent biogeographic studies as well (cf. Simberloff 1976); nonreproductive benthic populations maintained by larval settlement are described by Mileikovsky (1961, 1971), Gage & Tyler (1981*a*, and references therein), and, on a microgeographic scale, by Strathmann *et al.* (1981).

Larval dispersal can also mask older biogeographic patterns. For example, the endemic elements of the Hawaiian biota may have been derived in part by integration of island groups on the Pacific Plate into the Hawaiian–Emperor chain (Rotondo *et al.*, 1981), as reflected in the affinities of the terrestrial biota. However, the endemic mollusks of Hawaii show a greater affinity with wide-ranging Indo–West Pacific mollusks than with the mollusks of the islands of the Pacific Plate, probably as a consequence of continued dispersal of porpagules from the west after integration of the island chain had taken place (e.g. Zinsmeister & Emerson, 1979).

Recognition of differential dispersal capability can provide considerable insight into processes underlying temporal changes in faunal similarities among regions. Just as species with teleplanic larvae can be used to reconstruct paleocurrent systems, species with low-dispersal larvae can be used to infer continuity among continental shelves. One would predict a progressive decrease in faunal similarity as lithospheric plates separated, with nonplanktotrophic groups being the first to develop endemic taxa, and teleplanic groups being the last to lose intercontinental faunal smilarities. Conversely, groups with teleplanic larvae would be the first to anticipate continental collisions, while nonplanktotrophic groups would be unlikely to show pronounced similarity of faunal elements until a virtually unbroken continental shelf was established between the two previously separated plates. For example, if one accepts that Paleozoic articulate brachiopods were as exclusively nonplanktotrophic as their modern relatives, the appearance of European forms in the Early Silurian of North America, and particularly the abrupt replacement of endemic forms with European taxa (e.g. Sheehan, 1975), may document the interval in which essentially continuous continental shelf was established at the closing of the Proto-Atlantic Ocean (see also McKerrow & Cocks, 1976). Fürsich (1977, p. 381; see also Fürsich & Sykes, 1977, p. 154) attributes the scarcity of brachiopods in Boreal Late Jurassic assemblages in part to the inability of short-duration larvae to disperse from Tethyan source areas over unstable epicontinental regions to the north.

Turner (1973) attributed similarities in Late Cretaceous eastern North American (New Jersey) and European bryozoan faunas to a still unbroken continental shelf, which allowed stepwise larval dispersal in a group that today is strongly dominated by species having low-dispersal lecithotrophic larvae. Dissimiliarities between New Jersey and Arkansas faunas were attributed to a significant barrier to dispersal of species with a brief or absent planktic stage – a major deltaic system in the upper Mississippi Embayment. In contrast, Late Cretaceous oyster species in common between eastern North America and Poland (Pugaczewska, 1977, and personal communication) and the widespread occurrence of the Late Cretaceous *Turritella forgemoli* species group (North America, North Africa, Transcaucasia, U.S.S.R., Iran, Baluchistan: Sohl, 1977, p. 521) are more likely to be indicative of planktotrophic development in these groups (as is known for some of their extant relatives) than of proximity of habitat areas or continuity of favourable environments for adult occupation and reproduction.

The utility of partitioning planktotrophic and nonplanktotrophic faunal components for assessing the timing and nature of zoogeographic barrier formation is underscored by the work of Shuto (1974). He found that the number of nonplanktotrophic gastropod species shared among local faunas in the Philippine–Indonesian region declined steeply from the Late Miocene through the Pliocene and into the Early Pleistocene, while the percentage of shared planktotrophic species remained virtually constant throughout this interval. It was inferred that the Celebes Sea was forming at this time, presenting a bathymetric barrier to the species with low dispersal capability, but one insufficiently wide to disrupt gene flow among populations of species with planktotrophic larvae. A more complex explanation may be required, however, since recent geophysical studies indicate that the oceanic crust of the Celebes Sea is Late Cretaceous or Early Tertiary in age (Hamilton, 1979).

Because planktotrophic and nonplanktotrophic larvae are affected differentially by biogeographic barriers, recognition of this dichotomy in dispersal capability will permit a more critical assessment of paleobiogeographic hypotheses. For example, although it is reasonable to explain molluscan faunal similarities between the Indo–West Pacific and the eastern Pacific in terms of dispersal of teleplanic larvae from west to east (e.g. Emerson, 1978; Vermeij, 1978), the low dispersal capability of coral larvae led Heck & McCoy (1978) to reject a dispersal model for hermatypic corals in these regions (e.g. Dana, 1975) in favour of fragmentation and subsequent modification of an Early Tertiary pan-Tethyan biota. Rafting of sessile adults lacking planktotrophic larvae can also disperse species over wide geographic areas; this is probably the mechanism by which certain nonplanktotrophic bryozoans maintain their broad geographic ranges (Lagaaij & Cook, 1973), and may also be important in other species that characteristically attach to or bore into floating wood or plant material (e.g. Arnaud *et al.*, 1976; Hoagland & Turner, 1980). However, we concur with Kauffman (1975) and Scheltema (1977) that for most benthic species, free-swimming larvae are the most important agents of dispersal and gene flow.

Another little-explored approach is the use of present-day distributions of developmental modes, rather than of individual taxa of known dispersal type. For example, Foster (1974) attributed Late Eocene–mid Oligocene occurrence of marsupiate echinoids in southern Australia to the initiation of cold-water, circum-Antarctic currents at that time. Decline of this high-latitude mode of reproduction through the Oligocene and Miocene could reflect the return of warmer-water conditions, accompanying the drift of Australia into lower latitudes (see also Philip & Foster, 1971). Subsequent paleotemperature and molluscan biogeographic studies corroborate these hypotheses (Zinsmeister, 1982).

Finally, it is possible that significant changes in geographic dispersal might be related not only to the absence of barriers and availability of favourable habitats, but also to the physiological responses of the organisms to a changing environment. Beu (1976) cites major changes in distributions of several probably teleplanic tonnacean gastropods during the Pleistocene, and suggests that this was the result of slowing of development rate by decreased temperature (see also Lutz & Jablonski, 1978*b*) and thus increased planktic duration. However, large regions of the world ocean experienced a decrease in August sea temperatures of 2°C or less during the last glacial maximum (CLIMAP Project Members, 1976), which may not have been a sufficient temperature decrease to affect larval developmental rates in these regions (cf. Loosanoff *et al.*, 1951).

(3) *Paleoecology*

By aiding the assessment of the dynamics of fossil populations, the study of larval shell morphologies can contribute to progress away from the descriptive phase of marine paleoecology. The fecundities, potential for dispersal among habitats, and other demographic characteristics of benthic populations can be inferred through recognition of the two primary developmental modes, as discussed above, and in this way provide insights into the long-term ecological and evolutionary processes underlying the persistence or alteration of benthic assemblages in the fossil record. Moving from populations to species, the evolutionary data prsented above suggest that within a single assemblage, clades having different developmental types will have different speciation and extinction rates; this raises intriguing questions regarding the coherence of marine communities to evolutionary time scales (cf. Hoffman, 1979).

Larval–adult and larval–substratum interactions can also shape the composition of benthic communities. Perhaps the most familiar of these interactions is trophic group amensalism, in which adults of deposit-feeding species cause high mortality of newly settled juveniles (and later growth stages) by destabilizing the sediment–water interface (Rhoads, 1974; Woodin, 1976; Gray, 1981). Thayer (1979) has recently suggested that major long-term changes in the composition of benthic assemblages have been a consequence of increasing intensity of bioturbation since the Paleozoic. These ideas led Jablonski & Bottjer (1982) to suggest that larval capability for attachment to hard substrata at settlement was important in maintaining epifaunal suspension–feeding assemblages on soft substrata during the Cretaceous. By examination of early post-larval morphology, they found that virtually all of the abundantly shelled inhabitants of North American Late Cretaceous mid- to outer- shelf carbonate muds were attached during early ontogeny, suggesting that the scarcity of infaunal suspension feeders in such settings was at least partly attributable to a general inability of these species to attach to hard substrata at larval settlement.

Larval–adult interactions are also important on hard substrata. Overgrowth competition has been well documented as a determinant of the composition of epibiont communities in Recent faunas (e.g. Jackson, 1979, 1981), and has been invoked for ancient epizoan assemblages (e.g. Taylor, 1979*b*; Jackson, 1981). One remarkable recent finding on habitat selection in marine invertebrates has been that some larvae avoid settlement sites that are near superior competitors (Grosberg, 1981; Young & Chia, 1981). It is probable that similar behavioural adaptations played a part in determining the composition of ancient epizoan communities as well.

VI. SUMMARY

1. Modes of larval development play important roles in the ecology, biogeography, and evolution of marine benthic organisms. Studies of the larval ecology of fossil organisms can contribute greatly to our understanding of such roles by allowing us to race effects on evolutionary time scales.

2. Modes of development can be inferred for well preserved molluscan fossils because the size of the initial larval shell (Protoconch I in gastropods, Prodissoconch I in bivalves) reflects egg size. Other morphological criteria are also available, and a comparative approach based on related taxa with known development may be the most reliable method. By combining larval and adult traits, it is possible to recognize modes of larval development in at least some fossil bryozoans, brachiopods, and echinoderms as well.

(*a*) *Planktotrophic larvae* arise from small eggs, are released in enormous numbers with little parental investment per offspring, and suffer tremendous mortality during

and shortly after a planktic existence. These larvae feed on the plankton during development, and are commonly capable of a prolonged free-swimming existence, and thus wide dispersal.

(*b*) *Nonplanktotrophic larvae* (which include both planktic lecithotrophic forms and 'direct developers') generally arise from large eggs, with relatively few young produced per parent. Relative to planktotrophic larvae, nonplanktotrophic larvae generally receive greater parental investment per larva, and larval mortality is generally lower. These larvae rely on yolk for nutrition during development, and planktic durations are generally much briefer than for species with planktotrophic larvae, so that dispersal capability is considerably less. Energetic investment per egg is generally higher than in planktotrophs, but as there are lower fecundities as well it is difficult to generalize about the total energetic cost of one mode of reproduction against the other.

3. Owing to the high dispersal capability of planktotrophic larvae, it has been suggested that species with such larvae will be geographically widespread, geologically long-ranging, and exhibit low speciation and extinction rates. Species with nonplanktotrophic larvae will tend to be geographically more restricted, geologically short-ranging, and exhibit high speciation and extinction rates (again, as a consequence of their characteristically low larval dispersal capabilities).

4. Recognition of differential dispersal capabilities can play a role in paleobiogeographic analyses. Concurrent study of the distribution of groups with contrasting modes of development will permit testing of hypotheses concerning timing, magnitudes and frequencies of migration and vicariance events.

5. Larval types are not randomly distributed in the oceans, but relationships with other aspects of the organisms' biology and habitats are very complex. Mode of development varies with:

(*a*) *Ecology*. A simple r–K model of adaptive strategies is clearly insufficient to explain the observed relationships: while many 'equilibrium' species have nonplanktotrophic larvae, and organisms living in less prdictable environments often have planktotrophic larvae, some of the most opportunistic marine species have nonplanktotrophic larvae. Nonetheless, planktotrophic development seems most suited for exploitation of patchy but widespread habitats.

(*b*) *Latitude*. At shelf depths, planktotrophy is predominant in the tropics, and decreases sharply at high latitudes.

(*c*) *Depth*. Incidence of planktotrophy decreases with depth across the continental shelf, at least in some taxa. Beyond the shelf, many deep-sea organisms are nonplanktotrophic (e.g. most bivalves, peracarid crustaceans), but planktotrophic development appears to be present in other groups (prosobranch gastropods, ophiuroids, and bivalves inhabiting transient habitats such as sunken wood and hydrothermal vents).

These trends in developmental types will be accompanied by trends in evolutionary rates and patterns as outlined above. The study of larval ecology by paleobiologists will yield insights into the processes that gave rise to ancient evolutionary and biogeographic patterns, and will permit the development and testing of hypotheses on the origins of the patterns observed in modern seas.

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IX. ADDENDUM

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