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# **Lower Eocene Crustacean Burrows (Israel) Reflect a Change from K- to r-Type Mode of Breeding Across the K-T Boundary Clarifying the Process of the End-Cretaceous Biological Crisis**

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## **1. Introduction**

Crustacean burrows filled with chalk were found at the lowermost part of the Lower Eocene sequence in southwestern Israel. They are exposed on both sides of a road-cut about 40 m long (Fig. 1) on the way leading from the city of Be'er Sheva to the Israeli-Egyptian border (Fig. 2A; site A; N 30° 57' 36", E 34° 39' 20"). The road-cut exposes grey-greenish clay of the upper part of the Paleocene Taqiya Formation, overlain by white chalk with chert nodules of the Lower Eocene Mor Formation (Fig. 2B). The burrow system consists of horizontal galleries leading to heart-shaped flattened casts of chambers embedded in 12-cm-thick argillaceous chalk (Fig. 2B). This single type of chamber cast preserves on its surface ovoid blister-like elevations with transversal fine scratches. These peripheral structures are identical to those on the phosphatic casts of Campanian crustacean burrow-system chambers described from another exposure along the same road, some 18 km to the east where two types of chamber fillings were found (Lewy & Goldring, 2006). One is circular (D=45 mm) and replicates the arched ceiling with finely scratched elevated ovoid structures, whereas the cast of the floor comprises rings of about eight tubercles replicating pits 4 mm in diameter and 3.0-3.5 mm in depth. The pits were interpreted to host and protect large eggs in a brood chamber. The second kind of chamber changes shape and dimensions from circular (D=45 mm) to arrowhead-shaped up to 100 mm in length with one end rounded and tapering towards the opposite end. This gradually enlarged chamber was suggested to host the young (nursery chamber) and perhaps store food or provide gardening sites. The Lower Eocene burrow system lacks the brood chamber, whereas the heart-like chamber looks as a shortened modification of the Campanian arrowhead chamber, preserving the wall structure of the Campanian chambers. The diameter of the galleries of the Campanian burrows is about 14-17 mm compared to 10-15 mm of the Lower Eocene ones, and the greatest width of the Campanian chambers (about 7 cm) is similar to that of the Lower Eocene ones. Accordingly, the Campanian and Lower Eocene crustacean burrows into pelagic chalk have a similar structure of horizontal galleries connecting between chambers

of similar dimensions and wall sculpture. These common features attest to a similar body structure. The main difference between these two burrow systems is the lack of brood chambers during the Lower Eocene, which reflects a change in breeding strategy sometime between the Campanian and the Early Eocene. Both burrow systems are in pelagic chalk and thus external ecological factors turned the specially constructed brood chamber useless. These local ecological changes were probably associated with the global biological turnover at the K-T boundary. Their evaluation in comparison with other biological changes clarifies the natural processes which resulted in the end-Cretaceous biological crisis.



Fig. 1. Road-cut exposing Taqiya Fm. greenish clay overlain by Mor Fm. chalk (M. Kitin pointing at the fossiliferous bed).

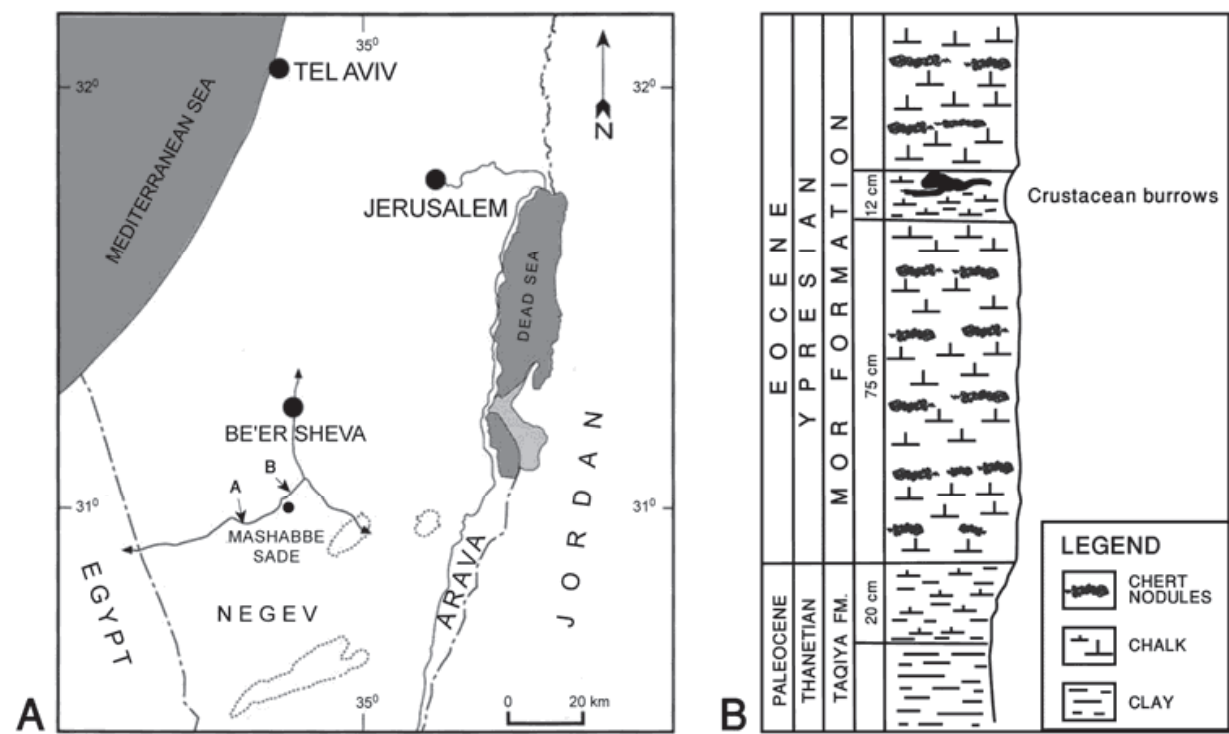


Fig. 2. A. Location map. B. Columnar section of the Upper Paleocene-Lower Eocene fossiliferous interval.

## 2. Crustacean burrows in pelagic chalk

### 2.1 Lower eocene burrows

The road cut exposes the upper part of the greenish clay of the Taqiya Formation (Fig. 2) containing the latest Paleocene (Thanetian) planktonic foraminifer *Morozovella velascoensis* (Cushman). It ranges into the overlying 20 cm of argillaceous chalk which forms a lithological transition to chalk of the Lower Eocene (Ypresian) Mor Formation. The formation begins with 75 cm of lithified chalk with chert nodules containing the Lower Eocene *Morozovella formosa* Bolli and *Morozovella aragonensis* (Nuttall). The layer above is comprised of 12 cm of argillaceous chalk with secondary gypsum at the base and the crustacean burrow system in the upper part. The overlying sequence consists of 0.5-1.0 m thick units of hard chalk with chert nodules alternating with 10-15 cm thick beds of argillaceous chalk. The chalk-filled crustacean burrows consist of horizontal galleries connecting between chambers. Vertical shafts are not preserved. The present elliptical shape of the horizontal galleries attests to sediment compaction to 60-65% of the original vertical dimensions of the galleries as well as of the chambers. The periphery of these chalky casts is friable and part of the external features of the chamber cast is erased. None of the gallery fillings shows any scratches and their walls seem to have been smooth, forming tubes of 1.0-1.5 cm in diameter (Fig. 5G). About 27 heart-shaped casts were collected, probably representing the only kind of chamber fill. Their orientation in the layer is with the heart-shape on the horizontal plane. A gallery enters into the middle of the floor and another one is connected close to the constricted end of the chamber ceiling, pointing a little upward and continues horizontally (Figs. 3, 4B). The chamber casts vary a little in dimensions and proportions whereby the longitudinal length (along the connecting galleries) may be shorter than the transversal width in some specimens. Length ranges between 55-75 mm and width between 55-73 mm. Despite sediment compaction, the thickness (chamber height) of all these casts decreases toward the end with the gallery opening (Figs. 4C, F, H, 5C, E) strengthening the pear-shape of the chamber in side view. Well-preserved casts show ovoid blister-like elevations 5-6 mm broad and 5-9 mm long covering the whole cast, being compressed on the flanks by later compaction. These ovoid structures on the chamber ceiling (upper surface without a gallery entrance) of some specimens tend to orient into transversal lines forming slightly arched ribs about 7 mm in width (Fig. 5B). The horizontal galleries and the flattened chamber casts are concentrated in the upper half of the 12-cm-thick layer.



Fig. 3. Lower Eocene burrowing crustacean chamber and connecting gallery within the chalky sediment (80% of natural size).

The absence of any relict of vertical shaft indicates the truncation of the unconsolidated sediment reaching close to the horizontal burrows. This sediment removal from the deep sea bottom by deep marine currents could have occurred before the fill of the burrows by the following deposition of foraminiferal ooze, or after sediment filled the burrows and formed a stabilized level at which sediment removal stopped.



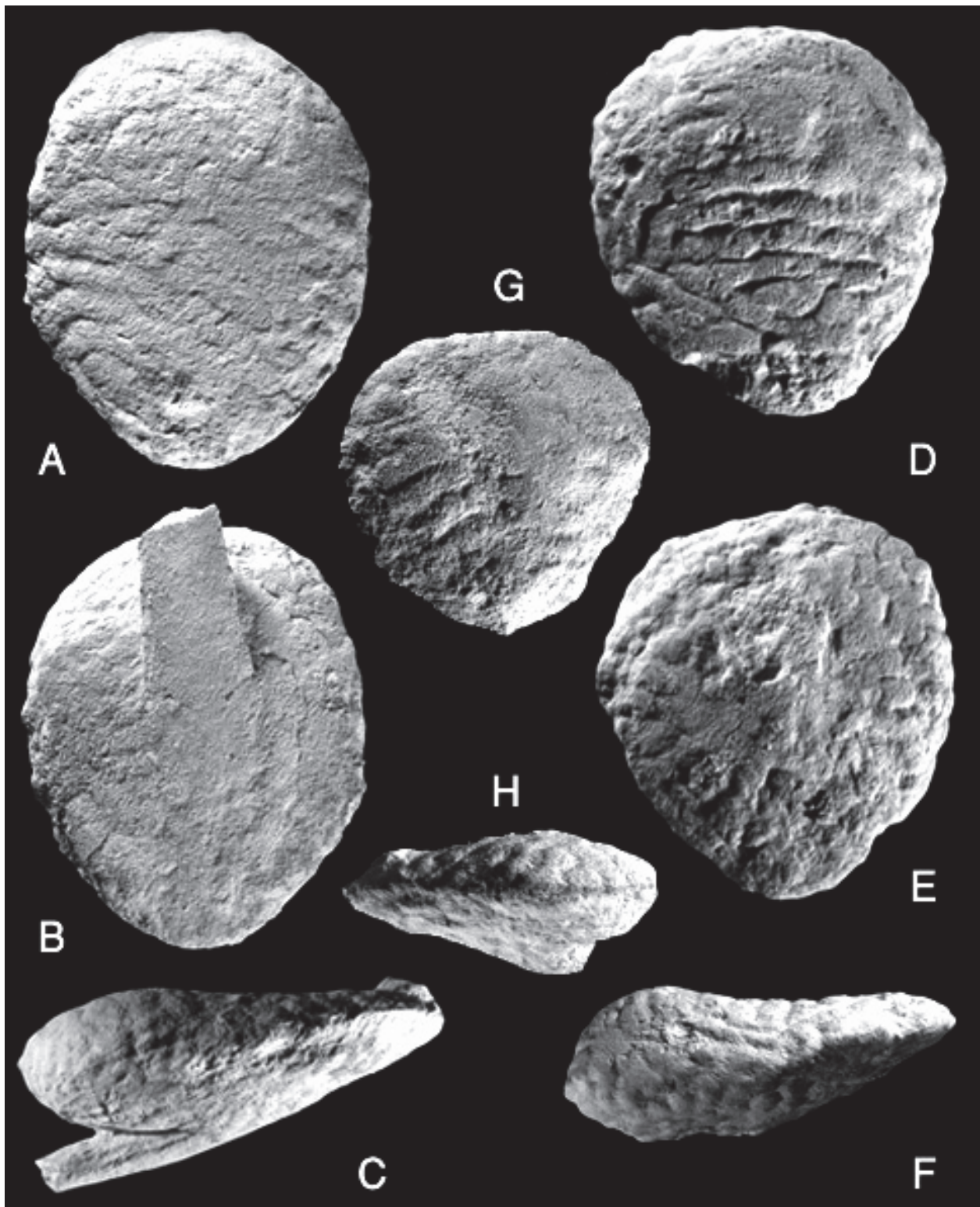


Fig. 4. Lower Eocene, burrowing crustacean, chamber casts (85% of natural size). A: Upper side with relic of broken gallery at the lower (narrow) end. B: Lower side with the gallery exiting from the middle; C: Side view with relics of both galleries. D: Upper side; E: Lower side; F: Side view; G-H: Smallest chamber cast; G: Upper side; H: side view; (A-C sample GSI 8990:1; C-F sample GSI 8990:2; G-H: sample GSI 8990:5).

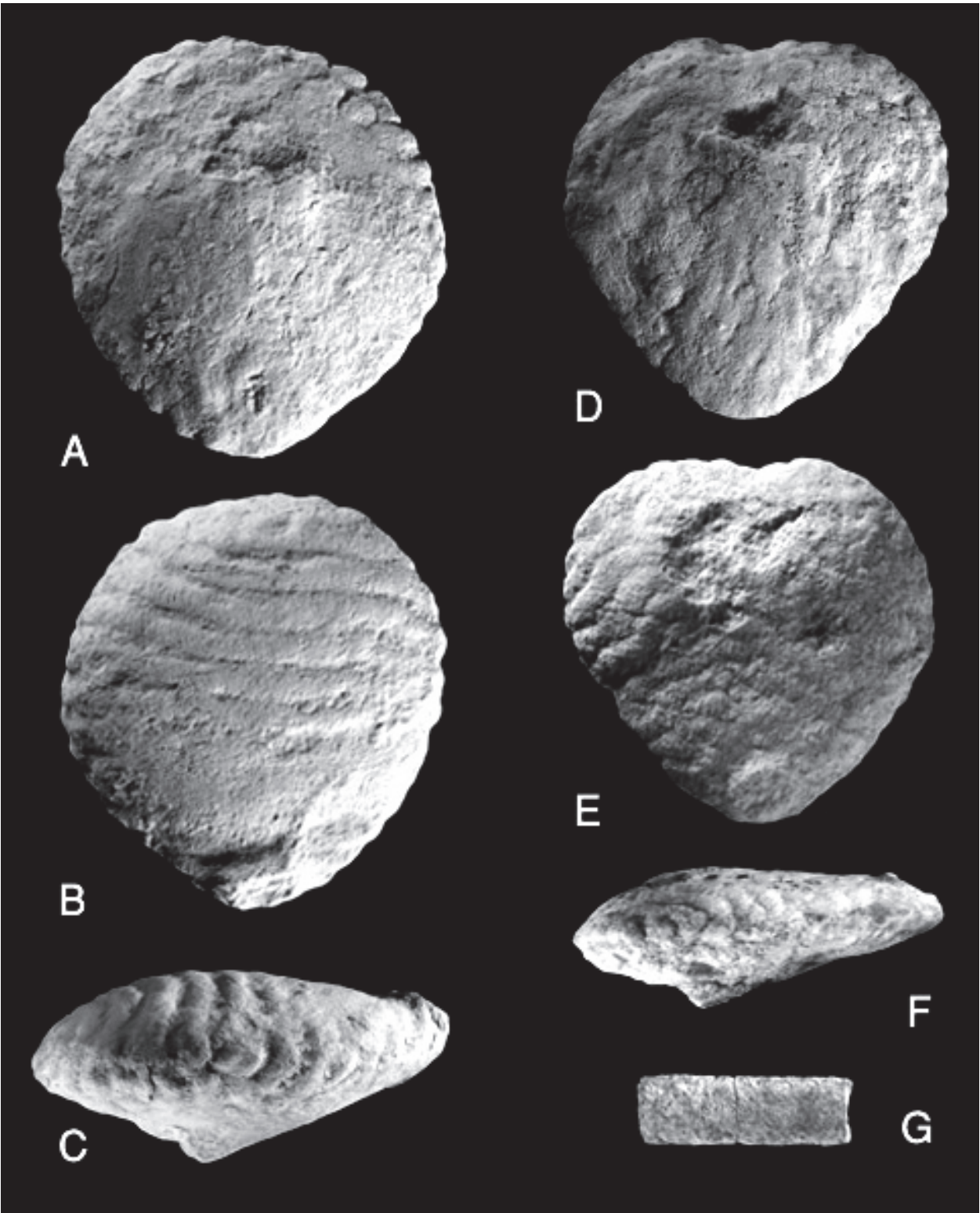


Fig. 5. Lower Eocene, burrowing crustacean, chamber casts (85% of natural size). A: Lower side; B: Upper side showing ovoid blister-like elevations arranged 80% of transversal direction; C: Side view. D: Lower side of heart-shaped specimen; E: Upper side; F: side view; G: Gallery fragment without any distinct sculpture (A-C sample GSI 8990:3; D-F sample GSI 8990:4; G Sample 8990:6).

## 2.2 Campanian burrows

The Campanian crustacean burrows into chalk filled with granular phosphorite were described by Lewy & Goldring (2006). They comprise straight and slightly bent casts of galleries covered by longitudinal scratches. Most of them were compressed by sediment compaction but some preserve the circular cross-section of 14-17 mm in diameter. One of the two kinds of chamber casts occurs in a constant size and a rounded shape 45 mm in diameter. The biscuit-like chamber cast has a gently arched ceiling, with circular to ovoid blister-like elevations covered by transversal fine ribs replicating scratches. The lower surface of the cast comprises rings of about 8 tubercles 4 mm in diameter and 3.0-3.5 mm high in a honeycomb pattern extending over the whole surface (Fig. 6 C, D). The tubercles are smooth, but in an unfinished state of chamber the few tubercles bear fine scratches. On opposite sides of the cast are relics of the pair of connecting galleries. This structure construction replicates a pitted chamber-floor in which the honeycomb configuration of the pits enables crustaceans to cross the chamber by stepping on the floor in the center of the pit rings. This carefully constructed chamber floor comprises 60-70 pits which were interpreted as individual sites for a large egg in a brood chamber within the network of the burrow system. The other chamber type is represented by different shapes and dimensions suggesting its continuous enlargement. The smallest chamber cast is flattened and biscuit-like of a diameter of 4-5 cm, with both sides covered by the finely scratched blister-like elevations. Further enlargement changes the round periphery into an arrowhead shape with one end broad and rounded, tapering toward the opposite end (Fig. 6B). Above a length of 9-10 cm the enlargement of the chamber is vertical (Fig. 6A). The scratched elevations cover the whole cast up to the longitudinally scratched gallery casts on both ends of the elongated cast (Fig. 6B). Only movable objects could be stored in these gradually enlarged chambers. Therefore they were interpreted as nursing chamber for the young, for storing food, and perhaps also as gardening sites.

## 2.3 Comparison between the campanian and the lower eocene burrow systems

Both crustacean burrow systems were dug into pelagic chalk suggesting rather deep marine bottom conditions of several hundred meters in depth. Both occur in the same region, which at the time of deposition were on the seaward flank of the anticlinal structures of the Syrian Arc fold system (Krenkel, 1924), which has been operating and intensifying the folded structures from the Late Coniacian to the Middle Eocene. The chambers in both systems possess the same wall structure carved by the crustacean appendages, and the similar diameter of the galleries in both systems suggest morphological similarity of the producers. The crustaceans living in the Campanian burrow system had to cross the chambers. Therefore the brood chamber was carefully constructed to avoid damage to the eggs. The size of the pits ( $D=4$  mm) attests to the rather large size of the eggs hosted in the brood chamber, probably being cared for until hatching. It seems that only the large eggs laid by the females were kept to assure total recovery (K-type breeding) whereby the number of the young of each hatching phase was the same, keeping more or less a constant size of the community. The construction of the brood chamber, exclusively for egg development, required to transfer the hatchling (larvae) to a nursery chamber where the young developed.

The Lower Eocene burrow system lacks the brood chamber and the single type of chamber has a nearly constant flattened heart-like shape as if it was a concise shortened modification of the Campanian nursery chamber. The entrance and exit at the opposite ends of the Campanian nursery chamber, which required the crustaceans to cross the whole length of



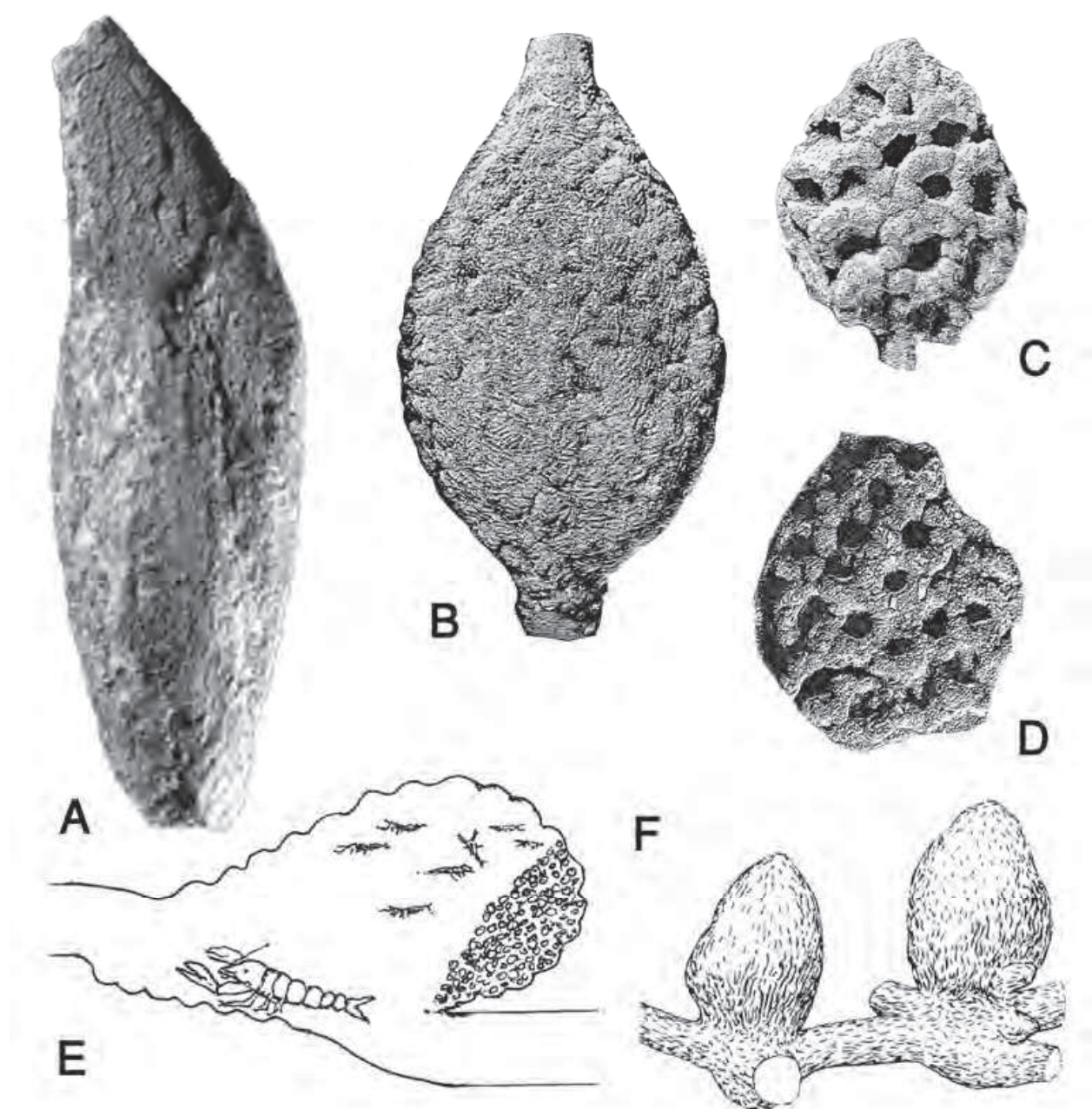


Fig. 6. A-D: Phosphatic molds of the two types of chambers in Campanian crustacean burrow system (samples GSI 5597). A & B: Nursery and storage chambers. A: Side view of vertically enlarged chamber; B: The pattern of the chamber wall consisting of low, circular to ovoid, blister-like elevations in irregular orientation of their length as indicated by fine transversal scratches in different directions. C & D: Casts of chamber floor comprising rings of pits arranged in a honeycomb pattern, leaving alternating non-pitted parts of the floor, which enables crustacean to cross the chamber without stepping on the pit's content. The pits were interpreted as protected sites for individual large eggs in a brood chamber. E: Sketch of the single type of chamber of Lower Eocene burrowing crustaceans suggesting the position of the egg-mass and the hatched young in relation to adult crustaceans crossing the chamber within the burrow network. F: Sketch of Pleistocene *Spongiomorpha sicula* (Sicily, Italy; D'Alessandro & Bromley, 1995). All figures in 80% natural size.



the room, shifted in the Lower Eocene single chamber type to a new position. One gallery tube enters into the middle of the floor and the other tube exits from the upper narrow end of the chamber (Figs. 3, 4C). In that way, a large part of the space is not disturbed while crustaceans cross the chamber. In most chamber casts, the horizontally narrow part is also vertically smaller than the opposite side, which forms a greater space undisturbed by crustaceans crossing the chamber mainly over the floor. This constant chamber configuration attests to its special functions which required digging all chambers in the same design. When compared to the functions of the two Campanian chambers, the single Lower Eocene type of chamber probably fulfilled the necessary functions of brood chamber and nursery room. The lack of special sites protecting the eggs does not mean that the brood was released into the water and the carefully constructed chambers served for storing food and gardening. It is more reasonable to assume that in this case the whole brood mass laid by several females was concentrated in one place in the chamber, protected underground from potential predators and undergoing minimal brood-care. Accordingly total recovery was not expected and the brood consisted of numerous, hence small eggs which in previous Late Cretaceous times would not have been preserved. This breeding strategy reflects the early stages of r-type mode of breeding which in its fully developed stage the brood of numerous small eggs laid by each female was shed into open water. Thus, a small number of hatchling survived to maturity enough to maintain the species' population size relative to the associated organisms. The Lower Eocene hatched young probably developed in a corner where the eggs were concentrated. These free-swimming young swam within the chamber above the egg mass on the bottom of the broader part of the chamber (Fig. 6E).

The communal organization concluded for the Campanian burrowing crustaceans (Lewy & Goldring, 2006) can be extended to the Lower Eocene ones, which were constructed of one type of chamber where the brood of several females was assembled and the hatching young were cared for in another corner.

#### **2.4 Possible cause for the change in breeding strategy**

The Campanian brood chambers were constructed to host each of the selected eggs in individual pits, where they were protected from incidental damage by the crustacean crossing the chamber while swimming through the burrow network. The size of the pits ( $D=4$  mm) suggests that the largest (yolk-rich) eggs were selected from the brood of the females whereas small eggs were not included in the processed brood of every breeding season. Each brood chamber comprised a limited number of eggs, yielding 60-70 hatchlings under full recovery. This limited number of young probably maintained the community, reflecting optimal living conditions under 'luxurious' stable ecological settings. The disappearance of the brood chamber indicates that their function lost its previous significance, though underground protection of the brood continued in the Lower Eocene single type of chamber. What probably rendered these brood chambers useless seems to have been a change toward more eggs in every breeding season, which would require less attention and will supply offspring in the quantity required to maintain the size of a living community. It is suggested that the small eggs which were previously discarded were now gathered into an egg-mass placed at a corner of the underground chambers. These continued to provide a connecting passage within the burrow system and probably served as nursery and storage rooms as well (Fig. 6E). This multifunction may have involved some damage to the free-lying eggs, but their large quantity assured the maintenance of the population size and even an increase in the number of hatchlings. The unlimited number of

eggs that could be obtained in the Eocene brood seasons is in sharp contrast to the Campanian brood in which the number of eggs was limited by the number of pits in the brood chambers, and hence the number of hatchlings even if all the eggs were fertile. The interpreted reduction in egg size did not affect the size of the mature crustaceans as attested to by the similar range of diameters of the Campanian ( $D=14-17$  mm) and Lower Eocene ( $D=10-15$  mm) galleries. This reflects a change in breeding strategy that is neither the result of changes in body or population size, nor of food shortage. It reflects a transition to a more economic mode of life to which the Lower Eocene (or earlier) crustacean population had to adapt under ecological pressure within the same pelagic habitat of their Late Cretaceous ancestors. The reduction in egg size increased the number of eggs that each female laid and hence the overall quantity of eggs in each breeding period. It probably increased the number of hatchlings despite some egg loss due to reduced brood-care. This interpreted need for more hatchlings must have compensated for the loss of individuals being killed while swimming outside the underground tunnel network to look for food. This fatal threat of predation has profoundly increased during the Late Cretaceous as evidenced by other faunal groups (discussed herein).

The evolutionary trend expressed by changes in crustacean burrowing systems can be extended to Early Pleistocene times as exemplified by a burrow system of *Spongeliomorpha sicula* D'Alessandro & Bromley (1995) from Sicily, Italy. Cylindrical vertical shafts and horizontal galleries about 10 mm in diameter bear longitudinal fine ridges replicating scratches. Plum-shaped chamber casts 30 mm high and 25 mm in diameter with similar longitudinal striations occur at gallery junctions every few centimeters (Fig. 6F). They are associated with much shorter cylindrical inflations. The plum-shaped chambers were interpreted as microbial gardening sites (D'Alessandro & Bromley, 1995). Following the study of the Campanian and Lower Eocene burrow systems, we are inclined to refer these chambers to brood and nursery chambers as in the Lower Eocene example. However, in the Pleistocene example each chamber has its own entrance from the lower side, whereby the chamber content is not jeopardized by chamber-crossing crustaceans as in the Eocene example. The associated sediments indicate shallow marine environments which were rich in food sources and should not require production of special nourishment in specially constructed gardening chambers. On the other hand, eggs and larvae shed into the shallow marine water were subjected to rapid consumption by many predators. Thus keeping the hatchlings until they were capable to defend and feed themselves would have been needed to protect the species. This interpretation coincides with the evolutionary trend in this group of burrowing crustaceans from the Late Cretaceous to almost present times. The interpreted care for the brood and the young attests to communal organization at least until the Early Pleistocene and probably might be detected in extant *Spongeliomorpha* species. It seems that these burrowing Crustaceans have maintained communal organizations from times when they inhabited deep water bottoms exposed to predators, and continued to experience the benefits of this co-operation in shallower marine environments.

### 3. The ecological affinities of the upper part of the Cretaceous Period

MacLeod (2005) summarized the characteristic affinities of the Cretaceous Period which ranged between 145.5-65.5 Myr and is generally divided at the Albian-Cenomanian boundary (99.6 Myr) into the Lower and Upper Cretaceous. The warm equable climate (warmer than today) extended into the high latitudes, and the poles were probably without

ice cover most of the year (Hay, 2008). High sea-levels with their peak during the Turonian characterized the general transgressive trend of the oceans throughout the Upper Cretaceous and the Lower Tertiary. The continental plates continued to move toward their present-day position whereby the Atlantic Ocean further opened perpendicular to the Tethys Ocean improving the north-south water circulation. This global plate movement triggered local tectonic movements which differentiated plate margins and intensified the reduction of the previous Albian-Cenomanian-Turonian broad (50-300 km wide) shelves, where rudistid bivalves thrived together with sessile ostreids and chondrodontids. These could survive temporary exposure or cover by sediment, in contrast to hermatypic corals which occupied protected regions in this shallow marine ecosystem. A broad intertidal flat extended landward of this rudistid reefal belt, where calcareous detritus (bioclasts) accumulated and was partly dolomitized under the high salinity of the lagoon and sabkha settings. The abundance of calcitic mollusk conchs highly increased during the middle part of the Cretaceous Period, represented by the shallow marine rudists, oysters and chondrodonts, with Inoceramidae inhabiting the deeper water. The expansion of pelagic environments during the Upper Cretaceous was associated with an increase in the diversity and abundance of planktonic foraminifera and calcareous nannoplankton (Coccolithophorida) all having calcitic endoskeletons. This abundance of biologically precipitated calcite suggested a very low Mg/Ca ratio in Cretaceous seawater (MacLeod, 2005). Keeled planktonic foraminifera diversified from the uppermost part of the Lower Cretaceous (Albian) onward throughout the Late Cretaceous, and were associated with globular forms. Their calcitic tests accumulated as foraminiferal ooze in the outer shelf and deeper marine bottoms forming chalk characterizing the Upper Cretaceous, such as the Lower and Upper Chalk in northwest Europe. The gradual increase in the plankton bloom in the broad oceans triggered a gradual rise in marine productivity evidenced in the later Upper Cretaceous (Campanian-Maastrichtian) by extensive accumulations of organic-rich ('bituminous') chalk with chert (from dissolved diatoms and radiolarians) and phosphorite beds mainly in the Tethys ocean (Lucas & Prévot-Lucas, 1996). These optimal living conditions are corroborated by the increasing diversity of the marine fauna and the development of gigantic organisms. The largest ammonite *Parapuzosia seppenradensis* (Landois) with a diameter of about 2.50 m (Summesberger, 1979) and *P. bradyi* Miller & Yongquist (D=1.37 m) from Wyoming, USA (Larson et al., 1997) are from the Lower Campanian. Large inoceramid bivalves with an axial length of 1 m, and occasionally over 2-3 m in size of the genus *Platyceramus*, occur in the Santonian-Lower Campanian of Colorado (USA) (Kauffman et al., 2007). Marine reptiles related to plesiosaurs and mosasaurs grew to a length of 9-15 m (MacLeod et al., 1997). Their flying relatives (Pterosauria) reached in latest Cretaceous time wide wing spans up to 11-12 m in *Quetzalcoatlus* (Langston, 1981). The marine high productivity extended into early Cenozoic times (Lower Eocene) despite the profound change in zoo- and phytoplankton composition, suggesting that the Late Cretaceous marine physical and chemical properties were neither affected by the Deccan volcanism (India) nor by the asteroid impact. These marine conditions were controlled by the continuing movement of the plates and the general transgressive trend of the widening oceans during the Late Cretaceous and Early Tertiary. Thereby the size of the shelves and the neritic habitats were considerably reduced. Organisms living within the 'reefal' habitat of the rudistid and ostreid buildups decreased in abundance and disappeared from many shrinking shallow marine environments, surviving only in restricted regions. The expansion of the pelagic habitats increased the abundance of the nektonic organisms which comprised



the top predators and thus changed prey-predator relationships. Micropaleontological analyses of Late Maastrichtian pelagic sediments detect short-term paleotemperature fluctuations (Li & Keller, 1998). A progressive cooling trend between ~66.8-65.45 Myr was followed by rapid extreme warming 400-200 Kyr before the end of the Maastrichtian, which was succeeded by a cooler climate during the last 100 Kyr of this stage (Abramovich & Keller, 2002; Abramovich et al., 2010).

#### **4. Victims of disturbed prey-predator relationships under climatic and ecological instability**

Despite the overall flourishing of the Upper Cretaceous marine fauna and flora, the local balance of prey-predator relationship was very fragile, threatening this global paradise. Optimal living conditions on land increased animal diversity, populations size and the dimensions of individuals (gigantism), as in the marine environments. However, any temporary ecological disturbance might have reduced reproduction, resulting in much less young, which played a significant role in the food-chain. The further collapse of the food chain, as the result of increased predatory stress, is examined herein, by comparing the affinities of the organisms which became extinct at the end of the Cretaceous Period to those which survived the biological crisis. The present study builds on the detailed analysis of the geological record of most faunal and floral groups around the K-T boundary, carried out by a large team of experts (MacLeod et al., 1997). They pointed out the terrestrial and extraterrestrial factors which affected life on Earth during a long period as well as short-catastrophic processes close to the K-T boundary. However, the control of the extinction-survivorship pattern was not defined. Re-evaluation of the characteristics of representative marine and terrestrial faunal groups will demonstrate that all those which became extinct at the end of the Cretaceous, were at some stage of their life unable to avoid their predation, thus being victims of temporary extreme predatory stress. This selective over-predation of the vulnerable organisms was caused by the collapse of the food chain as the result of climatic and ecological instability. These are partly reflected by paleotemperature fluctuations of the oceans surface water and deeper levels (Li & Keller, 1998; Abramovich & Keller, 2002), as well as reduction in oxygen content in seawater and dwarfing in marine calcareous planktonic microorganisms. All these phenomena can be related to fluctuations in the intensity of the volcanoclastic dust screening the sunlight, hence affecting photosynthetic activity of the flora and disturbing the biological clock of animals in the sea and on land.

##### **4.1 Vertebrates: Reptiles and fishes**

The disappearance of the dinosaurs close to the end of the Cretaceous Period is presented in scientific and popular publications and films as evidence to the most impressive catastrophic event in Earth history. These reptiles ruled over the land while their flying relatives (pterosaurs) and the marine ones (e.g., plesiosaurs and mosasaurs) were the top predators in the sky and the sea. They diversified during the Late Cretaceous and many of their species grew to giant dimensions (9-15 m long mosasaurs; 11-12 m wing-span of the pterosaur *Quetzalcoatlus*). Their apparent simultaneous disappearance from over the whole world was puzzling. Whatever caused it did not kill the related crocodiles and did not harm the sensitive frogs and salamanders. This selective elimination of the most skillful predators resulted from their early ontogenetic stage. Dinosaurs and pterosaurs were oviparous,

laying 1-7 eggs (or more) in nests on a rather flat land, such as sea-shores (Sanz et al., 1995), tidal flats (López-Martínez et al., 2000) and beside estuaries, lagoons, marshes and fluvial plains (Vianey-Liaud & Lopez-Martinez, 1997). Despite brood-care by the adults, the eggs and the hatchlings were frequently exposed to potential predators and could be snatched from the nest or consumed on site after the distraction of the parent. Dinosaurs and pterosaurs living in this region were probably involved in the killing of their kind. This common process among birds was suspected to have occurred in dinosaurs as indicated by the name *Oviraptor*=‘egg stealer’, given to a dinosaur situated in an egg nest. Other oviparous reptiles such as crocodiles, land lizards and sea-turtles hid the brood and only experienced predators knew were to search for them, whereby most of the eggs hatched and the young quickly looked for shelter. The marine reptiles gave birth to young which were likewise vulnerable to predation at this stage as hinted by bones of small, probably young mosasaurs in Upper Campanian sediments in southern Israel. The dinosaurian branch of birds survived this predatory threat thanks to their rather small body, and hence their egg size. These could be laid in nests high above the ground hidden in trees, in bushes or at inaccessible sites such as on cliffs. The threat to the brood was thus minimized and restricted to the few predators which could discover and reach these breeding sites. The extant large ostrich exemplifies the mode of breeding of the dinosaurs on open ground whereby some of the 10-12 eggs might be consumed by predators.

MacLeod et al. (1997) summarize the record of the Upper Cretaceous cartilaginous **fishes** many of which survived into the Tertiary like many of the bony fishes. Among those which became extinct are *Enchodus* and *Stratodus*. *Enchodus* species reached 1 m of length whereas *Stratodus* species were over 3 m long (Lewy et al., 1992). These rather large bony fishes, as well as most of the cartilaginous ones seem to have swum as individuals in contrast to present-day small fish, forming vortex-like swarms, hence confusing predators. Thus the surviving potential of these small fish is higher than of individual large ones, despite their skills as vicious predators which could be overcome by larger sharks and by big marine reptiles.

## 4.2 Cephalopods

**Ammonites** are another example of a large group seemingly to suddenly disappear at the end of the Cretaceous Period like the dinosaurs. These conch bearing cephalopods diversified during the Upper Cretaceous, providing excellent biostratigraphic markers. Ammonite species gradually disappeared during the Upper Maastrichtian, with 12 reaching close to the K-T boundary in the section exposed in northern Spain, in which other species disappear in groups or individual species during the Upper Maastrichtian (Marshall & Ward, 1996). This is probably the most complete latest Cretaceous sedimentary sequence with ammonites. The simultaneous disappearance of twelve species close to the K-T boundary gives the impression of a catastrophic event that killed all ammonites in this area and seems to corroborate the total elimination of the order Ammonoidea throughout the world.

Lewy (1996, 2002a, b) analyzed the functional morphology of ammonites (ammonoid conchs), especially of heteromorphs, but also of the planispirally coiled ones. Most of the heteromorph ammonites (except for the Baculitidae) developed a U-shaped terminal whorl with an upward facing aperture, which in some species was partly occluded by the previous whorls. Some planispiral ammonites changed the shape of the last whorl, inflating it and

constricting the terminal aperture. Others added apertural appendages. All of these modifications in the last growth stage limited the mobility of the ammonoid by the constricted or upward oriented aperture, complicated nourishment, and in some cases must have resulted in death of starvation. These rather fatal modifications could not have been intended to live further in a different way (Westermann, 1990) and were interpreted to have served the last and most important biological duty of breeding by providing protected brood chambers (Lewy, 1996). The female was situated beside numerous tiny eggs (detected in fossil ammonites) being drifted by currents across the ocean while the eggs developed. This drifting process is corroborated by the wide distribution of many of these non-streamlined heteromorph ammonite species along the Tethys Sea, which could not have been explained by swimming. Such mode of breeding in cephalopods is known in extant octopods which carry out two breeding strategies. The common one is laying large, yolk-rich eggs in bundles attached to submarine substrates ('stationary' mode of breeding), in which both parents care for the brood during several months without eating. They die of starvation close to when the young hatch, each with some yolk for their nourishment during the first hours of free swimming. In the single group of argonautids the female *Argonauta* (larger than the male) secretes from the expanded edge of two of its tentacles a thin calcitic, widely-coiled shell. It situates itself in this boat-shaped shell and lays numerous tiny spherical eggs about 1 mm in diameter, similar in shape and size to spheres detected in fossil ammonites (Lewy, 1996). Together they drift over the sea while the eggs develop ('pelagic' mode of breeding) and the young are shed into the water to cope with life. The shapes of all of the argonautid brood chambers (several fossil and extant species) are identical to latest Cretaceous ammonites. This fragile conch cannot protect its content and merely carries the female and the brood. For this purpose, a smooth boat-shaped shell would be sufficient and the ammonite-like complex sculpture cannot be explained by convergent evolution. Argonautid egg-cases occur since the Late Oligocene (Saul & Stadum, 2005). It is unlikely that only then the 'pelagic' mode of breeding was introduced into octopod breeding strategy. It is more reasonable to explain the first occurrence in Late Oligocene times of fossils of ammonite-like argonautids by the preservation of their calcitic shell. This brood-case might have been made in earlier times of an organic substance (conchiolin) which disintegrated close to after burial in the marine sediment. Octopods have neither an external conch nor an internal hard feature, which renders their geological record sparse. The earliest fossil octopod is an imprint from the Middle Jurassic, but the development of these cephalopods must have been earlier. The few octopod fossils preserved in restricted environments of unusual burial conditions resulted in the dispute over their systematic position among cephalopods. The comparison between the anatomy and physiology of extant octopods and the functional morphology of ammonites suggests close genetic relationships between these two cephalopod groups, one of which survived the end-Cretaceous biological crisis (Lewy, 1996, 2002).

The straight (orthocone) baculitids are heteromorph ammonites which did not modify the last growth stage and probably had another breeding strategy. All baculitid species seem to have formed local evolutionary lineages and were hence indigenous species like several planispiral ammonites, which characterize biogeographic provinces in contrast to the 'cosmopolitan' distribution of most heteromorphs. The 'pelagic' mode of breeding resulted in the wide distribution of these species, whereas in the 'stationary' mode of breeding the hatchlings remained in the area where they hatched and formed indigenous species. This



means that the two modes of octopod breeding occurred in ammonoids and controlled their distribution. The similarity of the argonautid brood cases to Upper Cretaceous ammonites strengthens these ammonoid-octopodid relationships, suggesting phylogenetic connections. Lewy (1996) suggested that octopods descended from ammonoids in which the conch degenerated until total loss like in opisthobranch gastropods. This evolutionary trend can be explained by the diversification of fish, sharks, marine reptiles and belemnites (Lewy, 2009) predating, among others on slow swimming ammonites which their conch did not protect anymore from these skillful hunters. On the other hand, the conch limited the expansion of the mantle cavity and hence the expelled water jet which controlled swimming speed. The lack of an external conch overcame these restrictions and improved maneuverability, while additional strategies improved octopods' escape from predators. The earliest octopods descended from several ammonoid groups, whereby some carried out the 'stationary' mode of breeding and the others- the 'pelagic' mode. These conchless creatures were physiologically required to carry out the two modes of breeding in which the 'pelagic' one a floating egg-case was needed. Empty ammonites floated for some time over the Jurassic and Cretaceous seas before sinking into the depths. These were occupied by the relevant octopods and amended into suitable egg-cases. In Late Cretaceous times, the common ammonites *Hoplitoplacenticeras*, *Jeletkytes* and *Phylloceras* were amended into floating egg-cases by the breaking off of the terminal part of the conch and its extension in an uncoiling shape, enabling the octopod female to enter and care for the brood. This added part was probably made of conchiolin secreted from glands developed at the end of two tentacles as reflected by extant argonautid octopods. The disappearance of floating conchs in earliest Cenozoic times forced the surviving octopods to produce the whole brood-case, which they did in the shape of the Late Cretaceous ammonites, which their ancestors had learned to construct. The short longevity of extant octopods (1-3 years), when applied to ammonoids provided an explanation to the function of the fluted margins of ammonite septa (Lewy, 2002a), ammonoid high evolution rate and other phenomena in ammonoids (Lewy, 2002b), corroborating the deduced ammonoid-octopodid genetic relationships as hinted by other common characteristics (Lewy, 1996). Accordingly, the order Ammonoidea did not completely disappear at the K-T boundary, but only the conch-bearing ones. In this respect the Ammonoidea are comparable to those dinosaurs from which the birds descended.

The endoskeleton of the cephalopod order of **Belemnitida** has been suggested to balance the horizontal orientation in the water while the belemnoid preys and swallows skeletal fragments (Lewy, 2009). These were mainly made of calcareous composition of a specific gravity twice that of flesh, being temporarily stored in the frontal crop. The change in weight in the anterior side through the accumulation and regurgitation of these fragments was balanced by water-gas exchange in the phragmocone. The rapid evolution of the belemnites since the Early Jurassic was associated with the appearance of calcitic opercula (aptychi) in ammonites. This calcification of the pair of 'wings' of the lower jaw in the shape of the aperture was intended to protect the ammonoid by preventing crustacean claws, belemnite tentacles and other means of predation from penetrating into the conch. Most aptychi are found associated with belemnites suggesting prey-predator relationships. The same ammonite genera (e.g., *Baculites*) in regions without belemnites, lack any associated aptychi plates (Lewy, 2009). Some Late Cretaceous belemnites reduced the size of the guard (rostrum) up to complete disappearance (e.g., *Naefia*, *Groenlandibelus*) suggesting a change in their diet comprising less skeletal parts- a fact which was attributed to the profound reduction in the abundance of ammonites as prey. These latest Cretaceous belemnites share

common morphological affinities with Early Tertiary sepiids (Coleoidea) suggesting an evolutionary transition across the K-T boundary rather than belemnoid extinction (Lewy, 2009).

Five Late Cretaceous **nautiloid** genera crossed the K-T boundary (Kummel, 1964). Many had a spherical shape which was not easy to catch and crush, despite the fact that the ammonoids and the nautiloids were preyed by mosasaurs (Kauffman, 2004). All cephalopod groups descended from ancestral nautiloids and the extant ones have similar anatomical features, except for nautilids. The latter have a primitive eye structure, two pairs of gills and numerous small tentacles in contrast to vertebrates-like eyes, a single pair of gills and ten or eight tentacles as seen, for example in cuttlefish, squids and octopods. These anatomical and physiological differences suggest that the extant nautilid adapted to darkness and oxygen deficiency, such as exists in the deep ocean where they are found today, restricted to the southwestern Pacific Ocean (Kummel, 1964). Mesozoic fossil nautiloids occur in shallow and deep marine sediments. It is reasonable to assume that nautiloids swimming in open marine waters were attacked by sharks, large fish, large octopods and squids. The slow swimming nautiloids escaped into deeper marine environments already millions of years ago during which their anatomy and physiology considerably changed and therefore cannot be applied to Mesozoic and older nautiloids (Lewy, 2000). This trend explains how nautiloid genera survived the Late Cretaceous biological crisis which affected their associated coelate ammonites. This crisis was not caused by acid rain (Prinn & Fegley, 1987) which would have killed most nektonic organisms, but reflects an increase in predation pressure (as reflected by other faunal groups) from which nautiloids escaped into deeper water and less menacing habitats.

#### 4.3 Bivalvia

Most bivalves are burrowers into the sediment and are thus hidden from predators, in contrast to epifaunal species. Among the few groups which did not survive into the Cenozoic are the sessile, epifaunal, gregarious **incoceramid** bivalves, which thrived in large communities on rather deep marine bottoms of calcareous shale and chalk. These sediments preserved organic matter in some places, suggesting temporary reduced oxygen content and hence living conditions unfavorable to other organisms (Kauffman et al., 2007). The decimeter to over a meter long bivalves are found up to the base of the Upper Maastrichtian, with questionable relics at higher levels. Their small relative *Tenuipteria* survived to the end of the Maastrichtian (Dhondt, 1983; Marshall & Ward, 1996). This selective extinction can be explained by increased predation by sharks and mosasaurian reptiles (Kauffman, 1972), which dived into the deep bottom for the easy prey due to the fragile nature of the prismatic shell structure of these sessile, rather large bivalves, which until the beginning of the Upper Maastrichtian coped with the usual predation rate.

**Rudists** were individual marine bivalves attached to substrates or reclining on the soft sediment. Whether or not they hosted photosynthesizing zooxanthellae, they concentrated in shallow water where food supply and aeration were optimal. They probably had a short larval stage and could not have drifted far from their ancestral rudists before settling down and undergoing metamorphism. Therefore the young rudists are found attached beside, or on top of the previous generation accumulating into wide thickets forming the carbonate-platform framework, or building elongated or lenticular biogenic buildups (bioherms) with or without hermatypic corals, stromatoporoids, calcareous algae and other attached faunal groups. Some rudists reclined on the bottom in the low-energy neritic zone. The general

narrowing of these neritic habitats during the Late Cretaceous reduced rudistid abundance (e.g., central-eastern Mediterranean and Middle East region; Steuber and Löser, 2000) and the associated 'reefal' communities. Late Cretaceous rudist buildups prevailed in restricted regions of the Tethys Sea, such as in the Caribbean province (e.g., Jamaica; Mitchell et al., 2004) where a few genera reached the K-T boundary and became suddenly extinct probably as the result of the asteroid impact at the Yukatan Peninsula in the same region (Steuber et al., 2002). The following initiated tsunami waves might have broken and killed the rudists or covered them by sediment (e.g., Scasso et al., 2005; Bralower et al., 2010; with references). However, the dating of these turbulence-induced deposits relative to the age of the asteroid impact and the K-T boundary are still controversial (Keller et al., 2007).

Most **oysters** are attached to substrates in shallow marine environments tending to concentrate and form oyster banks. A few genera recline on soft bottoms in low-energy environments (e.g., *Gryphaea*, *Pycnodonte*). The 'tribe' Exogyriini (Stenzel, 1971) was highly abundant in the Cretaceous neritic zone and their calcitic shells are well preserved in carbonate platform sediments beside the long-ranging *Ostrea*. Their attached (left) valve first grew in a spiral pattern which opened and straightened into an elongated or rounded cup-shape in which the posterior margin stretched over the substrate and the anterior margin was raised, whereby the flattened upper valve was inclined to the substrate. This mode of growth subjected these oysters to penetration of sedimentary particles in between the valves as well as total cover by sediment. The disadvantageous growth orientation in shallow marine environments added to possible exposure at low tide or predation, all of which resulted in the extinction of this group at the end of the Cretaceous. Thereby they differ from the subfamilies Gryphaeinae and Pycnodonteinae in which the lower valve grew in a nearly planispiral curvature into a cup-shape, whereby the valve commissure (margins) was elevated above the substrate and the flat upper valve was in horizontal orientation (Stenzel, 1971). The larvae of these oysters had to attach before undergoing metamorphism. The shallow marine habitats of the Upper Triassic-Jurassic Gryphaeinae consisted mainly of friable sediment such as sand and marl. Because these sediments lacked large firm substrates, any grain or small fragment served as attachment site as evidenced by the small attachment scar at the oyster beak. With further growth the small substrate lost its anchorage function and the oyster was tilted, raising the substrate above the ground whereby the ventral margins of the oyster nearly sunk into the friable sediment. To avoid the penetration of sedimentary particles, the oyster increased the upward growth of the lower valve whereby the oyster balance changed and required further tilt and upward growth. The resulting planispiral curvature increased the living space in between the two valves beyond the size of the mollusk which was compensated by secondary deposition of shell material on the inner surface of the lower shell (Lewy, 1976). However, the precipitated calcitic foliated shell structure increased the oyster total weight and enhanced its sinking into the sediment. Thereby the curvature and thickness of the Gryphaeinae lower valve reflect the plasticity of the sediment on which it reclined. The crucial effect of this secondary deposit in the lower valve was partly solved in Cretaceous times by changing the compact structure into a vesicular one which characterized the similarly looking Pycnodonteinae. These oysters thickened their valves by layers of light vesicular structures in between layers of foliated structures minimizing the weight of the secondary fill. Thereby the Pycnodonteinae could inhabit very soft bottoms and thrive on marl and planktonic foraminiferal ooze forming chalk in the Upper Cretaceous. Thanks to their adaptation to rather deep marine environments, the Pycnodonteinae survived the end-Cretaceous



biological crisis. This is in contrast to the Exogyrid tribe which lived attached to firm substrates and therefore inhabited mainly shallow marine environments such as gregarious oysters which were subjected to local exposure by long low-tides, being covered by sediment from terrestrial runoff, as well as predation. There they were associated with the oyster-like *Chondrodonta* which could withstand wave impact and thus thrived in high-energy environments and disappeared before the Exogyrids during the Upper Campanian (Stenzel, 1971). Perhaps *Chondrodonta* attained larger dimension and had a thin fragile shell in contrast to *Exogyra* species. The pectinid *Neithea* Group thrived in Upper Cretaceous neritic and continental-slope sediments and probably disappeared at the end of the Mesozoic (MacLeod et al., 1997). After an early byssate stage they reclined on the sea bottom and occasionally leaped for a short distance, thus being exposed most of the time to diving predators, subject to over predation and extinction at the end of the Cretaceous Period.

#### 4.4 Gastropoda

Most gastropod families crossed the Cretaceous-Tertiary boundary nearly unaffected except for the *Nerineidae* and *Actaeonellidae*. These two families comprised rather large gastropods which thrived on the Tethyan warm-water carbonate platforms and their marginal mainly low-salinity zones (Sohl & Kollmann, 1985). The elongated nerineids had a thick external shell reinforced by folds of the inner shell layer. Actaeonellids likewise had a thick shell and most of them formed ovate conchs which probably slipped through the teeth of predators, increasing the resistance of both gastropod groups to predation. Though these gastropods were mobile, they formed layered concentrations and in places lenticular structures. These accumulations suggest that these gastropods lived close below (shallow burrowers) or on the bottom and were thus subjected to exhumation and concentration by turbulent water in the neritic zone. Generally their representative species survived up to the end of the Cretaceous although some disappeared earlier from many provinces (Sohl & Kollmann, 1985, fig. 14) probably as the result of the reduction of the neritic zones and predation of previously untouched organisms.

#### 5. Marine microorganisms with symbiotic zooxanthellae

Marine floral and faunal microorganisms flourished and diversified throughout the Late Cretaceous. Therefore the disappearance of most of them at the end of the period seemed catastrophic (MacLeod et al., 1997). Close to the K-T boundary the calcareous tests of **nannoplankton** and the **planktonic foraminifera** reduced their size (dwarfing) and the assemblage became dominated by low-oxygen-tolerant small heterohelical foraminifera and the disaster opportunist nannofossil *Micula decussata* (Abramovich & Keller, 2002; Keller & Abramovich, 2009). These latest Maastrichtian affected microfossils occur in Indian Ocean drilling samples with volcanic sediments attributed to the Deccan volcanism, hinting to a connection between the intensive volcanism and the deterioration of the marine ecological systems (Tantawy et al., 2009).

#### 6. The end-Cretaceous biological crisis caused by the Deccan volcanism

The main volcanic phase, comprising ~80% of the total Deccan Trap volume, occurred around the K-T boundary and is interpreted as being active during a short time interval in

the middle of the paleomagnetic chron 29r (Keller et al., 2009, fig. 5). Oxygen isotope analyses (Li & Keller, 1998) and the response of microorganisms to water temperature (e.g., Abramovich & Keller, 2002; Abramovich et al., 2010) reflect fluctuations in surface and intermediate depth ocean water temperature during the Late Maastrichtian, especially in the latest 0.5 Myr. Fluctuating cool temperatures (average degrees of 9.9° C intermediate and 15.4° C surface water) during 66.85 and 65.52 Myr were followed by a short-term warming between 65.45 and 65.11 Myr which increased intermediate water temperatures by 2-3° C, and decreased the vertical thermal gradient to an average of 2.7° C (Li & Keller, 1998). A previous study by Stüben et al. (2003) on hemipelagic sediments of Tunisia differentiated three cool periods (65.50-65.55, 65.26-65.33, 65.04-65.12 Myr) and three warm periods (65.33-65.38, 65.12-65.26, 65.00-65.04 Myr). Tantawy et al. (2009, p. 85) point out that **“the biotic effects of volcanism have long been the unknown factors in creating biotic stress. The contribution of the Deccan volcanism to the K-T mass extinction remained largely unknown, although recent investigations revealed that the main phase of Deccan volcanism coincided with the K-T mass extinction”**. Keller et al. (2009, p. 723-4) refer to **“the dust clouds obscuring sunlight and causing short-term global cooling”** as the result of the volcanic eruptions, but **“how Deccan volcanism affected the environment and how it may have led to the mass extinction of dinosaurs and other organisms in India and globally is still speculative”**. The direct cause for seawater temperature fluctuations during the Maastrichtian last half million years and the dwarfed microfossils in this time interval (Keller, 2008) are herein related to sunlight screening by volcanoclastic dust from the Deccan volcanism, suggesting that its main activity extended over the same period.

Most Late Maastrichtian planktonic microorganisms reduced their size (dwarfing) at about 65.4 Myr (Keller, 2008) reaching sexual maturity at smaller dimensions and probably more rapid than their normally-sized ancestors. This assemblage became dominated by low-oxygen-tolerant small heterohelicids (Keller & Abramovich, 2009). All these globally detected abnormal morphological and ecological aspects of the latest Cretaceous marine microfossils attest to the deterioration of the ecological conditions, as the result of sunlight screening and darkening of the Earth to various extents and periods. Global darkening of the atmosphere by fine volcanoclasts decreased photosynthetic activity of the symbiotic zooxanthellae in extreme cases these useless symbionts were digested by their host. The dwarfing of the latest Maastrichtian microfossils was artificially demonstrated by the elimination of these symbiotic dinoflagellates from within the planktonic foraminifer *Globigerinoides sacculifer* (Bé et al., 1982). The loss of symbionts resulted in early gametogenesis (at small size), short life span of the foraminifer and its smaller shell size at sexual maturity (dwarfing), exactly as described from the latest Maastrichtian planktonic foraminifera and calcareous nannoplankton. When the tested live foraminifers were reinfected by zooxanthellae they resumed normal shell growth and size as before the removal of the symbiotic zooxanthellae (Bé et al., 1982). The lack of planktonic microfossils of normal size in the latest Maastrichtian 0.5 Myr indicates that solar radiation was, during this period, too low to resume symbiotic relationships between these photosynthesizing dinoflagellates and the microorganisms. The drastically reduced photosynthetic activity lowered the oxygen content in the upper water column as attested to by the increased abundance of low-oxygen-tolerant small heterohelicids and the blooming of the disaster

opportunistic *Guembelitra* (Keller & Abramovich, 2009). The shading of sunlight reduced the depth of the marine euphotic zone and affected water temperature. A thick cover by ash dust probably lowered sea-water and Earth surface temperature. A less dense screen may have resulted in a greenhouse effect, keeping the warmth of partially penetrating sunlight from escaping into the atmosphere. Paleotemperature fluctuations in the latest Maastrichtian marine environments (Li & Keller, 1998) are accordingly related to fluctuations in the intensity of the Deccan volcanic eruptions and world-wide dispersal of volcaniclasts.

The polyps of reef-building hermatypic **corals** house symbiotic zooxanthellae which are involved in the precipitation of the calcareous skeleton and in other physiological processes, but they can also become part of the coelenterate diet. Unlike in planktonic foraminifera these symbiotic relationships observed on extant corals in the Great Barrier Reef of Australia can be stopped for a while (coral bleaching) during which coral growth slows down while the polyps feed on other algae and microorganisms, organic debris and bacteria (Vernon, 1993). This may explain the survival of some hermatypic coral groups, though a great deal disappeared during the latest Cretaceous (MacLeod et al., 1997).

The fatal influence of the Deccan volcanism on the latest Cretaceous marine planktonic microorganisms applies to marine and large terrestrial creatures as well. The darkening of the atmosphere by dispersed volcaniclasts blurred the distinction between the annual seasons controlling plant growth and blooming, as well as the biological clock of animal reproduction, which provides a significant food source to carnivores after months of near starvation. Seasonality controls the timing of sperm and egg spawning into the water, most of which is consumed by predators awaiting this process. Mating and reproduction among larger animals is coordinated with availability of food supply (plant and meat) which will assure the survival and development of the young. Long-ranging darkness confused the instincts and physiology of animals, reducing birth rate and hence food supply crucial for predating mammals to feed the young as well as for reptiles and birds. The reduction in birth rate (including the laying of eggs) immediately reduced the food supply. The aggressive and large predators (mainly among the reptiles) were forced to consume part of the prey that smaller predators used to eat, whereby the 'normal' food chain collapsed, resulting in the intensive predation of the temporarily unprotected ones. These were dinosaurs and pterosaurs eggs in nests on flat-land and their hatched young, as well as mature ones sitting on the eggs, and other creatures which for a moment were careless. The over-predation of this easy prey reduced the size of the victim's population which gradually diminished until the remaining ones could not preserve the species, leading to extinction. The organisms which were not affected by the collapse of the food chain were small creatures which could escape and hide themselves or their brood such as crocodiles and turtles which covered their brood, birds which laid the small eggs in between plants, small mammals which could hide underground or among bushes, and amphibians and fishes capable of hiding in aquatic environments. The darkening effect of the Deccan volcaniclasts must have slowed down the metabolism of cold-blooded reptiles, among which were probably some large dinosaurs. During the severe darkening they were completely unable to defend themselves even from small predators. The selective elimination of the temporary vulnerable ones is an extreme example of **natural selection** as the result of catastrophic changes in the regular pattern of the long-operating ecological system in which organisms and plants lived in harmony. The additional destructive effect of a single or multiple



asteroid impacts (Keller, 2008) would have had little contribution to the gradual collapse of Earth's biological systems.

## 7. Early Tertiary biological recovery

The Deccan volcanic activity extended into the lowermost Tertiary (~64.8 Myr; Keller et al., 2009) and thereafter the climatic and ecologic systems began their recovery. Small globigerinid planktonic foraminifera survived the end-Cretaceous biological crisis and appear in Early Paleocene sediments (e.g., Orue-Etxebarria & Apellaniz, 2000). Their trochospiral coiling with 4-7 nearly globular chambers in the last whorl resembles other associated species such as *Parvularugoglobigerina eugobina* (Olsson et al., 1999). This general shape and size has been observed in one of the earliest planktonic foraminifer from the Lower Jurassic (probably Hettangian; ca 190 Myr) of Hungary (Görög, 1994). Keeled planktonic foraminifera appeared in the Upper Albian (*Rotalipora*) about 90 Myr later (Leckie, 1987). The earliest Tertiary keeled (pseudo-keel) planktonic foraminifer [e.g., *Morozovella angulata* (White)] appeared at the base of the Upper Paleocene (Thanatian, 58.7 Myr) about 6 million years after the recovery of the ocean ecological setting. This rapid introduction of the keel structure among pelagic foraminifera suggests that the survivors in a 'primitive' appearance preserved in their genome the ability to secrete keels and other morphologies under suitable conditions. The relative quick recovery of planktonic microorganisms after their near elimination at the end of the Cretaceous Period explains the similar recovery of life in the marine and terrestrial bioprovinces. Many Late Cretaceous species retreated to small-restricted niches protected from the side effects of the Deccan volcanism. They continued living in these numerous small habitats, adapting to the restricted ecological settings and thereby gradually changing their physiology, anatomy and the skeleton. With the recovery and stabilization of the ecological systems all of these 'hidden' communities tried to enter and adapt to the physical and chemical conditions of the open-large habitats and share the environment with other communities. Only those which succeeded to accommodate themselves in these extensive bioprovinces in large populations were discovered. The fossil record of all earlier small communities which lived in restricted areas is still missing, giving a misleading impression of a big hiatus in taxa ranges and sudden first appearance of new ones. These are actually members of evolutionary lineages, of which the earliest Paleocene ancestors have not been yet discovered. This all took part in an evolutionary biological continuum from the latest Mesozoic into the Cenozoic. The technical comparison of taxa names between these eras intensified the apparent catastrophic aspect of the end-Cretaceous biological crisis, being erroneously referred to a **mass extinction**.

## 8. Conclusion

Sunlight screening by volcanic dust from the Deccan volcanic eruptions blurred the distinction between annual seasons and disordered the biological clock of organisms and plants on land and in the sea. Flowering plants produced less fruits for vegetarians, reducing their birth-rate. The disturbed sexual cycle of carnivores likewise lowered their birth rate and drastically reduced the amount of food (eggs and young born), on which adults depended for feeding themselves and their young ones after a long period of near

starvation. Food shortage resulted in intensive predation of those which could not escape or hide. The comparison between Campanian and Lower Eocene crustacean burrow systems into pelagic chalk suggest a change in the mode of breeding from a few large eggs specially treated (K-type) to numerous tiny eggs partly cared for (transition to r-type) to compensate their over-predation. Dinosaur and pterosaur eggs were laid in nests on open-flat land such as estuaries, tidal-flats and shores. They and the few successfully hatched young provided easy prey, most probably to carnivorous reptiles living in the same region. The hatched young of marine reptiles were vulnerable to predation by other reptiles, sharks and large fishes. Reptiles which hid their brood (e.g., crocodiles, sea-turtles), birds laying their small eggs among plants or at sites inaccessible to non-flying organisms were not much affected by the predatory stress. The small mammals of that time could hide in the underground and in hidden places where they survived the predatory threat. The detected fluctuations in seawater temperature during the Cretaceous last half million years (Li & Keller, 1998) resulted from variations in the amount of volcanoclastic dust released into the atmosphere by the Deccan volcanic eruptions of different intensities and duration. A thick, long-lasting dust screen blocked the solar radiation resulting in the cooling of Earth's surface land and ocean-water. A thin volcanoclastic screen created a 'greenhouse' effect raising the temperature on the Earth. The associated darkening reduced the metabolism and the activity of cold-blooded reptiles, whereby the large ones living on land could not withstand even small predators. Darkening reduced and stopped the photosynthetic activity of the symbiotic zooxanthellae in planktonic foraminifera and calcareous nannoplankton lowering the oxygen content in the reduced euphotic zone as reflected by an increase in abundance of microorganisms tolerating low-oxygen conditions (e.g., Tantawy et al., 2009). The lack of these symbionts lowered the rate of calcium-carbonate precipitation, as attested to by smaller test sizes (dwarfing) of the planktonic microfossils during the last 0.5 Myr before the K-T boundary (Keller, 2008), being demonstrated in laboratory experiments on extant planktonic foraminifera (Bé et al., 1982). The recovery of most of the Late Mesozoic life forms during the Early Cenozoic suggests that all those organisms and plants survived predation thanks to their capabilities as well as by retreating to restricted and protected habitats. There they adapted to the local and changing ecological settings during a few million years until most of them succeeded in returning to the open-large marine and terrestrial habitats. Thereby they re-appeared in the fossil record, some in a new shape as the result of adaptation to changing settings during a few million years of the recovery of Earth's ecological systems. All of these seemingly new taxa took part in continuous evolutionary lineages ranging across the K-T boundary and during the aftermath of the biological crisis. They passed most of this period in hitherto undiscovered sites and therefore these intermediate evolutionary stages do not appear in the fossil record. The resulting different nomenclature of taxa between the Late Cretaceous and the Early Tertiary was erroneously referred to the mass extinction of the Cretaceous species. The end-Cretaceous biological crisis was actually an extreme example of natural selection caused by the Deccan volcanic activity.

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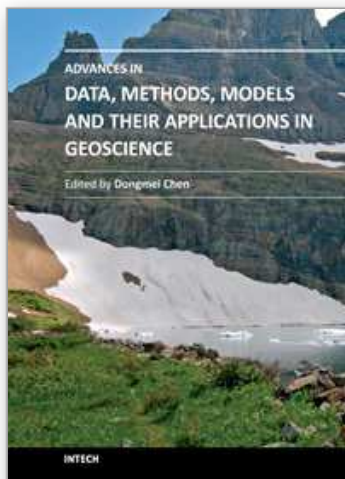
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