

## Punctuationalism and Gradualistic Evolutionary Trends of Eight Phylogenetic Lineages of Maastrichtian to Eocene and Recent Benthic Foraminifera from the Tethys

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### Abstract

Minor differences in the morphology of the test, wall structure, arrangement of chambers and apertures, size are recognized as being of decisive specific or subspecific value. Twenty four phylogenetic lineages were produced by punctuated equilibrium and gradualistic evolutionary trends which observed within 50 benthic foraminiferal species and subspecies belonging to 18 genera throughout the Maastrichtian to Priabonian forms in Tethys as well as one recent species by the present authors and others. In this study, new eight lineages are presented: *Clavulina parisiensis* d'Orbigny > *C. pseudoparisensis* Anan, *Laevidentalina granti* (Plummer) > *L. salimi* Anan, *Lenticulina carinata* (Plummer) > *L. turbinata* (Plummer) > *L. chitanii* (Yabe and Asano), *Percultazonaria ameerii* Anan > *P. allami* Anan, *Percultazonaria alii* Anan > *P. longiscata* (Nakkady), *Percultazonaria wadiarabensis* (Futyán) > *P. tuberculata* (Plummer), *Palmula woodi undulata* Nakkady > *P. w. woodi* Nakkady, *Gavelinella b. brotzeni* Said and Kenawy > *G. brotzeni paleocenica* Said and Kenawy. These lineages help, not only to define the major faunal changes at the Cretaceous/Tertiary (K/T) and the Paleocene/Eocene (P/E) boundaries, but also to emphasize the stratigraphic importance of them in different localities in the Tethys.

**Keywords:** Benthic foraminifera; Phylogeny; Lineages; Paleontology; Stratigraphy.

### Introduction

Many attempts have been made to interpret the phylogeny of fifty benthic foraminiferal species, which could have evolved from earlier stratigraphic species and used it in twenty four phylogenetic lineages by some authors: Nakkady [1], Anan [2,3,4,5,6,7]. Eight evolutionary lineages are recorded here which marked the changes in the stratigraphy, morphological characters, arrangement of chambers and ornamentation

of some benthic foraminiferal taxa throughout the Maastrichtian-Priabonian and Recent in the Tethys.

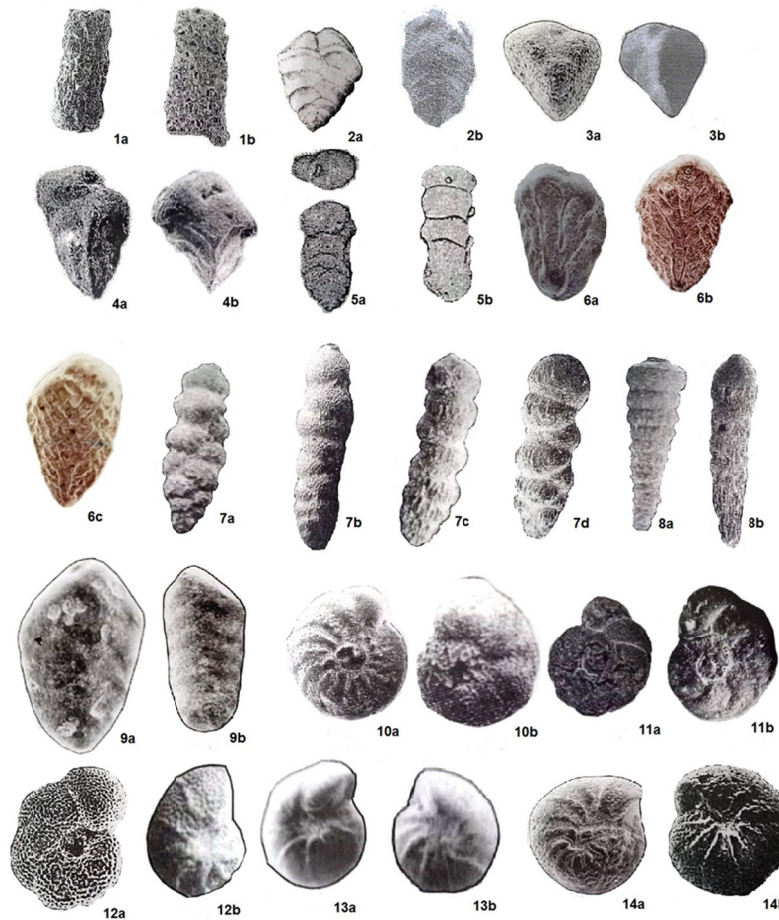
### Previous studies

Three lineage were presented by Nakkady [1]: *Orthokarstenia esnehensis* (Nakkady) > *O. eleganta* (Plummer), *O. esnehensis* (Nakkady) > *O. higazyi* (Nakkady) and *Cibicidoides abudurbensis* (Nakkady) > *C. pseudoacutus* (Nakkady). One lineage was proposed by Anan [2]: *Orthokarstenia oveyi* (Nakkady) > *O.*

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*applinae* (Plummer). Five lineage were presented by Anan [3]: *Verneuilina aegyptiaca* Said and Kenawy > *V. luxorensis* Nakkady, *Coryphostoma incrassata* (Reuss) > *C. midwayensis* (Cushman), *Anomalinoides rubiginosus* (Cushman) > *A. midwayensis* (Plummer), *Gyroidinoides girardanus* (Reuss) > *G. luterbacheri* Anan, and *Angulogavelinella nekhliana* Said and Kenawy > *A. avnimelechi* (Reiss). Another one lineage was proposed also by Anan [4]: *Cibicidoides pharaonis* (LeRoy) > *C. farafraensis* (LeRoy). Four lineage were proposed by Anan [5]: *Bathysiphon paleocenicus* El

Dawy > *B. saidi* (Anan), *Spiroplectinella knebeli* (LeRoy) > *S. paracarinata* (Said and Kenawy), *Gaudryina pyramidata* Cushman > *G. ameeri* Anan and *Siphogaudryina nekhliensis* (Said and Kenawy) > *S. africana* (LeRoy). Also one lineage was proposed by Anan [6]: *Orthokarstenia eleganta* (Plummer) > *O. nakkadyi* Anan > *O. higazyi* (Nakkady). Another one lineage was presented by Anan [7]: *Bolivinoides draco aegyptiacus* Anan > *B. d. draco* (Marsson) > *B. d. dorreeeni* Finlay (Plate 1).



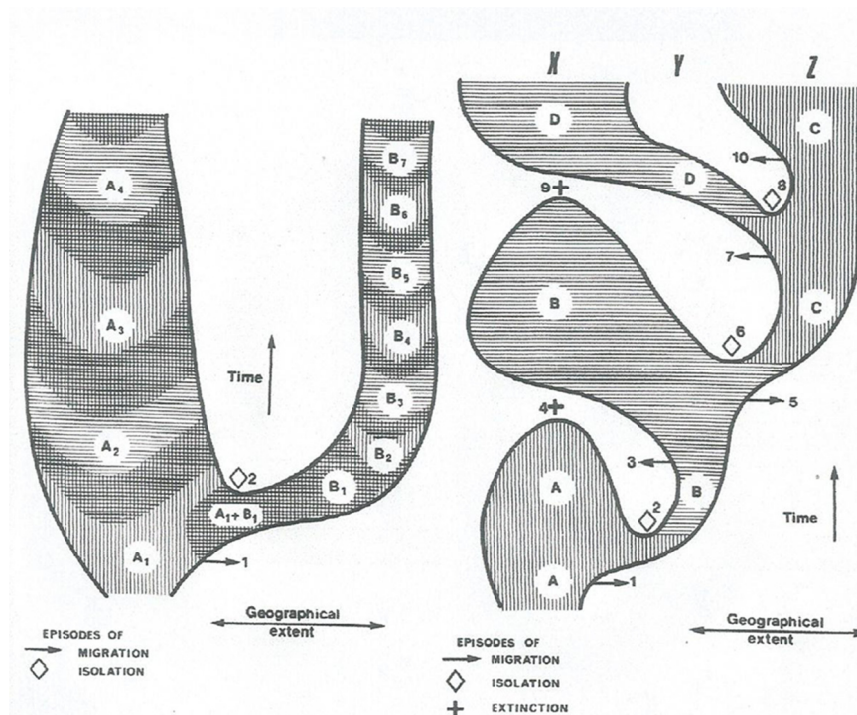
**Plate 1.** Figure: **1a:** *Bathysiphon paleocenicus* El Dawy, after Anan [6], **1b:** *B. saidi* (Anan) after Anan [20]. **2a:** *Spiroplectinella knebeli* (LeRoy [41]), **2b:** *S. paracarinata* (Said and Kenawy [32]), **3a:** *Verneuilina aegyptiaca* Said and Kenawy [32] after Anan [3], **3b:** *V. luxorensis* Nakkady [42] after Anan [3], **4a:** *Gaudryina ameeri* Anan [5], **4b:** *G. pyramidata* Cushman, after Anan [5]. **5a:** *Siphogaudryina africana* (LeRoy [41]) after Anan [5], **5b:** *S. nekhliensis* (Said and Kenawy [32]) after Anan [5]. **6a:** *Bolivinoides draco aegyptiacus* Anan [7], **6b:** *B. d. draco* (Marsson [49]) after Anan [7], **6c:** *B. d. dorreeeni* Finlay, after Anan [7]. **7a:** *Orthokarstenia esnehensis* (Nakkady [42]) after Anan [2], **7b:** *O. eleganta* (Plummer [23]) after Anan [2], **7c:** *O. higazyi* (Nakkady [1]) after Anan [2], **7d:** *O. nakkadyi* Anan, after Anan [29], **8a:** *O. oveyi* (Nakkady [42]) after Anan [2], **8b:** *O. applinae* (Plummer [23]) after Anan [2], **9a:** *Coryphostoma incrassata* (Reuss) after Anan [3], **9b:** *C. midwayensis* (Cushman) after Anan [3]. **10a:** *Cibicidoides abudurbensis* (Nakkady [42]) after Anan [3], **10b:** *C. pseudoacutus* (Nakkady [42]) after Anan [3]. **11a:** *Cibicidoides pharaonis* (LeRoy [41]) after Anan [4], **11b:** *C. farafraensis* (LeRoy [41]) after Anan [4]. **12a:** *Anomalinoides rubiginosus* (Cushman) after Anan [3], **12b:** *A. midwayensis* (Plummer [23]) after Anan [3]. **13a:** *Gyroidinoides girardanus* (Reuss) after Anan [3], **13b:** *G. luterbacheri* Anan [3]. **14a:** *Angulogavelinella nekhliana* Said and Kenawy [32] after Anan [3], **14b:** *A. avnimelechi* (Reiss) after Sztrákös [17].

**Taxonomy and stratigraphical value of benthic foraminiferal phylogenetic lineages**

Lemon [8] noted that a lineage in which one species or subspecies gradually evolves from another by a progressive shift in one or more morphological parameters is a process of speciation by phylogenetic trend (or phyletic gradualism or anagenesis) which produced a mixed morphologic character between the descendent species and the ancestral one, or by punctuated equilibrium trend, which means that a species migrates to another region and after some time back again to the previous region but with another morphological character to produce another species (Fig. 1). He also noted that the first occurrence of a new species within a sedimentary succession, assuming we are not dealing with an arbitrarily defined morphospecies within an evolutionary lineage, is not only abrupt but is unlikely to present the time of its appearance on earth. Hunter et al (9) noted that the documentation rates of evolution are not intermediate between the predictions of the punctuational and gradualistic models, rather they span the full spectrum of possibilities, and the foraminifera tend to evolve gradually, while the few well-documented cases of evolution in the macroinvertebrates suggests a rather more punctuated tempo. Very commonly the appearance of a species coincides with a change of lithology; this

may be because the species is facies-linked and migrated from elsewhere as the favorable habitat expanded. In such cases, it may be that more subtle alternations in the environment, such as changes in water temperature or salinity, might be sufficient to cause the appearance or disappearance of a particular species, but not to affect the character of the sediment being deposited. Fara and Langer [10] noted that a phylogenetic biochronology should rely on the historical relationships between ancestors and descendents. They also added that the taxa diagnosed by plesiomorphic characters are common among fossil taxa, and these potential ancestral forms are likely to be found in the fossil record.

The present study presented eight new evolutionary lineages based mainly on the change in shell morphological characters of some benthic foraminifera in the Maastrichtian-Priabonian stages, particularly around the Cretaceous/Tertiary (K/T), the Paleocene/Eocene (P/E) boundaries, and Recent in Egypt from many sections in Sinai, Farafra Oasis, Red Sea coast of Egypt and also other parts in the Tethys, which evolved by one of the two evolutionary models: phyletic gradualism (phyletic gradualism, model A) or punctuated equilibrium (model B). These new eight lineages: *Clavulina parisiensis* d'Orbigny > *C. pseudoparisiensis* Anan, *Laevidentalina granti*



**Figure 1.** The two trends or models of speciation: Phyletic Gradualism (left, model A) and Punctuated Equilibrium (right, model B), after Lemon [8].

(Plummer) > *L. salimi* Anan, *Lenticulina carinata* (Plummer) > *L. turbinata* (Plummer) > *L. chitanii* (Yabe and Asano), *Percultazonaria ameeri* Anan > *P. allami* Anan, *Percultazonaria alii* Anan > *P. longiscata* (Nakkady), *Percultazonaria wadiarabensis* (Futyán) > *P. tuberculata* (Plummer), *Palmula woodi undulata*

Nakkady > *P. w. woodi* Nakkady, *Gavelinella b. brotzeni* Said and Kenawy > *G. brotzeni paleocenica* Said and Kenawy (Fig. 2). The taxonomy for the studied 17 species and subspecies (belonging to 6 genera) used the scheme of Loeblich and Tappan [11] and presented in Plate 2.

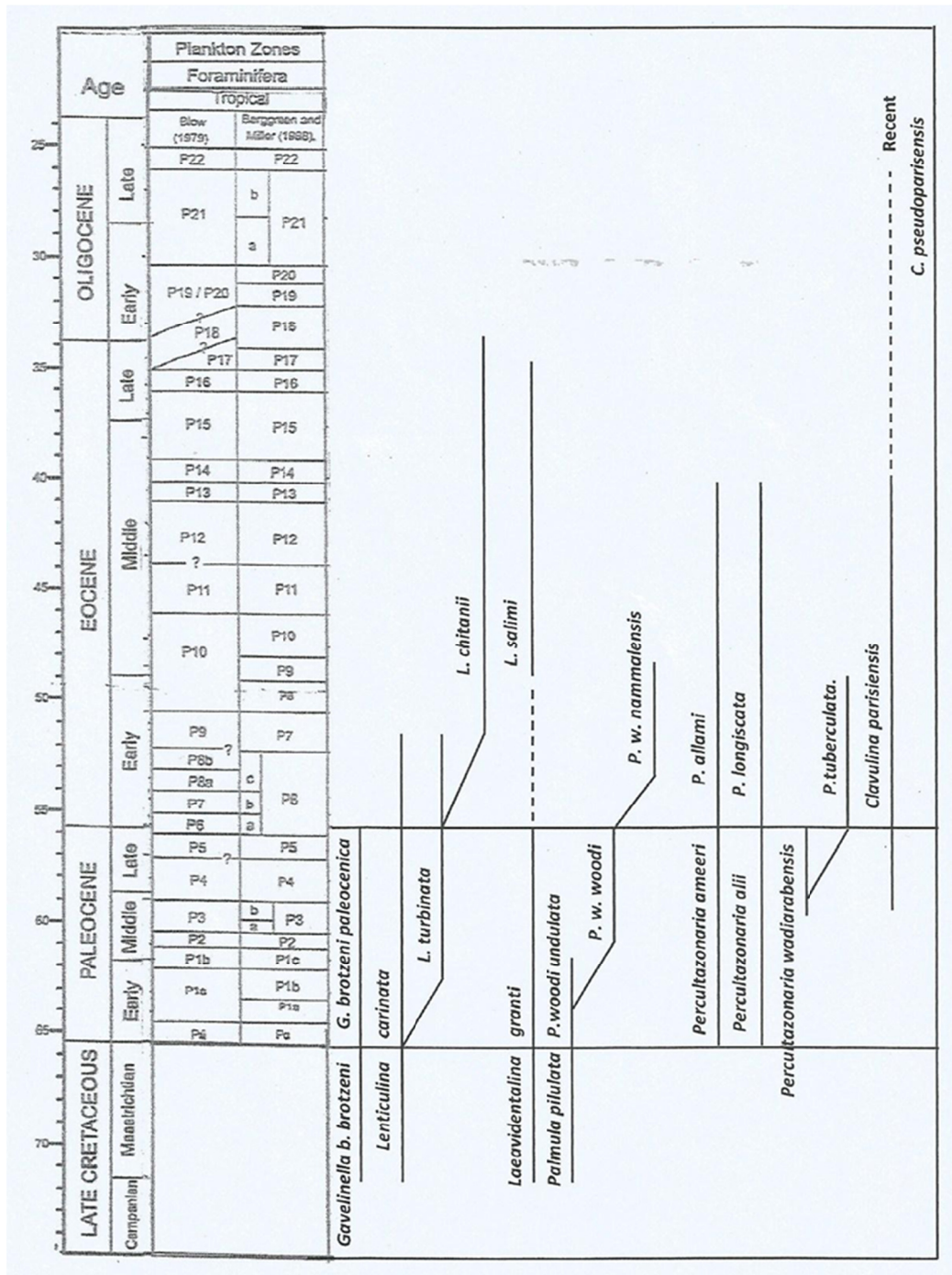
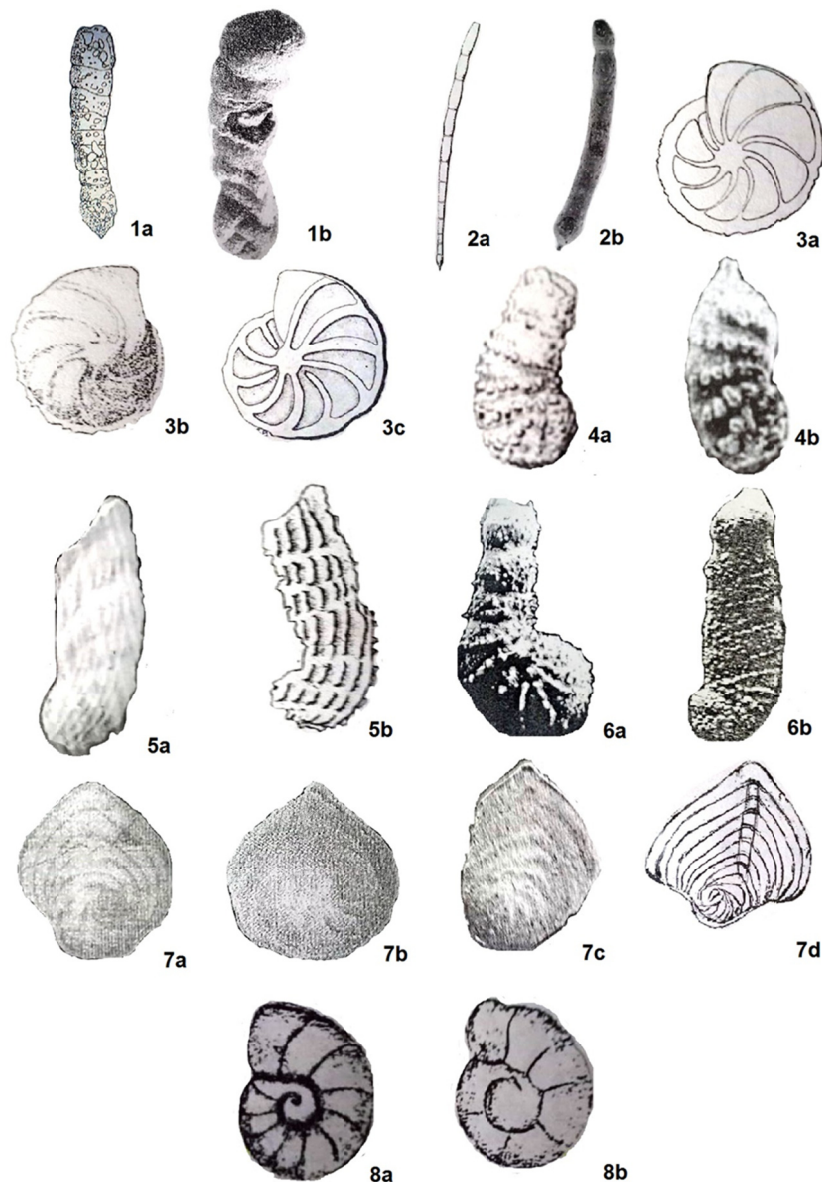


Figure 2. The eight phylogenetic lineages from Maastrichtian-Priabonian and Recent foraminiferal species and subspecies from the Tethys.



**Plate 2:** Figure: **1a:** *Clavulina parisiensis* d'Orbigny [12] after Sztrákos [17], **1b:** *C. pseudoparisensis* Anan [18], **2a:** *Laevidentalina granti* (Plummer [23]), **2b:** *L. salimi* Anan [29], **3a:** *Lenticulina carinata* (Plummer [23]), **3b:** *L. turbinata* (Plummer [23]), **3c:** *L. chitanii* (Yabe and Asano [36]) after Ansary [41]. **4a:** *Percultazonaria ameerii* Anan [40], **4b:** *P. allami* Anan [40], **5a:** *P. alii* Anan [40], **5b:** *P. longiscata* Nakkady [42] after Anan [40]. **6a:** *P. wadiarabensis* (Futyan [15]), **6b:** *P. tuberculata* (Plummer [23]) after Berggren and Aubert [34]. **7a:** *Palmula pilulata* Cushman [47], **7b:** *P. woodi undulata* Nakkady [42], **7c:** *P. w. woodi* Nakkady [42], **7d:** *P. w. nammalensis* Haque [14], **8a:** *Gavelinella b. brotzeni* Said and Kenawy [32], **8b:** *G. brotzeni paleocenica* Said and Kenawy [32].

Genus *Clavulina* d'Orbigny [12]

Type species *Clavulina parisiensis* d'Orbigny [12]

**1. *Clavulina parisiensis* d'Orbigny > *C. pseudoparisensis* Anan lineage:**

***Clavulina parisiensis* d'Orbigny [12] - (Pl. 2, Fig. 1a)**

*Clavulina parisiensis* d'Orbigny [12], p. 268, no. 3 -

Nakkady [13], p. 406, pl. 2, Fig. 6 - Haque [14], p. 48, pl. 5, Figs. 7-9 - Futyan [15], p. 521 - Parisi and Coccioni [16], p. 103, pl. 1, Fig. 3 - Sztrákos [17], p. 157, pl. 2, Fig. 6.

**Remarks:** This species has triangulate triserial stage then followed by elongate rounded discoidal uniserial chambers with agglutinated wall. The Paleocene-Middle

Eocene *Clavulina parisiensis* is considered here as the ancestor of the descendent Recent *C. pseudoparisensis* due to its discoidal chambers in the later portion of the uniserial stage than the triangular cross-section along the hole elongate triserial stage in the ancestor. It has wide paleogeographic record in the Tethys: Europe (Italy, France, Norwegian Sea), Africa (Egypt), Asia (Jordan, Pakistan).

***Clavulina pseudoparisensis* Anan [18] - (Pl. 2, Fig. 1b)**

*Clavulina pseudoparisensis* Anan [18], p. 239, pl. 1, Figs. 6,7 - El Deeb [19], p. 193, pl. 1, Fig. 8 - Anan [20], p. 55, pl. 1, Fig. 10.

*Clavulina tricarinata* d'Orbigny - Youssef [21], p. Fig. 12. 1.

**Remarks:** Test has triangular triserial stage followed by triangular early portion of the uniserial stage, but rounded chambers in its later uniserial portion. Wall agglutinated, arenaceous with calcareous cement and aperture terminal with single tooth. It originally described from the littoral coast of the Red Sea of Egypt and, later on, from the littoral coast of the UAE (Persian Gulf) and Saudi Arabia coast (Red Sea). It seems that the figured specimen of Youssef [22] from the Red Sea of Saudi Arabia is closely related to *Clavulina pseudoparisensis* Anan [18]. The *Clavulina parisiensis* > *C. pseudoparisensis* lineage most probably was produced by phylogenesis trend (model A).

Genus *Laevidentalina* Loeblich and Tappan [22]

Type species *Laevidentalina aphelis* Loeblich and Tappan [22]

**2. *Laevidentalina granti* (Plummer) > *L. salimi* Anan lineage:**

***Laevidentalina granti* (Plummer [23]) - (Pl. 2, Fig. 2a)**

*Nodosaria granti* Plummer [23], p. 83, pl. 5, Fig. 9.

*Dentalina granti* (Plummer) - Plummer [24], p. 149, pl. 11, Figs. 8, 9.

*Chrysalogonium granti* (Plummer) - Sztrákos [25], p. 184, pl. 12, Figs. 24, 25..

*Laevidentalina granti* (Plummer) - Ali [26], pl. 6, Fig. 7 - Hewaidy et al [27], p. 83, pl. 2, Fig. 35 - Anan [28], p. 274, Fig. 6.3.

**Remarks:** Plummer [23] noted that a concise description that covers completely the range of the variations of her species is difficult to compose. Some authors related this species to the genus *Laevidentalina*, which is followed here, due to very long, arcuate, cylindrical and smooth test with elongated chambers and apiculate rounded proloculus. It seems that the Middle-Late Eocene (LME) *Laevidentalina salimi* Anan [29] from UAE is most probably the youngest form of Maastrichtian-Paleocene *L. granti* Plummer. The *L.*

*granti* was originally recorded from USA, and later from Egypt and France.

***Laevidentalina salimi* Anan [29] - (Pl. 2, Fig. 2b)**

? *Stilostomella* sp.; Barr and Berggren [30], p. 187, pl. 3, Fig. 4.

*Laevidentalina salimi* Anan [29], p. 3, pl. 1, Fig. 2 - Anan [20], p. 55, pl. 1, Fig. 11.

**Remarks:** The Middle-Late Eocene (MLE) species *L. salimi* from UAE is characterized by its smooth surface test, apiculate rounded proloculus, second and later chambers are smaller than the globular proloculus, chambers nearly cylindrical and grow gradually, flush limbate sutures in the early uniserial chambers with almost parallel sides, then are slightly depressed in the latest chambers. It seems that the Late Eocene figured specimen of Barr and Berggren [32] from Libya is most probably belongs to *L. salimi*, which differs from the Maastrichtian-Paleocene *L. granti* by its more widely cylindrical than slender chambers and distinctive limbate sutures. *L. granti* is considered here as the ancestor of the descendent *L. salimi*. This lineage most probably was produced by punctuated equilibrium trend (model B).

Genus *Lenticulina* Lamarck [31]

Type species *Lenticulina rotulatus* Lamarck [31]

**3. *Lenticulina carinata* (Plummer) > *L. turbinata* (Plummer) > *L. chitanii* (Yabe and Asano) lineage:**

***Lenticulina carinata* (Plummer [23]) - (Pl. 2, Fig. 3a)**

*Cristellaria midwayensis carinata* Plummer [23], p. 41, text- Fig. 5 - Said and Kenawy [32], p. 130, pl. 2, Fig. 6 - Haque [14], p. 69, pl. 28, Fig. 2.

*Lenticulina midwayensis carinatus* (Plummer) - Bolli et al. [33], p. 109, Fig. 29. 1, 2.

**Remarks:** Plummer [23] noted that this Cretaceous species genus has gradually increased in species and numbers during the Tertiary. It is having conspicuous peripheral flanges, raised limbate curved sutures and wide biconvex test. It was originally described from USA, and later from the Paleocene-Early Eocene of Sinai (Egypt), Pakistan Trinidad (Caribbean Sea).

***Lenticulina turbinata* (Plummer [23]) - (Pl. 2, Fig. 3b)**

*Cristellaria turbinata* Plummer [23], p. 93, pl. 7, Fig. 4.

*Robulus turbinatus* (Plummer) - Haque [14], p. 65, pl. 29, Fig. 8.

*Lenticulina turbinata* (Plummer) - Berggren and Aubert [34], p. 158, pl. 1, Fig. 3 - VahdatiRad et al. [35], p. 6, pl. 2, fig. 3 - Anan [28], p. 277, Fig. 6. 9.

**Remarks:** This Paleocene-Early Eocene species has considerably compressed circular test and ragged

flanges. It has been widely reported in many Tethyan localities, so far: USA, Spain, Tunisia, Egypt, UAE, Iran and Pakistan.

***Lenticulina chitanii* (Yabe and Asano [36]) - (Pl. 2, Fig. 3c)**

*Robulus chitanii* Yabe and Asano [36], p. 100 - Ansary [37], p. 56, pl. 1, Fig. 16.

*Lenticulina chitanii* (Yabe and Asano) - Anan [29], p. 6, pl. 1, Fig. 5- Aly et al. [38], p. 90, pl. 2, Fig. 1.

**Remarks:** Its central boss, keeled periphery and thick raised sutures mark this species. It was recorded from the Eocene of Egypt and UAE. Ansary [18] consider both species of Plummer *Lenticulina carinata* and *L. turbinata* in the synonym list of the MLE *L. chitanii*. The Cretaceous *Lenticulina carinata* is considered here as the ancestor of the descendent Paleocene-Eocene *L. turbinata* then to MLE *L. chitanii*. This lineage most probably was produced by phylogenesis trend (model A).

Genus *Percultazonaria* Loeblich and Tappan [22]

Type species *Cristellaria subaculeata* Cushman [39]

**4. *Percultazonaria ameeri* Anan > *P. allami* Anan lineage :**

***Percultazonaria ameeri* Anan [40] - (Pl. 2, Fig. 4a)**

*Marginulinopsis tuberculata* (Plummer) [23] - Ali [26], pl. 5, Fig. 25 (non figs. 23, 24, 26, 27)

*Marginulinopsis* sp.; LeRoy [41], p. 39, pl. 4, Figs. 6, 7.

*Percultazonaria ameeri* Anan [40], p. 17, pl. 1, Fig. 4.

**Remarks:** This Paleocene species has large test, early portion closed coiled and making up about the third of test, later portion uncoiled, slightly increasing in size as added and gently curved and nearly circular in cross section, sutures gently curved, surface ornamented by sporadic numerous well-defined nodes running continuously throughout the test, periphery subrounded. It can be recognized by its large size test, and conspicuous sutural nodes along the coiled and inclined uniserial portions of the test. *P. ameeri* is considered here as the ancestor of the descendent *P. allami*. This lineage most probably was produced by punctuated equilibrium trend (model B).

***Percultazonaria allami* Anan [40] - (Pl. 2, Fig. 4b)**

*Percultazonaria cristobalensis* Aly et al. [38], p. 92, pl. 3, Fig. 3.

*Percultazonaria allami* Anan [40], p. 17, pl. 1, Fig. 3.

**Remarks:** This Paleocene-Middle Eocene species has closed coiled initial portion of the test, elongate 4-5 chambers in inclined uncoiled portion, ornamented by sporadic numerous well-defined nodes, periphery slightly convex with a narrow keel, aperture on neck at

peripheral margin. It has inner margin slightly curved, while the outer margin is curved with keel.

**5. *Percultazonaria alii* Anan > *P. longiscata* Nakkady lineage:**

***Percultazonaria alii* Anan [40] - (Pl. 2, Fig. 5a)**

*Marginulina* sp.; Ali [26], pl. 6, Fig. 1.

*Percultazonaria alii* Anan [40], p. 16, pl. 1, Fig. 2.

**Remarks:** This Paleocene species has elongate and compressed test, early portion closed coiled, later uncoiled portion is slightly increasing in size as added, sutures gently curved, wall smooth, surface ornamented by ridges running continuously throughout the test and not interrupted at the sutures, periphery slightly convex with a narrow keel, aperture at the peripheral margin. Its running ridges along the two portions of the test, differs from Early Eocene *P. longiscata* of Nakkady by its interrupted ridges at sutures. Anan [40] noted that his new Paleocene species *P. alii* has running ridges along the two portions of the test, which differs from Early-Middle Eocene *P. longiscata* Nakkady by its interrupted ridges at sutures. *P. alii* is considered here as the ancestor of the descendent *P. longiscata*. This lineage most probably was produced by punctuated equilibrium trend (model B).

***Percultazonaria longiscata* Nakkady [42] - (Pl. 2, Fig. 5b)**

*Marginulina wetherilli* Jones var. *longiscata* Nakkady [42], p. 684, pl. 89, Fig. 13.

*Vaginulinopsis fragaria* (Gümbel); Bignot [43], p. 437, pl. 1, Fig. 8.

*Marginulina longiscata*; Anan [4], p. 41, Fig. 2.

*Percultazonaria longiscata*; Anan [40], p. 22, pl. 2, Fig. 12.

**Remarks:** Nakkady [42] noted that this species is a further stage of Nakkady's intercostata, which has higher ridges and more elongated. It seems that the Middle Eocene figured specimen Bignot's *fragaria* from the marginal Ivorian Ridge, Central Atlantic Ocean is related to Nakkady's *longiscata*. It was recorded, so far, from Early Eocene of Luxor, Farafra, Duwi sections of Egypt and Central Atlantic Ocean.

**6. *Percultazonaria wadiarabensis* (Futyan) > *P. tuberculata* (Plummer) lineage:**

***Percultazonaria wadiarabensis* (Futyan [15]) - (Pl. 2, Fig. 6a )**

*Vaginulinopsis wadiarabensis* Futyan [15], p. 524, pl. 81, figs. 7-9.

*Percultazonaria wadiarabensis* (Futyan) - Anan [40], p. 24, pl. 2, Fig. 15.

**Remarks:** This Late Paleocene species has planispirally large coiled part, proximal portion have flanged spinose periphery, heavily ornamented with

short spines, raised sutures with low sharp spines, three inflated chambers in uniserial part which perpendicularly on the coiled one, terminal aperture with neck. It differs from *P. tuberculata*, in a stouter and flanged test, larger coiled part, spinose periphery and surface. It was recorded from Jordan and Egypt. *P. wadiarabensis* is considered here as the ancestor of the descendent *P. tuberculata*. This lineage most probably was produced by punctuated equilibrium trend (model B).

***Percultazonaria tuberculata* (Plummer [23]) - (Pl. 2, Fig. 6b)**

*Cristellaria subaculeata* var. *tuberculata* Plummer [23], p. 101, pl. 7, fig. 2, pl. 14, Fig. 1.

*Marginulinopsis tuberculata* (Plummer) - Berggren and Aubert [34], p. 127, Fig. 5 - Anan [44], p. 315.

*Marginulinopsis* sp. 1.- Barr and Berggren [30], p. 187, pl. 3, Fig. 6.

*Marginulina wetherelli intercostata* Nakkady - Ali [26], pl. 6, Fig. 2.

*Percultazonaria tuberculata* Nakkady - Anan [40], p. 23, pl. 2, fig. 14 - Anan [28], p. 278, Fig. 6. 10.

**Remarks:** The Paleocene-Early Eocene Plummer's *tuberculata* is treated here to belong to the genus *Percultazonaria*. Plummer [23] noted that her variety *tuberculata* is strictly an upper Midway species and partially similar forms are very common in Tertiary formations in Europe and everywhere. The *P. tuberculata* is distinguished by its compressed elongate test, first six-seven plano-spiral with medium size followed by a linear succession of compacted 6-7 chambers, sutures are marked by rows of distinct beadlike tubercles best developed on the coiled portion of the test and giving place to more ridgelike elevations between later chambers. A long list of a recorded forms have an ill-treatment by some others, i.e.: Said and Kenawy [32], Luger [45], because most of these illustrated forms have lacking a rectilinear uncoiled chambers after the coiling stage. It was recorded, so far, from USA, Tunisia, Libya, Egypt and UAE.

Genus *Palmula* Lea [46]

Type species *Palmula sagittaria* Lea [46]

**7. *Palmula pilulata* Cushman > *P. woodi undulata* Nakkady > *P. w. woodi* Nakkady > *P. w. nammalensis* Haque lineage:**

***Palmula pilulata* Cushman [47] - (Pl. 2, Fig. 7a)**

*Palmula pilulata* Cushman [47], p. 37, pl. 6, Fig. 2 - Cushman [34], p. 84, pl. 32, Figs. 18-21.

**Remarks:** This Cretaceous form is distinguished by its very gradually increasing chamber size, extending backward at the sides but including much of the early coiled ones, and each of them ending at the inner end in a raised and slightly elongate beaded ornamentation.

Wall smooth except for the slightly raised sutures. The *Palmula pilulata* of Cushman is considered here as the ancestor of the descendent Maastrichtian *P. w. undulata* Nakkady.

***Palmula woodi undulata* Nakkady [42] - (Pl. 2, Fig. 7b)**

*Palmula woodi* var. *undulata* Nakkady [42], p. 685, pl. 89, Fig. 25.

*Palmula woodi undulata* Nakkady - Anan [29], p. 35, pl. 1, Fig. 3.

**Remarks:** This subspecies differs from the typical form *Palmula w. woodi* in the undulation of the outer periphery which results from the shortening of the chambers as noted by Nakkady [42]. The Maastrichtian *P. w. undulata* is considered here as the ancestor of the descendent Paleocene *P. w. woodi*. This lineage most probably was produced by phylogenesis trend (model A).

***Palmula w. woodi* Nakkady [42] - (Pl. 2, Fig. 7c)**

*Palmula woodi* Nakkady [42], p. 684, pl. 89, Fig. 24 - Futyan [15], p. 521 - Luger [45], p. 84, pl. 5, Fig. 9.

*Palmula w. woodi* Nakkady - Anan [29], p. 35, pl. 1, Fig. 4.

**Remarks:** *Palmula w. woodi* of Nakkady [42] has compressed test except in the early coiled which rises above the general level. It was originally recorded from the Late Paleocene shales of Duwi section. It is also recorded from Jordan (Futyan [15]).

***Palmula w. nammalensis* Haque [14] - (Pl. 2, Fig. 7d)**

*Palmula w. nammalensis* Haque [14], p. 91, pl. 3, Fig. 3.

**Remarks:** The early coiled portion of the Early Eocene *P. w. nammalensis* has astrocoline-shape and below the general level of the test. It is considered here as the ancestor of the descendent Late Paleocene *P. w. woodi* Nakkady. This lineage most probably was produced by phylogenesis trend (model A).

Genus *Gavelinella* Brotzen [48]

Type species *Discorbis pertusa* Marsson [49]

**8. *Gavelinella b. brotzeni* Said and Kenawy > *G. brotzeni paleocenica* Said and Kenawy lineage:**

***Gavelinella b. brotzeni* Said and Kenawy [32] - (Pl. 2, Fig. 8a)**

*Gavelinella brotzeni* Said and Kenawy [32], p. 147, pl. 4, Fig. 47

**Remarks:** Dubicka and Peryt [50] noted that Loeblich and Tappan [11] described the *Gavelinellinae* as possessing a trochospirally coiled test, an aperture as an interiomarginal equatorial arch that may continue on the umbilical side of the umbilicus, where it is partially



covered by distinctive flaps of successive chambers commonly visible in the umbilical area. Some of the Cretaceous genera which are included in the Gavelinellinae are *Angulogavelinella* Hofker (roughly Maastrichtian) and *Gavelinella* Brotzen (Barremian-Upper Paleocene). This subspecies were originally recorded from the Maastrichtian rocks of Sinai, Egypt.

***Gavelinella brotzeni paleocenica* Said and Kenawy [32] - (Pl. 2, Fig. 8b)**

*Gavelinella brotzeni paleocenica* Said and Kenawy [32], p. 148, pl. 4, Fig. 44.

**Remarks:** This Paleocene subspecies differs from the typical form *Gavelinella b. paleocenica* in having a more compressed test, a less open umbilicus and limbate sutures on the dorsal side. This lineage is presented here for the first time. *Gavelinella b. brotzeni* is considered here as the ancestor of the descendent *G. brotzeni paleocenica*. This lineage most probably was produced by punctuated equilibrium trend (model B).

## Results

A study of abundant, well preserved Maastrichtian-Priabonian benthic foraminiferal species of Plummer [24] in USA and other localities in the Middle East/Tethys, shows an increasing phylogenetic plasticity through modifications of morphological features first appearing in the ancestors, led to the following some evolutionary trends:

1. Three phylogenetic lineages were presented by Nakkady [1] in the Maastrichtian-Early Eocene rocks of Egypt: (1) *Orthokarstenia esnehensis* (Nakkady) > *O. eleganta* (Plummer), (2) *O. esnehensis* (Nakkady) > *O. higazyi* (Nakkady) (3) *Cibicidoides abudurbensis* > *C. pseudoacutus* (Nakkady).

2. In this study, one agglutinated lineage is added throughout the Eocene to Recent: *Clavulina parisiensis* d'Orbigny > *C. pseudoparisensis* Anan, and another seven calcareous lineages are added throughout the Maastrichtian-Priabonian time, particular around the K/T and P/E boundaries, which have a stratigraphic value in evaluating the faunal changes throughout the stratigraphic intervals: (1) *Laevidentalina granti* (Plummer) > *L. salimi* Anan, (2) *Lenticulina carinata* (Plummer) > *L. turbinata* (Plummer) > *L. chitani* (Yabe and Asano), (3) *Percultazonaria ameeri* Anan > *P. allami* Anan, (4) *Percultazonaria alii* Anan > *P. longiscata* (Nakkady), (5) *Percultazonaria wadiarabensis* (Futyan) > *P. tuberculata* (Plummer), (6) *Palmula woodi undulata* Nakkady > *P. w. woodi* Nakkady, (7) *Gavelinella b. brotzeni* Said and Kenawy > *G. brotzeni paleocenica* Said and Kenawy.3. The

evolutionary lineages may be produced by one of the two evolutionary models: phyletic gradualism (phylogenesis, model A) or punctuated equilibrium (model B).

4. The species used in those evolutionary trends are originally erected from different parts in the Tethys, from west (North Atlantic) to east (Indian Ocean) via Mediterranean and Red Sea, and exhibits an affinity with the Midway Type Fauna (MTF) of the Gulf Coast (east USA) and in different parts of the Tethys (i.e. France, Tunisia, Libya, Egypt, Jordan, Iraq, UAE, Iran, Pakistan).

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