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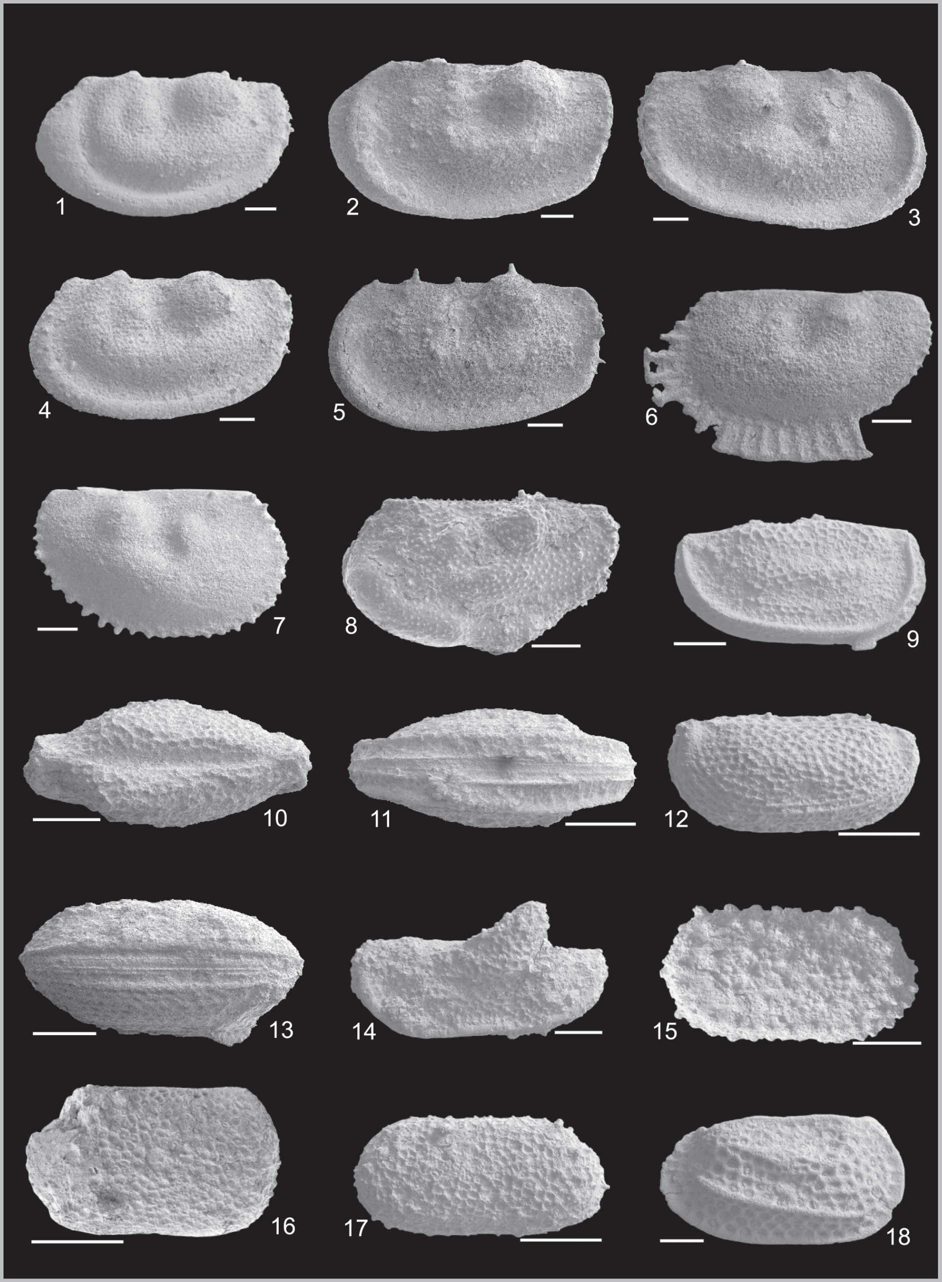

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*Cover: Ostracods from the Upper Permian of Northwest Iran. Scale bar: 200 µm. Microphotographies by Wolfgang Mette.*

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# On a rare Carboniferous red alga (*Urtasimella*, Ungdarellaceae) from southwestern Spain

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## Resumen

Las ungdarellaceas forman un grupo prolífico de algas rojas de distribución mundial que es muy abundante en carbonatos marinos someros. El género *Urtasimella* se encuentra muy bien representado en la sección Viseense superior de Valdemilano (cuenca de Los Pedroches, sudoeste de España). El género siguió siendo un *nomen nudum* durante catorce años, pero recientemente fue propuesto formalmente por Chuvashov y Anfimov (2007). Se caracteriza por un hipotalo pobremente diferenciado. Las muestras estudiadas están constituidas por numerosos ejemplares de *Urtasimella parallela* (Kulik, 1973) comb. nov., una especie reconocida por la proliferación de las celdas peritálicas.

**Palabras clave*:*** Algas rojas, Ungdarellaceae, Viseense superior, sudoeste de España, cuenca de Los Pedroches, taxonomía.

## Abstract

The ungdarellaceans form a prolific group of red algae that have a worldwide distribution and are a major component of shallow-marine carbonates. The rare *Urtasimella* is encountered in great number at the late Visean Valdemilano section (Pedroches basin, southwestern Spain). The genus remained a *nomen nudum* for fourteen years, but was recently formally proposed by Chuvashov and Anfimov (2007). It is characterized by a poorly differentiated hypothallus. The Spanish material is composed of numerous *Urtasimella parallela* (Kulik, 1973) comb. nov., a species recognized by the proliferation of perithallic cells.

**Key words**: Red algae, Ungdarellaceae, late Visean, southwestern Spain, Pedroches basin, taxonomy.

## 1. INTRODUCTION

The ungdarellaceans (Maslov, 1956) constitutes a prolific group of red algae that was very common during the Carboniferous–Early Permian, when they formed bioconstructions in the shallow-marine environment. However, large taxonomic problems and confusions around the ungdarellaceans have emerged throughout time. Lately, Chuvashov and Anfimov (2007) discussed the history of the Ungdarellaceae and described three new genera (*Ungdarelloides, Urtasimella* and *Suundukella*) based on specimens coming from Middle Carboniferous carbonate rocks of the Subpolar and Southern Ural Mountains. Intensive geological survey in the Lower Carboniferous successions of the Pedroches basin in southwestern Spain (Cózar *et al.*, 2006; Armendáriz, 2008), has recently resulted in the recognition of abundant, very-well preserved representatives of the recent genus *Urtasimella* Chuvashov and Anfimov, 2007. The aim of this work is to review and describe better the new taxon and place it in the systematics of the prolific ungdarellaceans.

## 2. GEOLOGICAL SETTING

The studied samples were obtained from the Carboniferous (Mississippian) succession of the Pedroches basin. The Pedroches basin constitutes a major tectonic element in the segment of the Variscan Belt exposed in southern Iberia (Fig. 1A; Quesada *et al.*, 2006). It developed as a syn-orogenic foredeep in response to sinistral oblique reactivation of the tectonic boundary between the Central Iberian and Ossa Morena zones of the Iberian Massif during the Late Palaeozoic Variscan collision between Gondwana and Laurussia (Fig. 1A; Quesada *et al.,* 1990; Ribeiro *et al.,* 1990; Quesada, 1991; Gabaldón *et al.,* 2004; Armendáriz, 2008; Armendáriz *et al.,* 2008*a*). Due to syn- and late-orogenic deformation, the Pedroches basin is extremely fragmented into various structural units (Fig. 1B). Among them, the Central Guadiato unit (Fig. 1B) shows an exceptional record of carbonate sedimentation, mostly represented by chaotic units (olisthostromes and olistholiths) but, also locally, by *in situ* carbonate platform deposits (e.g. Cózar and Rodríguez, 1999*a*, 1999*b*, 2004; Rodríguez Martínez *et al.,* 1999, 2000, 2003; Cózar *et al.,* 2004, 2006; Rodríguez Martínez, 2005; Armendáriz, 2006, 2008; Armendáriz *et al.,* 2007, 2008*b*).

Relics of *in situ* carbonate platform deposits of latest Visean age have been recognized in the surroundings of the Adamuz village (Fig. 1B; Armendáriz, 2006, 2008; Cózar *et al.,* 2006; Armendáriz *et al.,* 2007, 2008*b*). These carbonate deposits have not yet been defined formally, but they have been recently described informally as Los Conventos platform (Armendáriz, 2008). The Los Conventos platform is characterized by the occurrence of microbialite and carbonate mud mounds in relatively shallow shelf environments. These deposits grade downslope into marls and marly nodular limestones with sponges and large brachiopods deposited in open shelf environments below the storm wave base (Armendáriz, 2006, 2008; Cózar *et al.,* 2006).

## 3. SAMPLING LOCALITY

Within the Los Conventos platform, the Valdemilano section is one of the most prolific in red algae (Figs. 1B–2; Armendáriz, 2006, 2008; Cózar *et al.,* 2006, Armendáriz *et al.,* 2008*b*). The Valdemilano section begins with a marly package with intercalated decimetre-thick sandy-bioclastic limestones (Fig. 2). Above this package, the suc-

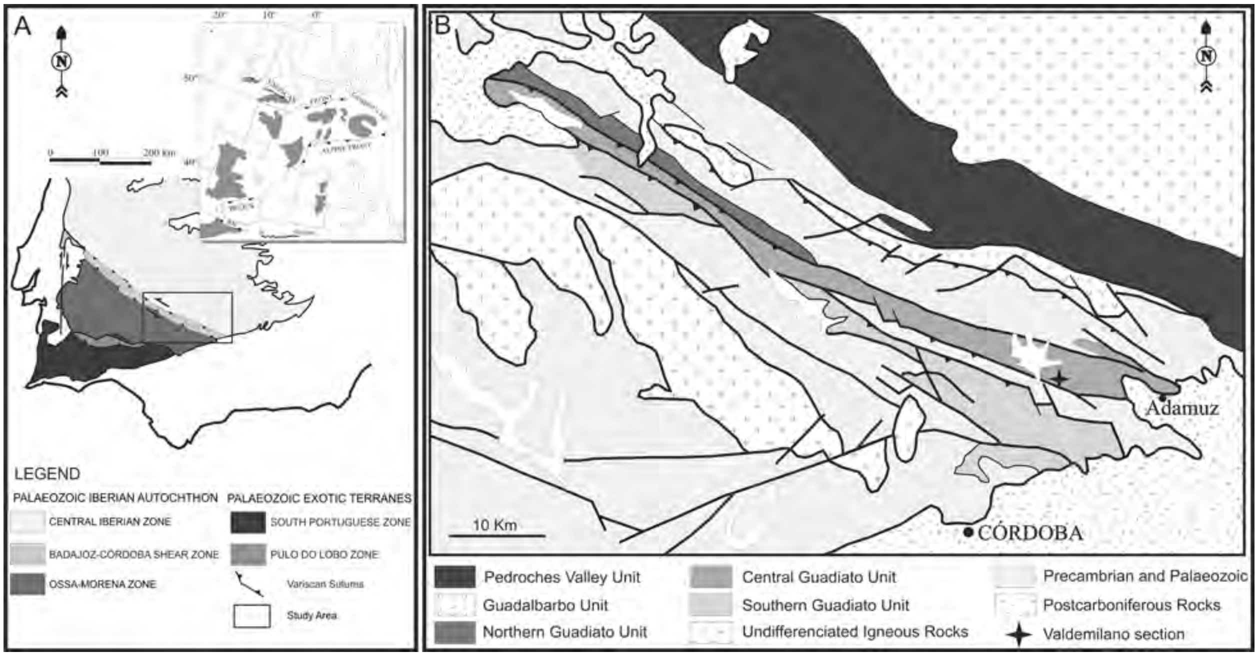

Figure 1. A, Location of the Pedroches basin in the southern Iberian Massif (after Julivert *et al.*, 1974; Quesada, 1991). B, Simplified geological map showing the Pedroches basin units and the location of Valdemilano section (based on Mapa Geológico de España 1:1.000.000, I.G.M.E., 1995).

cession follows with intraclastic-oolitic-skeletal limestone beds (Fig. 2). Towards the top, there are marls and nodular limestones, which grade upwards into micritic massive and nodular limestones (Fig. 2).

The sampling was carried out in the first 14 m of the section, which are constituted by the basal marly package with sandy-bioclastic limestone intercalations and by the intraclastic-oolitic-skeletal limestone levels.

Within the basal marly package, sandy-bioclastic limestones appear in planar to lens-shaped thin layers (up to 18 cm thick), which alternate with decimetre-thick bioturbated marls. Microfacies of the skeletal limestones correspond to quartz-bearing packstones with crinoids, “algae” fragments (*Stacheoides* sp., *Fasciella* sp., *Girvanella* sp.), bivalves and foraminifers (*Earlandia* sp., *Pseudoendothyra* sp.). Minor bryozoans, ostracodes, gastropods, echinoderms and sponge spicules are also found.

Above them, limestones corresponding to coated intraclast-ooid-skeletal grainstone to packstone are also identified. They form bedded layers (0.7–2 m thick) that extend laterally for tens to a few hundred metres. The non-skeletal grains comprise large amounts of coated intraclasts together with ooids. The accompanying biota consists largely of crinoids, “algae” (*Girvanella* sp., *Coelosporella* sp.), shell fragments (bivalves, brachiopods), foraminifers (e.g. *Earlandia* sp.) and minor proportion of corals, bryozoans, echinoderms and gastropods.

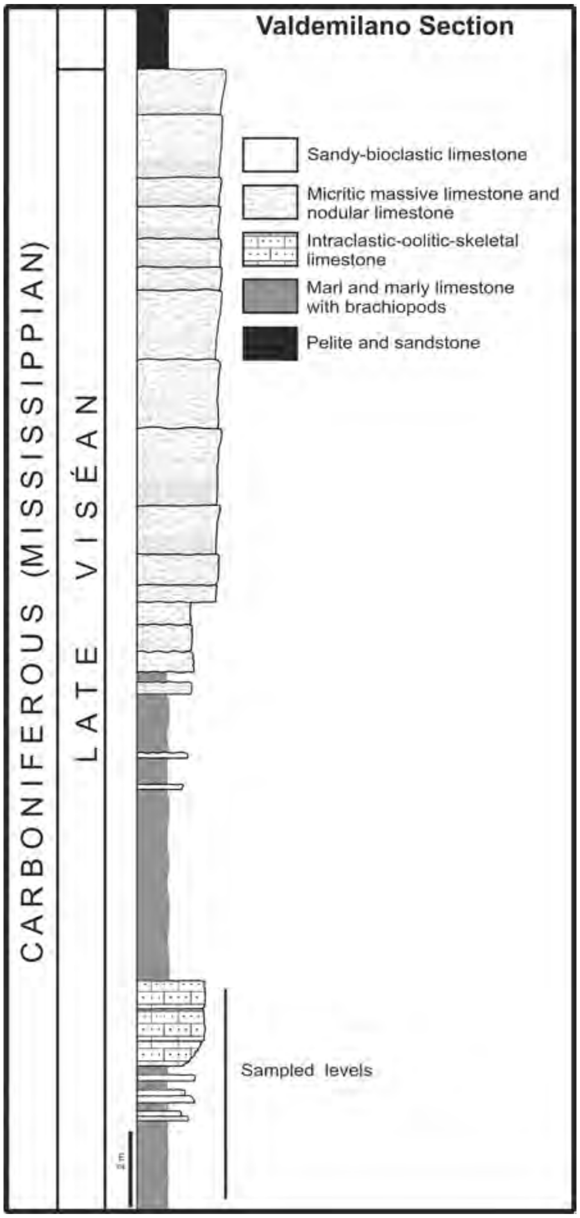

Figure 2. Valdemilano stratigraphic section (Pedroches basin, Central Guadiato unit) showing the location of the studied samples.

## 4. SYSTEMATIC PALAEONTOLOGY

### 4.1. Introduction

The family Ungdarellaceae was erected by Maslov in 1956 and based on the controversial new genus *Ungdarella* that Maslov attributed to himself as *Ungdarella uralica* Maslov, 1950. An attempt of diagnosis is as follows. Thalli are subcylindrical, erect, ramified, non encrusting and non articulated. Hypothallus composed of rows of grossly quadratic cells. Perithallus of similar composition. Cell rows (“filaments”) are perpendicular or oblique towards the axis. Wall of hyaline iron-rich, yellowish calcite.

Further confusion was introduced by Wilson *et al.* (1963) who considered *Ungdarella* as a stromatoporoid, a suggestion that died later on. The same applies to the attribution to hypercalcified sponges by Termier *et al.* (1977), later expanded by Vachard (1981). Ischyrosponges do not have a hyaline clear, iron-rich calcite wall. Therefore the sponge attribution as the stromatopore proposal died rapidly.

A list of 44 publications and a hundred photographs illustrates the concept of *Ungdarella uralica* since over fifty years in Mamet *et al.* (1987) and Mamet and Villa (2004). Although the problem of the original description is unsolved, the stability of *uralica* concept is assured.

These taxonomic problems are regrettable as ungdarellaceans were very common during the Carboniferous-Early Permian, when they formed bioconstructions in the marine euphotic-disphotic zone. With the exception of South America, they are present in all the continents.

## 4.2. Review of the published taxa

The family has considerably increased the number of taxa with the passing of time (Poncet, 1989). They can be classified as:

- *Ungdarella* (see discussion above). One central row of rectangular cells and oblique insertion of perithallic rectangular cells. Branches widespread.
- *Komia* Kordé, 1951 (type: *Komia abundans* Kordé, 1951). Numerous rows of central elongated rectangular cells. Perpendicular insertion of rectangular numerous cells. Thallus branching widespread.
- *Petschoria* Kordé, 1951 (type: *Petschoria elegans* Kordé, 1951). Numerous central rows of wavy elongated cells and perpendicular insertion of tabular cells. Thallus branching widespread.
- *Pseudokomia* Rácz, 1966 (type: *Pseudokomia cansecoensis* Rácz, 1966). Numerous rows of central elongated cells and perpendicular insertion of tabular cells. Thallus cylindrical.
- *Cheggatella* Poncet, 1989 (type: *Cheggatella lenticula* Poncet, 1989). Numerous rows of elongated wavy central cells and oblique insertion of perithallic rows of wavy undulating cells. Branching widespread.
- *Ungdarellina* Mamet, 2002 (type: *Ungdarella peratrovichensis* Mamet and Rudloff, 1972). Discrete, crustose layers of subquadratic cells without clear hypo-perithallic differentiation.
- *Ungdarellita* Mamet and Villa, 2004 (type: *Ungdarellita articulata* Mamet and Villa, 2004). Grossly cylindrical series of barred shaped segments. Central hypothallic stem and bundles of regular perithallic cells without oblique insertion.

The genus *Pechorella* mentioned by Chuvashov in a private correspondence is probably a *nomen nudum*. Finally the subgenus *Urtasimella* also mentioned by Chuvashov in the same letter is supposed to derive from Chuvashov and Anfimov (1991), but that publication does not have trace of the taxon.

Recently, Chuvashov and Anfimov (2007) proposed new genera, *Ungdarelloides* and *Suundukella* that have a succession of spherical perithallic cells. This is the result of recrystallization that can be observed in many families (e.g. spheroid cells among *Stacheinae*). Thus the recent taxa are not recognized here.

The first mentions of *Urtasimella* are to be found as *Ungdarella (Urtasimella) laxa* Chuvashov and Anfimov published in Chuvashov, Shuysky and Ivanova (1993; no description, Plate 12, Figs. 9–10, South Urals, Berdyansk River, Bashkirian).

It is followed by *Ungdarella (Urtasimella) concentrica* Chuvashov and Anfimov, same publication, no description, Plate 12, Fig. 11, South Urals, Bolshoy Urtasym River, Bashkirian.

## 4.3. Systematics

The material is housed in the Geominero Museum of the Instituto Geológico y Minero de España of Madrid (under the prefix MGM).

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Plate 1. Graphic scale 100 µm. All figured specimens from the late Visean Valdemilano section, Pedroches basin (southwestern Spain). *Urtasimella parallela* Kulik, 1973. *1,* Sample 30d (MGM-748H-d). Longitudinal section that synthesizes the characteristics of the genus: (1) thallus cylindrical, branching; (2) few central stems, with angular/rectangular hypothallic cells; (3) numerous perithallic cells, much more regular and smaller than the hypothallic cells and; (4) subparallel disposition of the rows. *2,* Sample 30g (MGM-748H-g). Longitudinal section in the center of a branch, with large hypothallic and smaller perithallic cells. *3–4,* Samples 30e (MGM-748H-e) and 38b (MGM-754H-b). Perpendicular sections through the center of a branch. *5,* Sample 31f (MGM-749H-f). High longitudinal section with the regular perithallic rows. *6,* Sample 98Aa (MGM-755H-a). Longitudinal section of two branches. The section is well oriented as both hypo- and perithallic cells are observed. *7,* Sample 31g (MGM-749H-g). Base of dichotomic branching.

**Plate 1**

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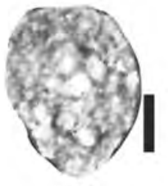

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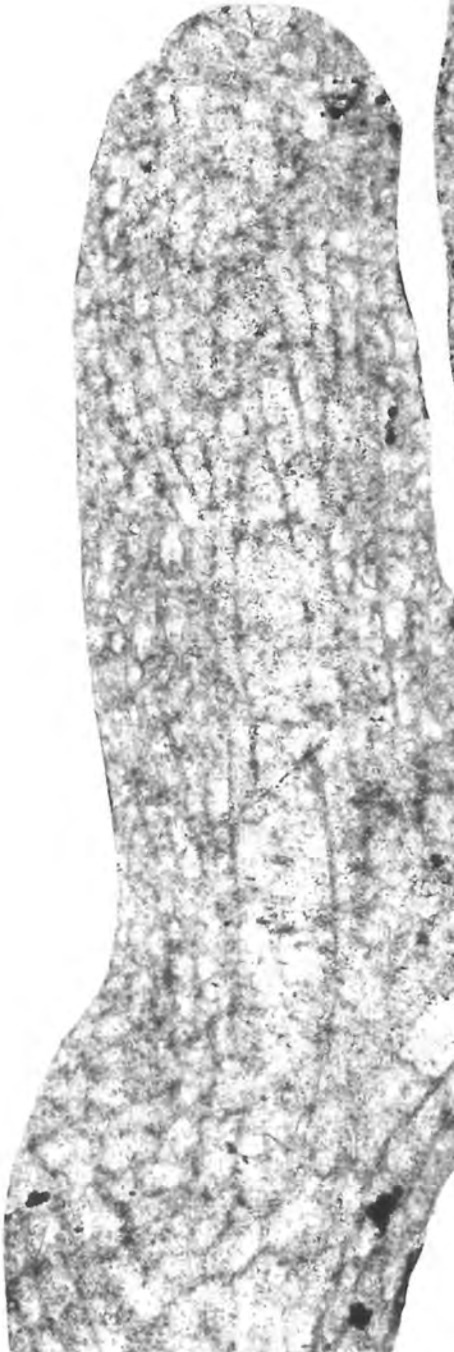

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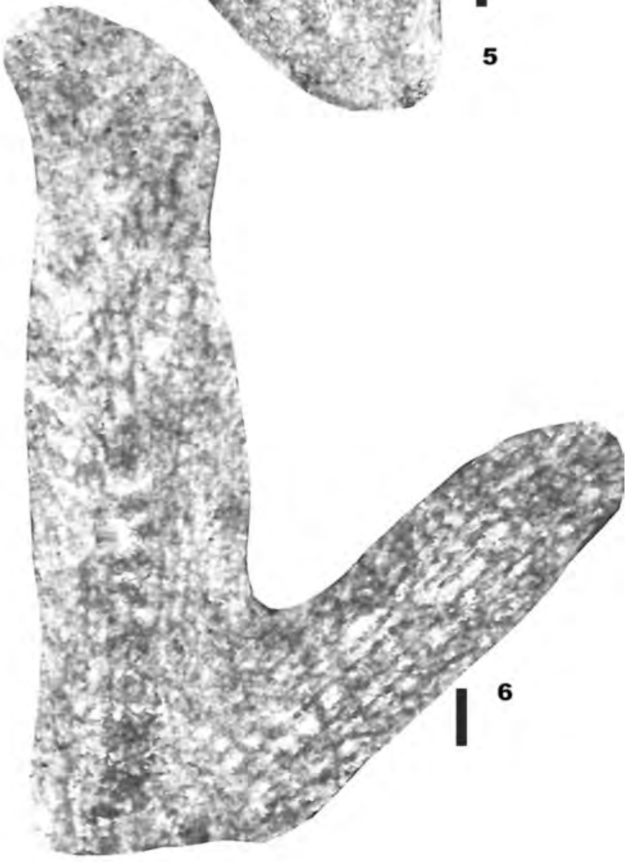

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Division RHODOPHYTA Papenfuss, 1946
Family UNGDARELLACEAE Maslov, 1956
Genus *Urtasimella* Chuvashov and Anfimov, 2007

*Type species.–* *Urtasimella concentrica* Chuvashov and Anfimov, 2007, from the Subpolar and Southern Urals Mountains.

*Diagnosis.–* Thallus erect, grossly cylindrical, with numerous branches in all directions and at all dichotomic angles. Branches variable, some have approximately the same diameter as the main trunk. Central hypothallic stem with a few rows of subquadratic cells. Little hypo-perithallic differentiation. Numerous rows of perithallic cells, small, subquadratic, closely parallel to the central stem.

*Comparison.–* *Urtasimella* is an intriguing mixture of *Komia* and *Ungdarella* morphologies.

*Distribution and stratigraphical range.–* Europe. Latest Visean, Serpukhovian, Bashkirian and Moscovian.

***Urtasimella parallela* (Kulik, 1973) comb. nov.**
(Pl. 1, Figs. 1–7; Pl. 2, Figs. 1–13)

1973 *Ungdarella parallela* Kulik, p. 47, pl. 4, fig.10.
1990 *Ungdarella parallela* Kulik; Bogush *et al.*, p. 25, pl. 24, fig. 4.
1993 *Urtasimella parallela* (Kulik); Chuvashov *et al.*, no description, pl. 11, fig. 10.

*Holotype.–* Akad Nauk SSSR, Collection 3498/136/63, Shartym River, Bashkirian.

*Material.–* 19 specimens. MGM-747H-c; MGM-748H-d-e, g-h; MGM-749H-f-h; MGM-750H-a, d, i; MGM-752H-b; MGM-754H-b, c; MGM-755H-a, c, d, g, h.

*Description.–* Thallus cylindrical, heavily branched. About 6-8 branches at variable dichotomic angles (usually, 30-40 degrees). Common diameter from 300 to 600 µm, more at branching point. Central stem of 2–8 rows of hypothallic cells, around 30-50 µm in diameter, subquadratic but often round by corrosion. Around one hundred perithallic rows of subquadratic cells, smaller and more regular (10-20 µm).

*Remarks.–* The average dimensions given here have to be interpreted with caution. A great variability is encountered and in particular very elongated and slender forms are observed (see Pl. 2, Figs. 9-10) but they have the same cell morphologies.

*Comparison.–* Chuvashov *et al.* (1993) mention the existence of a similar *Urtasimella laxa* Chuvashov and Anfimov (1991), but this taxon is a *nomen nudum*. Our material is nearly identical to Kulik's species.

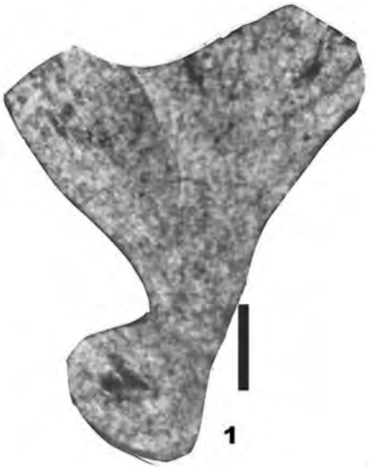
*Distribution and stratigraphical range.–* *U. parallela* is mentioned in Russia from the Early Bashkirian. Our material is latest Visean. At the time being, it is restricted to the Urals and Spain.

## 5. CONCLUSIONS

The genus *Urtasimella* is recognized in the Visean of Spain and added to the already prolific red Ungdarellaceae. At the time being, the genus appears restricted to Europe, but as most representatives of the family have widespread to cosmopolitan distribution, it is to be expected that the geographic extension will be expanded.

Plate 2. Graphic scale 200 µm. All figured specimens from the late Visean Valdemilano section, Pedroches basin (southwestern Spain). *Urtasimella parallela* Kulik, 1973. *1,* Sample 36b (MGM-752H-b). Upper part: high oblique section at branching level; lower part: perpendicular section of branch with central stem cells. *2–3,* Samples 38c (MGM-754H-c) and 30h (MGM-748H-h). High longitudinal sections with branches at various dichotomic angles. *4,* Sample 31h (MGM-749H-h). Longitudinal section at branching level, showing the central stem cells. *5,* Sample 12c (MGM-747H-c). Longitudinal section of a branched thallus. Rectangular central stem cells and numerous parallel perithallic cells. Tiny bead perpendicular to the viewer. *6,* Sample 98Ac (MGM-755H-c). Slightly oblique section of a branch. *7,* Sample 98Ag (MGM-755H-g). Perpendicular section of a bead similar to that observed at Plate 2, Figure 5. Numerous departures of hypothallic rows. *8,* Sample 98Ah (MGM-755H-h). Oblique section of branch with numerous perithallic cells. *9–10,* Samples 32d (MGM-750H-d) and 32i (MGM-750H-i). Unusual elongated, slender thalli. *11,* Sample 98Aa (MGM-755H-a). Central longitudinal section with rectangular central stem cells. *12,* Sample 98Ad (MGM-755H-d). At the base: central longitudinal section with central stem cells and numerous perithallic cells; at the top: perpendicular section with a dissolved stem surrounded by perithallic cells. *13,* Sample 32a (MGM-750H-a). Longitudinal section. Regular disposition of quadratic cells.

**Plate 2**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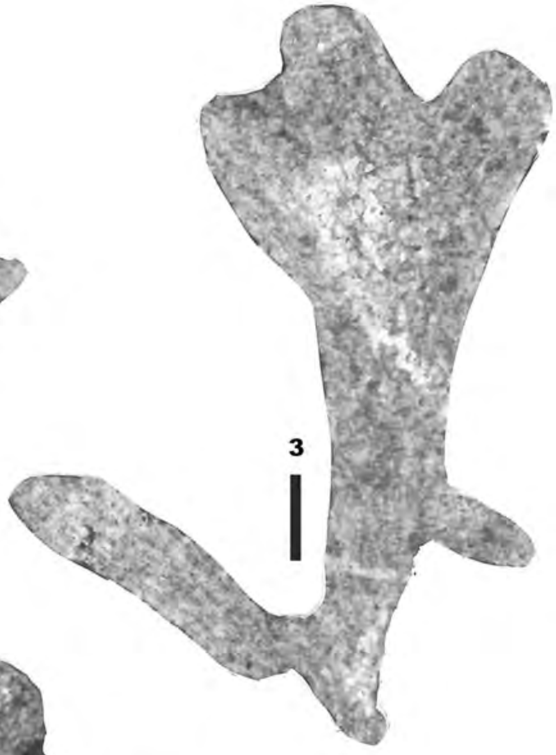
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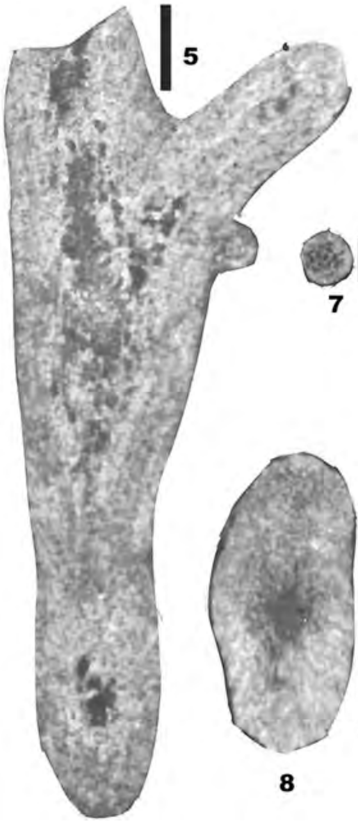
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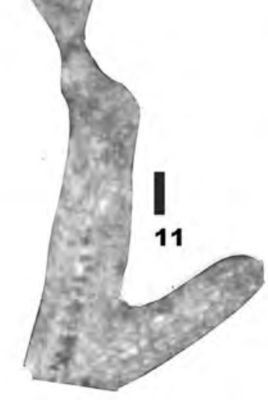
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# Ostracods from the Upper Permian and Permian/Triassic boundary interval of Northwest Iran

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## Resumen

Las asociaciones de ostrácodos del Pérmico superior y Triásico más inferior del noroeste de Irán se encuentran representadas por 35 especies, entre las que se han descrito cuatro nuevas: *Kirkbya jolfaensis, Cavellina jolfaensis, Bairdia zaliensis* y *Bairdiacypris zaliensis*. Los ostrácodos del Pérmico superior muestran un fuerte carácter endémico. Algunas especies de estas asociaciones constituyen probablemente nuevos taxones, pero se describen aquí en nomenclatura abierta debido a su mala conservación. En el Dzhulfiense los representantes de Kirkbyoidea y Bairdioidea son más abundantes e indican un ambiente marino de aguas someras. Las asociaciones del Dorashamiense son de baja diversidad y los abundantes Bairdioidea indican un ambiente neritico más profundo. Los ostrácodos del Pérmico más superior – Griesbachiense inferior reflejan la extinción en masa del límite P/T y agrupan especies pandémicas que han sido interpretadas como "disaster taxa".

**Palabras clave**: Ostracoda, taxonomía, Pérmico superior, Triásico inferior, Irán.

## Abstract

Ostracod assemblages from the Upper Permian and lowermost Triassic of Northwest Iran comprise 35 species including the new species *Kirkbya jolfaensis, Cavellina jolfaensis, Bairdia zaliensis* and *Bairdiacypris zaliensis*. The Upper Permian ostracods show a strong endemic character. A number of the endemic species are considered as probably new but left in open nomenclature due to poor preservation or insufficient material. The Dzhulfian (Wuchiapingian) assemblages are dominated by Kirkbyoidea and Bairdioidea and point to an inner neritic environment. The Dorashamian assemblages are of lower diversity and comprise abundant Bairdioidea indicating greater water depth. Uppermost Dorashamian – lower Griesbachian ostracods reflect a complete faunal turnover across the Permian/Triassic event and include pandemic species which are interpreted as disaster taxa.

**Key words:** Ostracoda, taxonomy, Upper Permian, Lower Triassic, Iran.

## 1. INTRODUCTION

The present paper deals with the taxonomic analysis of ostracod asemblages which were recovered from the Upper Permian (Dzhulfian-Dorashamian) Jolfa and Ali Bashi formations and from the Lower Triassic (Griesbachian) Elika Formation at the Zal section in Northwest Iran. The section is located 22 km SSW of Jolfa and 2 km NNW of the village of Zal. The lower part of the section (Jolfa Formation, Zal I) is located about 400 m northwest of the upper part (Ali Bashi Formation and Elika Formation, Zal II). The geological setting, stratigraphy and facies of the Upper Permian and Lower Triassic of the investigation area as well as the biostratigraphical range and palaeoecology of the ostracod assemblages has been reported in Mette (2008). During recent years a number of studies were published which deal with the changes of ostracod faunas across the Permian/Triassic boundary (e.g.

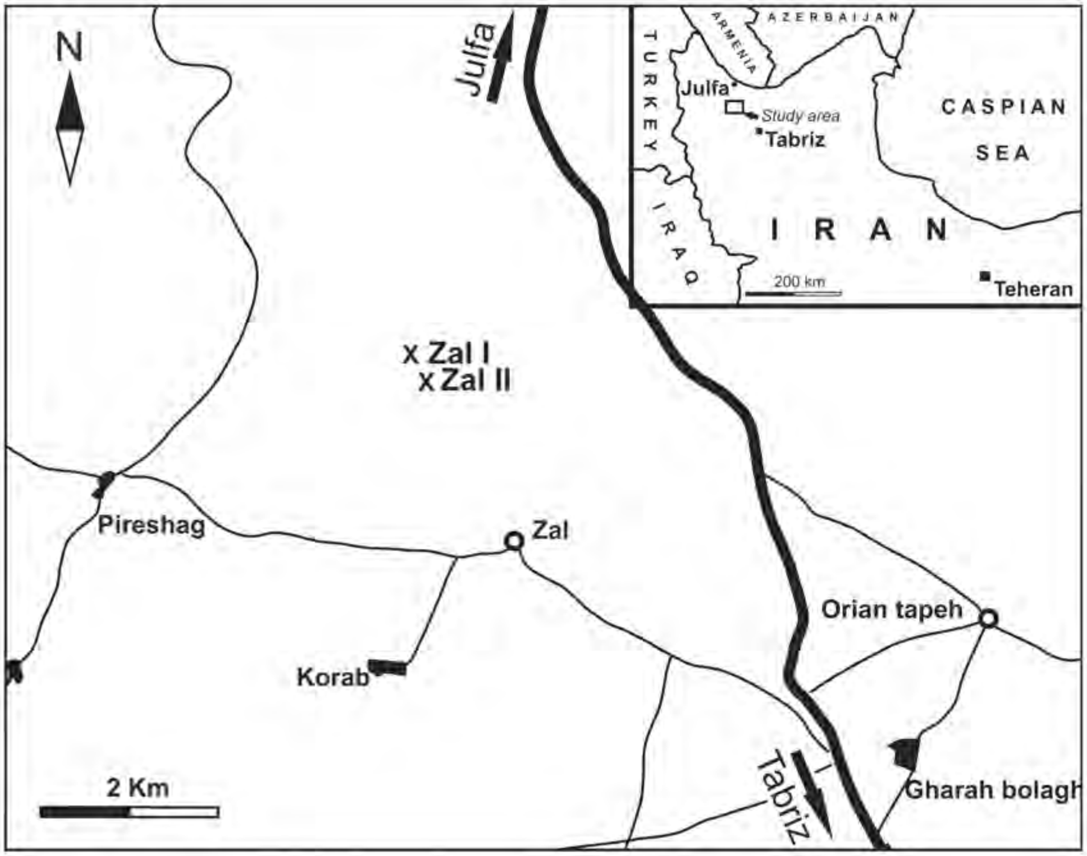


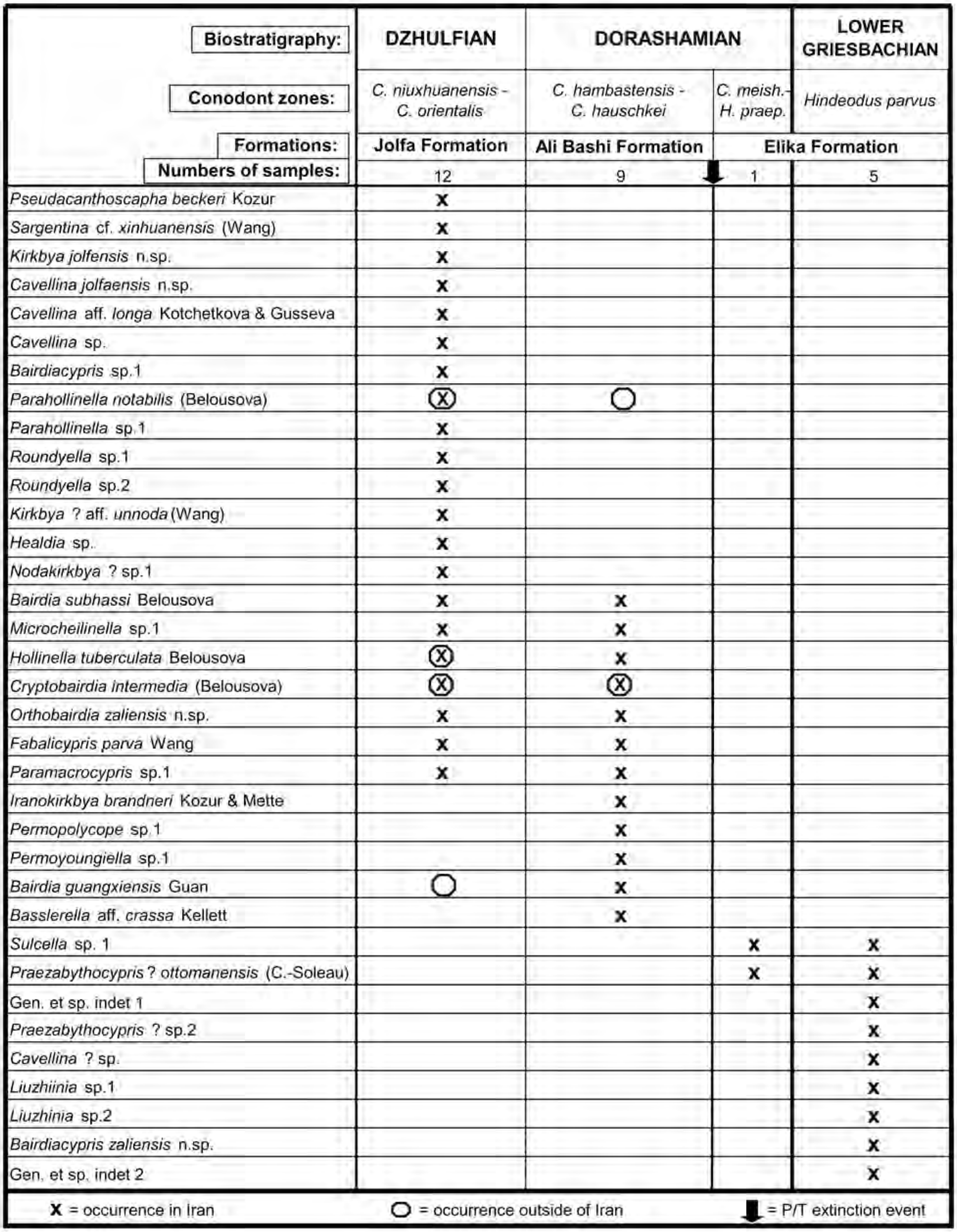
Figure 1. Location of the investigated section (Zal) and study area in detail.

Crasquin-Soleau *et al*., 2004; Crasquin-Soleau *et al*., 2007; Crasquin *et al*., 2008). The stratigraphical age of the P/T ostracods which are described in this study has been determined by detailed conodont biostratigraphy.

## 2. PALAEOECOLOGICAL AND PALAEBIOGEOGRAPHICAL ASPECTS

The sedimentological analysis and associated macrobenthic fossil content revealed that the early Dzhulfian ostracods lived in a relative shallow (shallow subtidal) normal marine shelf environment. A gradual deepening of the environment is recorded by the fossil associations of late Dzhulfian age. In the Dorashamian the habitat of the ostracod associations was a deeper well-oxygenated shelf. In the P/T boundary interval (upper *H. praeparvus* – *C. meishanensis* conodont zone / lower *H. parvus* conodont zone) a shallowing is indicated by sedimentological data and microfossil assamblages (Mette 2008). The ostracods from the P/T boundary interval and the earliest Triassic strata described herein are of particular significance because they show a total faunal turnover which was effected by the extinction event. The Boundary Clay (late Dorashamian) yielded a dwarfed fauna, dominated by small specimens of *Sulcella* sp.1 and indicating strong environmental stress. Some of the taxa which were recovered from the earliest Triassic beds such as *Liuzhinia* sp.1 and *Praezabythocypris*? *ottomanensis* (Crasquin-Soleau) show a pustulose ornamentation which may be due to changes in water chemistry.

With regard to palaeobiogeography the Upper Permian ostracods from Northwest Iran display a strong endemicity. In contrast the assemblages from the P/T boundary interval show a more pandemic character with abundant *P.*? *ottomanensis* which has also been recorded from Turkey and China (Crasquin-Soleau *et al*., 2004; Crasquin-Solaeu and Kershaw, 2005). The wide distribution of this taxon at the P/T boundary and in earliest Triassic beds strongly suggests that it was a disaster taxon. Another possible disaster species is *Liuzhinia* sp.1 which occurs in the uppermost



| **Biostratigraphy:** | **DZHULFIAN** | **DORASHAMIAN** | | **LOWER GRIESBACHIAN** |
|---|---|---|---|---|
| **Conodont zones:** | *C. niuxhuanensis - C. orientalis* | *C. hambastensis - C. hauschkei* | *C. meish.- H. praep.* | *Hindeodus parvus* |
| **Formations:** | **Jolfa Formation** | **Ali Bashi Formation** | **Elika Formation** | |
| **Numbers of samples:** | 12 | 9 ⬇ | 1 | 5 |
| *Pseudacanthoscapha beckeri* Kozur | **x** | | | |
| *Sargentina* cf. *xinhuanensis* (Wang) | **x** | | | |
| *Kirkbya jolfensis* n.sp. | **x** | | | |
| *Cavellina jolfaensis* n.sp. | **x** | | | |
| *Cavellina* aff. *longa* Kotchetkova & Gusseva | **x** | | | |
| *Cavellina* sp. | **x** | | | |
| *Bairdiacypris* sp.1 | **x** | | | |
| *Parahollinella notabilis* (Belousova) | ⊗ | ○ | | |
| *Parahollinella* sp.1 | **x** | | | |
| *Roundyella* sp.1 | **x** | | | |
| *Roundyella* sp.2 | **x** | | | |
| *Kirkbya* ? aff. *unnoda* (Wang) | **x** | | | |
| *Healdia* sp. | **x** | | | |
| *Nodakirkbya* ? sp.1 | **x** | | | |
| *Bairdia subhassi* Belousova | **x** | **x** | | |
| *Microcheilinella* sp.1 | **x** | **x** | | |
| *Hollinella tuberculata* Belousova | ⊗ | **x** | | |
| *Cryptobairdia intermedia* (Belousova) | ⊗ | ⊗ | | |
| *Orthobairdia zaliensis* n.sp. | **x** | **x** | | |
| *Fabalicypris parva* Wang | **x** | **x** | | |
| *Paramacrocypris* sp.1 | **x** | **x** | | |
| *Iranokirkbya brandneri* Kozur & Mette | | **x** | | |
| *Permopolycope* sp.1 | | **x** | | |
| *Permoyoungiella* sp.1 | | **x** | | |
| *Bairdia guangxiensis* Guan | ○ | **x** | | |
| *Basslerella* aff. *crassa* Kellett | | **x** | | |
| *Sulcella* sp. 1 | | | **x** | **x** |
| *Praezabythocypris* ? *ottomanensis* (C.-Soleau) | | | **x** | **x** |
| Gen. et sp. indet 1 | | | | **x** |
| *Praezabythocypris* ? sp.2 | | | | **x** |
| *Cavellina* ? sp. | | | | **x** |
| *Liuzhiinia* sp.1 | | | | **x** |
| *Liuzhinia* sp.2 | | | | **x** |
| *Bairdiacypris zaliensis* n.sp. | | | | **x** |
| Gen. et sp. indet 2 | | | | **x** |

**x** = occurrence in Iran ○ = occurrence outside of Iran ⬇ = P/T extinction event

Figure 2. Stratigraphic distribution of ostracods from the Upper Permian and the P/T-Boundary interval at Zal section.

Permian of China and may also be present in the lower Induan of Turkey (Chen and Shi, 1982; Crasquin-Soleau *et al*., 2004).

## 3. MATERIAL

The Upper Permian ostracods were recovered from twenty one samples. The uppermost Permian-lowermost Triassic strata yielded six ostracod assemblages. Thirty five species have been recorded and twenty seven species are described herein. The taxonomic composition of the associations, the distribution and relative abundance of the taxa was described in Mette (2008). The material is deposited at the Institute of Geology and Palaeontology at Innsbruck University (collection number Me 2004).

## 4. SYSTEMATIC DESCRIPTIONS

Taxonomically indicative internal features are not accessible and are therefore not described. "Dimensions" include the maximum and minimum values of length, height and width of adult specimens and thus show the intraspecific variability in size. All zones are conodont zones. Abreviations: L= lobus, S= sulcus, LV= left valve, RV= right valve.

Class OSTRACODA Latreille, 1806
Subclass PODOCOPA Sars, 1866
Order PALAEOCOPIDA Henningsmoen, 1953
Superfamily HOLLINOIDEA Swartz, 1936
Family HOLLINELLIDAE Bless & Jordan, 1971

### Genus *Hollinella* Coryell, 1928

### *Hollinella tuberculata* Beloušova, 1965

(Pl. 1, Figs. 1-8)

1965 *Hollinella* ? *tuberculata* Belousova sp. nov.. Belousova, p.254, Pl. 46, Figs. 2a, 2b.
? 1965 *Hollinella cushmanni* Kellett 1933. Belousova, Pl. 46, Fig. 1.
? 1987 *Hollinella tingi* (Patte). Shi & Chen, p. 30, Pl. 16, Figs. 2-5.
2008 *Hollinella* sp. Mette, Pl. 1, Figs. 1-2.

*Material*. – 217 valves and carapaces.

*Remarks*.– The most conspicuous characteristics of this species are the relatively large carapace size and the shape of the velum which is separated from the ventral lobus by a deep S1. The L1 is strongly developed and slightly overreaches the dorsal margin. The L2 is round and merges anteriorly with the L1. L3 is large, round, knob-like and protrudes strongly above the lateral surface and slightly overreaches the dorsal margin. L4 is completely reduced. Well-perserved specimens show a number of small spines at the posterior margin and one each at the dorsal part of L1, L3 and the dorsal prolongation of L2. Another small spine has been observed at the anterior cardinal angle. On the specimens from the Ali Bashi Formation the L1 and L2 are less distinct and L1 does not overreach the dorsal margin.

The adult males and females differ only in the shape of the velum which is broadened and incurved at the anterior and anteroventral part of the female carapace. The velum of the males is straight and of equal width all along the anterior, ventral and posterior margins. On the juvenile females the anterior and anteroventral part of the velum is strongly incurved and looks like an elongate brood chamber. The specimens from the Jolfa Formation (Dzhulfian) have a thicker shell than the specimens from the Ali Bashi Formation (Dorashamian) and the velum of the Dzhulfian specimens is bulge-like. Furthermore the average carapace size of the specimens from the Jolfa Formation is a little smaller. The different carapace calcification is interpreted as intraspecific variability due to different water depth and water turbulence because the Jolfa Formation was, according to the palaeoecological criteria deposited in a shallower shelf environment than the Ali Bashi Formation (Mette 2008).

*Dimensions (mm)*.– Jolfa Formation, sample Z10: length/height: of female RV: 1.30/0.78; 1.36/0.80; 1.38/0.84; 1.44/0.80; length/height of female LV: 1.40/0.82; 1.46/0.86; length/height of male RV: 1.30/0.68; 1.38/0.78; length/height of male LV: 1.40/0.84; 1.46/0.86; Ali Bashi Formation, sample Z 28: length/height of female RV: 1.50/0.90; 1.60/0.96; length/height of female LV: 1.42/0.92; 1.62/0.96; length/height of male LV: 1.42/0.84; length/height of male RV: 1.48/0.86.

*Discussion*.– The species which was described by Belousova (1965) as *Hollinella cushmanni* Kellett 1933 is possibly a juvenile specimen of *H. tuberculata*. This conclusion can however only be confirmed by direct comparison of the ostracod material of the present study and that of Belousova (1965). The species described as *Hollinella tingi* (Patte) in Hou (1954) from the Lower Permian of western Hupeh (China) is comparable to the specimens of the Zal section but according to the description of Hou (1954) the males of this species do not have a frill. In addition the second and the third lobes show a more elongate shape and merge into the ventral lobe. The specimens described as *Hollinella tingi* (Patte) from the Upper Permian (Changhsingian) of the Meishan section (Shi & Chen 1987) and the Upper Permian-Lower Triassic of the Zhenfeng section in South China and from Guizhou and Yunnan (Hao, 1996; Wang, 1978) also show affinity to the present material but are of much smaller size. In comparison to *Hollinella schreteri* Kozur (1985a) from the Middle Permian of Hungary the present species is more elongate in lateral outline and the males have a less broad velum.

*Stratigraphical and geographical distribution*.– *H. tuberculata* was first decribed from the Upper Permian of Azerbaijan (Belousova 1965). In Iran *H. tuberculata* occurs in the Dzhulfian-Dorashamian of Northwest Iran (Zal section). Another possible occurrence of the species is in the Upper Permian of the Meishan section (Shi & Chen, 1987).

Superfamily KIRKBYOIDEA Ulrich & Bassler, 1906
Family KIRKBYIDAE Ulrich & Bassler, 1906

### Genus *Kirkbya* Jones, 1859

#### *Kirkbya jolfaensis* n. sp.

(Pl. 1, Figs. 9-11)

2008 *Kirkbya* sp.1. Mette, Pl. 1, Fig. 5.

*Derivation of name*.– Referring to the town Jolfa which is located near to the type locality.

*Holotype*.– Zal 1,36, Pl. 1, Fig.9.

*Type locality*.– Zal section, 22 km southwest of the town Jolfa at the Iran-Azerbaijan boundary, Northwest Iran.

*Material*.– 72 carapaces and 22 valves.

*Type horizon*.– Lower Jolfa Formation (lithostratigraphical unit 1, sample 4), Lower Dzhulfian.

*Occurrence*.– Lower Jolfa Formation (lithostratigraphical unit 1, samples Z4,6,9,10), Lower Dzhulfian (sample 10=*Clarkina niuxhuanensis* zone), Northwest Iran.

*Diagnosis*.– *Kirkbya jolfaensis* is characterized by a more-or-less distinct median longitudinal ridge bordering the dorsomedian carapace inflation on its ventral side. The dorsal margin is strongly incised and the dorsal surface broadens in posterior direction attaining a maximum width at 1/4th of carapace length.

*Description*.– *Kirkbya jolfaensis* has a subrectangular outline in lateral view and a more or less convex lens-shaped outline in dorsal view. The posterior margin is more narrowly rounded than the anterior margin. Dorsal and posterior margins form an angle of 90° to 100° and between the dorsal and anterior margin the angle is 100° to 110°. Along the anterior, ventral and posterior margins a relative strong inner carina and a more delicate outer marginal carina occur which are separated by two rows of small fossules. In lateral view the outer carina is visible at the anterior and posterior margins and hidden behind the inner carina at the ventral margin. On the right valve the outer carina is more strongly developed than on the left valve. Dorsal and ventral margins are parallel or slightly converging with the ventral margin inclined at about 5° towards the posterior margin. The kirkbyan pit is small and distinct. The dorsomedian carapace inflation is bordered ventrally by a more or less distinct ridge, just above the kirkbyan pit. Along the dorsal margin this carapace inflation develops a more-or-less strong elongate bulge bordering the v-shaped dorsal surface. The ventral, lateral and dorsal surface areas are finely reticulated. In the central part of the lateral surface the round fossules build an irregular meshwork. In the ventral, anterior and posterior parts of the lateral surface and on the dorsal surface the fossules are arranged in rows parallel to the valve margins. The dorsal margin is distinctly incised and overreached by the dorsomedian carapace inflation.

*Dimensions (mm)*.– Jolfa Formation, sample Z4: length/height/width of carapace: 0.88/0.42/0.36; 0.84/0.40/0.40;

0.90/0.50/-; 0.76/0.38/-; 0.92/0.46/-; sample Z6: length/height/width of carapace: 0.78/0.40/0.34; 0.74/0.36/0.34; 0.84/0.39/-; 0.76/0.38/-; 0.84/0.42/-; 0.88/0.42/-.

*Discussion*.– *Kirkbya jolfaensis* shows a strong similarity to *Kirkbya permiana* (Jones) with respect to carapace outline and ornamentation. It can however be distinguished from the latter species by the lack of a posterventral knob and longitudinal ribs and occurrence of a median longitudinal ridge at the lateral surface. Furthermore the dorsal surface of *K. permiana* is symmetrical and not broadened posteriorly. *Kirkbya* sp. from the Middle Permian of Texas (Sohn 1954) seems also to be closely related to the present species but differs by the more elongate lateral carapace outline and subdued lobation of the lateral surface. *Kirkbya clarocarinata* Knight, 1928 in Harlton (1928) from the Pennsylvanian of Texas differs from the Iranian species by the more symmetrical lateral carapace outline, occurrence of nodes near the dorsal margin and absence of a longitudinal ridge. Furthermore, the carapace of the latter species is laterally much more inflated. Another similar species is *Kirkbya firma* Kellett from the Upper Pennsylvanian-Lower Permian of Texas (Kellett, 1933) which differs from the present species by the occurrence of four fossule rows between the inner and outer carina, the elongate shape of the fossules and the greater carapace size. A greater number of fossule rows between the inner and outer carina was also recorded from *Kirkbya inornata* Roth 1929 which is very similar to the present species with regard to carapace outline and ornamentation.

*Stratigraphical and geographical distribution*.– The species is known from the lower part of the Jolfa Formation (unit 1) at Zal section in Northwest Iran which corresponds lithostratigraphically to the *Codonofusiella* beds of the Jolfa section and of the Dorasham section at the Iran-Azerbaijan border and belongs to the lower Dzhulfian. According to the conodont biostratigraphy sample 10 has been attributed to the *Clarkina niuxhuanensis* Zone (Mette, 2008).

### ***Kirkbya*? aff. *unnoda* (Wang, 1978)**

(Pl. 1, Figs. 12-13)

? 1978 *Kirkbya unnoda* sp. nov. Wang, p. 283, Pl. 1, Figs. 12a, 12b.
? 1999 *Knightina unnoda* (Wang, 1978). Crasquin-Soleau *et al.*, Pl. 1, Fig. 14.
? 2002 *Shleesha unnoda* (Wang). Shi & Chen, p. 60, Pl. 1, Figs.5-8.
2008 *Kirkbya* sp.2. Mette, Pl. 1, Fig. 6.

*Material.* – 4 carapace and 7 valves.

*Remarks*.– The species is characterized by an evenly convex and regularly reticulated lateral surface and a low outer carina. The carapace is laterally constricted at the anterior and posterior cardinal angles. On the ventral, anterior and posterior parts of the lateral surface and on the dorsal surface the reticulation meshes are oriented parallel to the margins and the longitudinal elements of the reticulation meshes build more or less distinct concentric ribs along the free margins. On the central and dorsal parts of the lateral surface the reticulation does not show a preferred orientation. The dorsal margin is slightly incised.

*Dimensions (mm)*.– Jolfa Formation, sample Z9: length/height/width of carapace: 0.78/0.40/0.41; length/height of LV: 0.86/0.44; 0.77/0.36; 0.90/0.43; 0.76/0.37; 0.78/0.40; length/height of RV: 0.78/0.38; 0.80/0.42.

*Discussion*.– The present specimens have a similar carapace outline, shape and ornamentation to *Kirkbya unnoda* Wang from the Upper Permian of China, but the latter species is about 30% bigger and the figured specimens in Wang (1978) and in Shi & Chen (2002) do not show concentric ribs along the free margins. Therefore it is assumed that *K.* aff. *unnoda* may represent a subspecies of the Chinese species or a new species. For a final decision a direct comparison of the present material with the type material of *K. unnoda* would be necessary. According to the definition of the genus *Kirkbya* by Jones (1859) the taxon shows two marginal rims/carinae. The assignment of the present material to *Kirkbya* is questionable because of the absence of an inner carina. The type of ornamentation is reminiscent of the Carboniferous genus *Reviya* but in contrast to the latter genus the present species has a different lateral carapace outline and shows a more regular reticulation and rib pattern. *Knightina* cf. *K. hungarica* Kozur 1985 from the Upper Permian of Israel (Honigstein *et al.*, 2006) differs in possessing a posterodorsal shoulder and a more variable reticulation and rib pattern on the lateral surface.

*Stratigraphical and geographial distribution*.– *Kirkbya*? aff. *unnoda* occurs in the lower Jolfa Formation (unit 1) which has an early Dzhulfian age (*C. niuxhuanensis* conodont zone).

### Genus *Nodokirkbya* Kozur, 1991

#### *Nodokirkbya*? sp.1

(Pl. 1, Fig.14)

2008 *Nodokrikbya* sp. Mette, Pl. 2, Fig. 3.

*Material*.– 1 valve.

*Remarks*.– The present species is represented by only one poorly preserved left valve. Because of its lateral outline and type of ornamentation it is thought to belong to the genus *Nodokirkbya* Kozur, 1991. But this assignment is questionable because the details of ornamentation are not preserved and the present species is almost four times larger than the type species of this genus.

A relationship to *Semipetasus* or *Permokegelites* also seems possible. *Semipetasus unicornus* Fohrer from the Upper Carboniferous of the Carnic Alps (Fohrer 1991) is very similar with regard to lateral outline and ornamentation. The present specimen does not however, in contrast to the genera *Semipetasus* and *Permokegelites,* show a dorsomedian swelling or an inner carina and subcentral node respectively.

*Stratigraphical and geographical distribution*.– The present species occurs in the middle part of the Jolfa Formation (unit 2) dated as Dzhulfian (*C. leveni* zone).

### Family AMPHISSITIDAE Knight, 1928

### Genus *Parahollinella* Zalanyi,1974, emend. Kozur, 1985a

#### *Parahollinella notabilis* (Belousova, 1965)

(Pl. 1, Fig.18, Pl. 2, Figs.1-3)

1965 *Amphissites notabilis*. Belousova, p. 255, Pl. 46, Figs. 3a,b.
? 1987 G. et sp. indet. 4. Gerry *et al.*, p. 213, Pl. 2, Fig. 25.
? 2006 G. et sp. indet 4 sensu Gerry *et al.*, 1997. Honigstein *et al.*, p. 420, Pl. 3, Fig. 10.
2008 *Parahollinella notabilis* (Belousova, 1965) subsp.1. Mette, 2008, Pl. 1, Figs. 8,9.

*Material*.– 120 valves and carapaces.

*Remarks*.–The species is characterized by a coarse reticulation and a strong inner carina extending from the posterior to the anteroventral part of the lateral surface and between the kirkbyan pit and the ventral margin. Anteriorly the inner carina is turned up parallel to the anteroventral margin. The posterodorsal node is usually well-developed and the subcentral node is transformed into a short, more or less distinct subcentral ridge which is located just above mid-height and runs parallel to the ventrolateral rib towards the posterodorsal node. The outer carina runs parallel to the free margins starting at the posterodorsal margin and ending at the anterior cardinal angle. Posteriorly the outer carina shows a wing-like extension at mid-height. The dorsal margin is overreached by a high dorsal ridge extending from the anterior cardinal angle to the posterdorsal node and diverging in posterior direction. The kirkbyan pit is relatively small and sometimes almost indistinguishable from the neighbouring reticulation meshes. At the peripheral parts of the lateral surface and at the dorsal surface the reticulation meshes are oriented parallel to the valve margins and at the central part parallel to the inner carina and subcentral ridge.

*Dimensions (mm)*.– Jolfa Formation, sample Z4: length/height of RV: 0.78/0.44; 0.95/0.46; 0.72/ 0.39; length/height of LV: 0.78/0.40; 0.84/0.45; 0.76/0.42; sample Z9: length/height/width of carapace: 0.92/0.45/0.48; 0.85/0.45/0,46; 0.82/0.46/0.50; sample Z11: length/height of LV: 1.02/0.64; 1.10/0.56; length/height of RV: 1.10/0.62; 1.02/0.62; length/height/width of carapace: 0.88/0.44/0.50.

*Discussion*.– The specimens described by Gerry *et al.* (1987) as G. et sp. indet 4 and also recorded by Honigstein *et al.* (2006) from the Upper Permian of Israel are similar in carapace outline, ornamentation and size to *P.*

*notabilis* (Belousova) but their poor preservation precludes a definite assignment. A species which is probably closely related to the present species was described as *Amphissites biambonaria* from the Changhsingian of southern China (Hao, 1992, 1993, 1994). *A. biambonaria* was also described as *Neoamphissites costatus* Becker & Wang in Becker & Wang (1992) and in Becker (1997). The species from China shows some similarity with the present species in carapace outline and type of ornamentation. It differs from *P. notabilis* by the occurrence of a long and distinct subdorsal carina instead of a short ridge, the absence of a posterodorsal node and a much finer reticulation.

*Stratigraphical and geographical distribution*.– Belousova (1965) recorded *P. notabilis* from the Upper Permian (Dzhulfian - Dorashamian) of Azerbaijan. In NW Iran *P. notabilis* is restricted to the lower Jolfa Formation (unit 1- lower unit 2) which has been dated by conodonts as Dzhulfian (*Clarkina nixhuanensis* – lower *Clarkina leveni* Zone) (Mette, 2008).

### ***Parahollinella* sp.1**

(Pl. 2, Figs. 4-5)

2008 *Parahollinella notabilis* subsp.2. Mette, Pl. 1, Fig. 7.

*Material*.– 3 complete adult valves, 5 incomplete adult valves, 1 juvenile carapace, 3 juvenile valves.

*Dimensions (mm)*.– Jolfa Formation, sample Z24: length/height of RV: 1.08/0.62; length/height of LV: 0.98/0.62; 1.06/0.60; length/height/width of juvenile carapace: 0.90/0.52/0.52.

*Remarks*.– The species shows a similar carapace shape and type of ornamentation to *Parahollinella notabilis* (Belousova), but the inner carina is either very weakly developed or completely reduced. The outer carina, the dorsal ridge and the posterodorsal node are also strongly reduced in comparison to *P. notabilis* and the lateral surface is therefore more regularly convex. The kirkbyan pit is small and, similar to *P. notabilis*, on some specimens almost indistinguishable from the neighbouring reticulation meshes. The carapace size is also comparable to the latter species. Because of the above mentioned similarities and restriction to a younger biostratigraphical unit it is suggested that *Parahollinella* sp.1 is a descendant of *P. notabilis*. There is, however, insufficient material available for a detailed description and definition of this species.

*Stratigraphical and geographical distribution*.– The present species has been recorded from one sample in the upper part of the Jolfa Formation (unit 3), which belongs to the upper Dzhulfian (*C. transcaucasia* – *C. orientalis* conodont zone) (Mette, 2008).

Superfamily KIRKBYOIDEA? Ulrich & Bassler, 1906
Family SCROBICULIDAE Pozner, 1951

## **Genus *Roundyella* Bradfield, 1935**

### ***Roundyella* sp.1**

(Pl. 1, Fig. 15)

2008 *Roundyella* aff *kroemmelbeini* Kozur, 1985. Mette, Pl. 2, Fig. 6.

*Material*.– 2 valves and 3 carapaces.

*Dimensions (mm)*.– Jolfa Formation, sample Z24: length/height of carapace: 0.68/0.38; 0.68/0.40.

*Remarks*.– *Roundyella* sp.1 is represented by only a few poorly preserved specimens. Therefore a comparison with other species of *Roundyella* is difficult. The presence of a shallow marginal bulge at the anterior, posterior and ventral margins which is ornamented with papillae would suggest a close relationship to *Roundyella lebaensis* Krömmelbein from the Zechstein Limestone (Krömmelbein 1958). There is however a distinct irregulare and coarse reticula-

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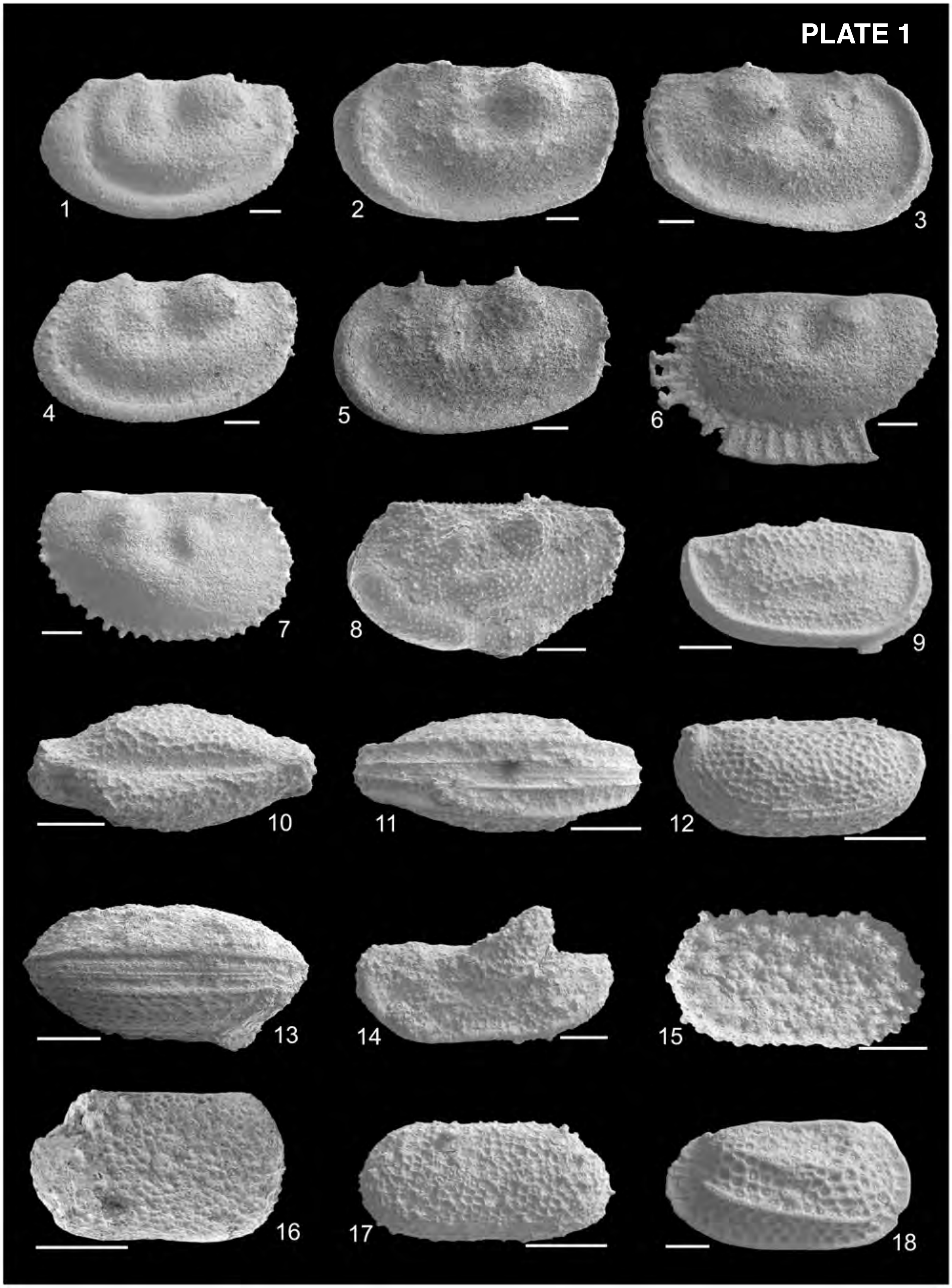
Plate 1. *1-8*: *Hollinella tuberculata* Belousova. 1: female, left valve (sample 10), 2: female, left valve (sample 28); 3: male, right valve (sample 28); 4: male, left valve (sample 7); 5: male, left valve (sample 28); 6: male juvenile, left valve (sample 28); 7: male juvenile, right valve (28); 8: female juvenile, left valve (sample 31). *9-11*: *Kirkbya jolfaensis* n.sp.. 9: carapace, holotype, right lateral view (sample 4); 10: carapace, dorsal view (sample 6); 11: carapace, ventral view (sample 6). *12-13*: *Kirkbya*? aff. *unnoda* (Wang). 12: carapace, left lateral view (sample 10); 13: carapace, ventral view (sample 9). *14*: *Nodokirkbya*? sp.1, left valve (sample 16,1). *15*: *Roundyella* sp.1, left valve (sample 24). *16*: *Roundyella* sp.2, carapace, left lateral view (sample 10). *17*: *Roundyella* sp., carapace, right lateral view (sample 4). *18*: *Parahollinella notabilis* (Belousova), right valve (sample 11). All figures of valves are external views. Scale bar = 200µm.

**PLATE 1**



tion on the lateral surface of *Roundyella* sp.1 which has not been recorded from adult specimens of *R. lebaensis*. Spines seem to be confined to the dorsal margin and the rest of the lateral and marginal surface is covered by coarse papillae. *Roundyella kroemmelbeini* Kozur from the Middle Permian of Hungary (Kozur, 1985a,b) lacks a marginal bulge at the anterior and posterior margins and shows long spines covering the complete lateral surface.

*Stratigraphical and geographical distribution*.– *Roundyella* sp.1. is recorded from the Dzhulfian (Jolfa Formation) of Northwest Iran.

### ***Roundyella* sp. 2**

(Pl. 1, Fig. 17)

? 2006 *Roundyella* cf. *R. papilliformis* Wang. Honigstein *et al.*, Pl. 3, Figs. 11, 12.

*Material.* – 1 carapace.

*Remarks*.– *Roundyella* sp. 2 shows a fine but strong reticulation and small papillae. There is a strong similarity in ornamentation and lateral carapace outline to *Roundyella* cf. *R. papilliformis* from the Upper Permian of Israel (Honigstein *et al.*, 2006). The latter authors did not give a description of this species. *Roundyella* sp. 2 is probably a new species but is left in open nomenclature because it is represented by only one incomplete and poorly preserved carapace.

*Stratigraphical and geographical distribution*.– *Roundyella* sp. 2 occurs in the lowermost Jolfa Formation dated as lower Dzhulfian (Mette, 2008).

Order PODOCOPIDA Müller, 1894
Suborder PLATYCOPINA Sars, 1866
Superfamily KLOEDENELLOIDEA Ulrich & Bassler, 1908
Family GEISINIDAE? Sohn, 1961

### **Genus *Sargentina* Coryell & Johnson, 1939**

### ***Sargentina* cf. *xinhuanensis* (Wang, 1978)**

(Pl. 2, Figs. 6-8)

? 1978 *Knoxiella xinhuanensis* n.sp.. Wang, p. 287, Pl. 2, Figs. 4a, 4b, 4c.
? 1996 *Knoxiella xinhuanensis* Wang. Hao, Pl. 1, Fig. 18.
2008 *Italogeisina* sp. Mette, Pl. 1, Figs. 10, 11.

*Material.* – 4 carapaces.

*Dimensions (mm)*.– Jolfa Formation, sample 4: length/height/width of carapace: 0.66/0.39/0.32; 0.70/0.42/0.34; 0.70/0.43/-; 0.64/0.39/-.

*Remarks*. - Due to the great similarity in carapace outline, overlap and shape of sulcus the present material is either conspecific or closely related to *Sargentina xinuanensis* (Wang) from the Upper Permian of China. A characteristic feature of this species is the sulcus which shows a distinct lateral extension in the subcentral part of the lateral surface. In contrast to the figured specimens in Wang (1978) and Hao (1996) the lateral extension of the sulcus at the present material is broader and shows a gradual peripheral shallowing. Furthermore, the lateral extension of the sulcus runs parallel and not oblique to the dorsal margin and the posterior lobe shows a more or less distinct node-like dorsal elevation which overreaches the dorsal margin in lateral view. Because of insufficient material (4 carapaces) it is not clear if these minor differences are due to intraspecific variability. *Sargentina transita* (Kozur) from the Dzhulfian of Hungary (Kozur, 1985a) also corresponds to the present material with regard to carapace outline in lateral view and overlap. Compared to the figured specimens from Hungary the present specimens show a stronger posterior lobe and a broader sulcus. The species from Hungary also lacks the subcentral extension of the sulcus and the present carapaces are also about 20% smaller than the specimens of Hungary. The material which was described as *Sargentina transita* (Kozur) from the Middle Permian of Oman by Crasquin-Soleau *et al.* (1999) is also similar to the present species but it differs from the Iranian material in the same morphological criteria as the species from Hungary and is of even greater size than the type material of *S. sargentina*.

*Stratigraphical and geographical distribution*.– *S.* cf. *niuxhuanensis* occurs in the lower part (unit 1) of the Jolfa Formation which is lower Dzhulfian (*C. niuxhuanensis* Zone). It is possibly also present in the Upper Permian of China.

### Family CAVELLINIDAE Egorov, 1950

### Genus *Cavellina* Coryell, 1928

### *Cavellina jolfaensis* n. sp.

(Pl. 2, Figs. 9-17)

2008 *Cavellina* aff. *arcuata* Coryell & Rogatz, 1932. Mette, Pl. 1, Figs. 12-14.

*Derivation of name*.– Referring to the town Jolfa which is located near to the type locality.

*Holotype*.– Zal 6,18, Pl. 2, Fig.9.

*Type locality*.– Zal section, 22 km southwest of the town Jolfa at the Iran-Azerbaijan boundary, Northwest Iran.

*Material*.– 520 valves and carapaces.

*Type horizon*.– Lower Jolfa Formation (lithostratigraphical unit 1, sample 9), Lower Dzhulfian (*Clarkina niuxhuanensis* zone).

*Occurrence*.– Lower Jolfa Formation (lithostratigraphical unit 1 – lower part of unit 2), Lower Dzhulfian (*Clarkina niuxhuanensis* – *Clarkina leveni* zones), Northwest Iran.

*Diagnosis*.– *Cavellina jolfaensis* is characterized by a subovate carapace with a symmetrically rounded (females) or angled (males) posterior margin in lateral view and a blunt posterior extremity in dorsal view.

*Description*.– The female carapace outline is subovate in lateral view and wedge-shaped in dorsal view with a blunt posterior end. Greatest width is located at 2/5th of length; greatest height at or just behind mid-length and greatest length at mid-height. The RV/LV overlap is weak at the anterior margin and strong at the dorsal and ventral margins with a maximum on the median part of the dorsal margin. No overlap occurs at the ventral part of the posterior margin. The adult females are strongly convex on the dorsal margin and gently convex to straight on the ventral margin. The dorsal margin is anteriorly slightly flattened and merges gradually into the anterior and posterior margins. The posterior margin is, like the anterior margin, almost symmetrically but more narrowly rounded; it gradually runs into the ventral margin. The female LV has a weakly arched dorsal margin; the anterior 3/5th part is almost straight and slightly inclined towards the symmetrically rounded anterior margin and the posterior 2/5th part broadly rounded and merging into the symmetrically rounded posterior margin. The ventral margin is straight to slightly convex.

The male shows a very similar lateral carapace outline but in contrast to the females the posterior margin of the right valve is more or less distinctly angled at mid-height. Furthermore, the male left valve differs from the female left valve in the angulation of the dorsal margin just behind mid-length and of the posterior margin at mid-height. Anterior and posterior parts of the dorsal margin are almost straight and the latter is distinctly inclined towards the posterior margin. Another difference between the males and females is the less convex, lens-shaped dorsal carapace outline of the males with the maximum thickness located at mid-length.

*Dimensions (mm)*.– Jolfa Formation, sample Z10: length/height of female RV: 0.96/0.66; 1.00/0.68; length/height of female LV: 0.96/0.53; 0.94/0.55; length/height/width of female carapace: 0.96/0.67/0.44; 0.96/0.66/0.44; length/height of male RV: 0.93/0.62; 0.92/0.59; length/height of male LV: 0.89/0.51;0.90/0.50; length/height/width of male carapace: 0.93/0.60/0.36; 0.90/0.62/0.40.

*Discussion*.– *Cavellina nebrascensis* (Geinitz) Kellett 1935 from the Upper Carboniferous-Lower Permian of Kansas has a very similar lateral carapace outline but the present species differs in the dorsal carapace outline with the maximum thickness located more anteriorly, the posterior end being more blunt and the sexual dimorphism being less distinct. The Iranian species is also about 10% smaller than *C. nebrascensis.* The same differences in dorsal carapace outline and size occur between *C. jolfaensis* n.sp. and *Cavellina fittsi* Kellett. *C. jolfaensis* can also be distinguished from *Cavellina ellipticalis* Hamilton from the Upper Permian of Texas (Hamilton 1942) by the different carapace outline in dorsal view with the greatest height located more anteriorly. Furthermore the ventral margin is not concave. In comparison to *Cavellina visnoyensis* Kozur from the Upper Permian of Hungary (Kozur, 1985a) the left valve of the present species has a less strongly arched dorsal margin and no concave ventral margin. *C.*

*jolfaensis* is also of greater size. *Cavellina subunica* Belousova does not show a dorsal convexity or angulation, the carapace outline in dorsal view is more slender with distinctly tapering extremities and it is of distinctly smaller size. In contrast to *Cavellina arcuata* Coryell & Rogatz, 1932 the present species does not show distinctly incised posterior and posteroventral margins and the posterior angulation is located at mid-height.

*Stratigraphical and geographical distribution*.– The species is recorded from the lower Jolfa Formation (unit 1- lower unit 2) of Northwest Iran (Zal section) which belongs to the lower Dzhulfian.

### ***Cavellina* aff. *longa* Kotschetkova & Gusseva, 1972**

(Pl. 2, Figs.18-19, Pl. 3, Figs.1-2)

? 1965 *Cavellina subunica* n. sp. Belousova, p. 255-256, Pl. 46, Figs. 4a, 4b.
? 1972 *Cavellina longa* n. sp. Kotschetkova & Gusseva, p. 21, Pl. 10, Figs. 1-6.

*Material*. – 4 carapaces and 4 valves.

*Dimensions (mm)*.– Jolfa Formation, sample Z4: length/height/width of male carapace: 1.0/0.53/0.35; length/height of male RV: 1.02/0.58; sample Z9: length/height/width of juvenile carapace: 0.80/0.40/0.28; 0.76/0.40/0.30; sample Z11: length/height/width of male carapace: 0.98/0.50/0.32; length/height of juvenile RV: 0.91/0.46; 0.88/0.48; length/height of juvenile LV: 0.82/0.46.

*Remarks*.– In lateral carapace outline and overlap the present male specimens coincede with the males of *Cavellina longa* from the lower Permian of the central Ural region (Kotschetkova & Gusseva, 1972). The present specimens, however, do not show a posterior carapace inflation. Due to the lack of adult female specimens and because of the differences in dorsal outline it is questionable if the Iranian material is conspecific with *C. longa*. Another similar species is *Cavellina subunica* Belousova from the Upper Permian of Azerbaijan (Belousova, 1965). According to the figured specimen of *C. subunica* in Belousova (1965) the present species seems to be more slender in lateral view. Therefore a direct comparison of *C.* sp.1 and the type material of *C. subunica* and determination of intraspecific variability would be necessary to assess their relationship. *Cavellina firma* Schneider from the Upper Permian of Russia (Schneider, 1966) has a concave ventral margin, a greater carapace size and the posterior margin of the right valve is only slightly angled.

*Stratigraphical and geographical distribution*.– *C.* aff. *longa* is restricted to the lower part of the Jolfa Formation (unit 1-2) dated as Lower Dzhulfian (*C. niuxhuanensis – C. leveni* Zone).

### ***Cavellina*? sp.**

(Pl. 3, Figs. 3-4)

2008 Cavellinidae? sp. Mette, Pl. 3, Figs. 1, 2.

*Material*. – 3 carapaces.

*Remarks*.– *Cavellina*? sp. is represented by only a few specimens which are preserved as steinkerns. The presence of a strong posterior swelling suggests that the species may be a representative of *Cavellina*. A similar steinkern was described by Sohn (1970) from the Lower Triassic (Spathian) of Pakistan as *Reubenella*? sp. A species described as *Kloedenellitina* sp.1 with a similar carapace outline was recorded from the Upper Permian of Saudi Arabia (Crasqun-Soleau *et al*., 2005). These specimens have their shells preserved and therefore cannot be directly compared.

*Stratigraphical and geographical distribution*.– *Cavellina*? sp.1 is present in the lowermost Griesbachian (*H. parvus* zone) at the Zal section (Northwest Iran).

Plate 2. *1-3: Parahollinella notabilis* (Belousova). 1: left valve (sample 11); 2: carapace, dorsal view (sample 11); 3: carapace, ventral view (9). *4-5*: *Parahollinella* sp.1. 4: right valve (sample 24); 5: carapace, dorsal view (sample 24). *6-8*: *Sargentina* cf. *xinhuanensis* (Wang). 6: carapace, left lateral view (sample 4); 7: carapace, left lateral view (sample 4); 8: carapace, dorsal view (sample 4). *9-17*: *Cavellina jolfaensis* n. sp.. 9: female, carapace, holotype, left lateral view (sample 9); 10: female, right valve (sample 11); 11: female, left valve (sample 11); 12: female, left valve (sample 11); 13: male, right valve (sample 11); 14: male, right valve (sample 11); 15: male, left valve (sample 11); 16: male, carapace, dorsal view (sample 9); 17: female, carapace, dorsal view (sample 9). *18-19*: *Cavellina* aff. *longa* Kotchetkova & Gusseva. 18: carapace, left lateral view (sample 11); 19: right valve (sample 11). All figures of valves are external views. Scale bar = 200µm.

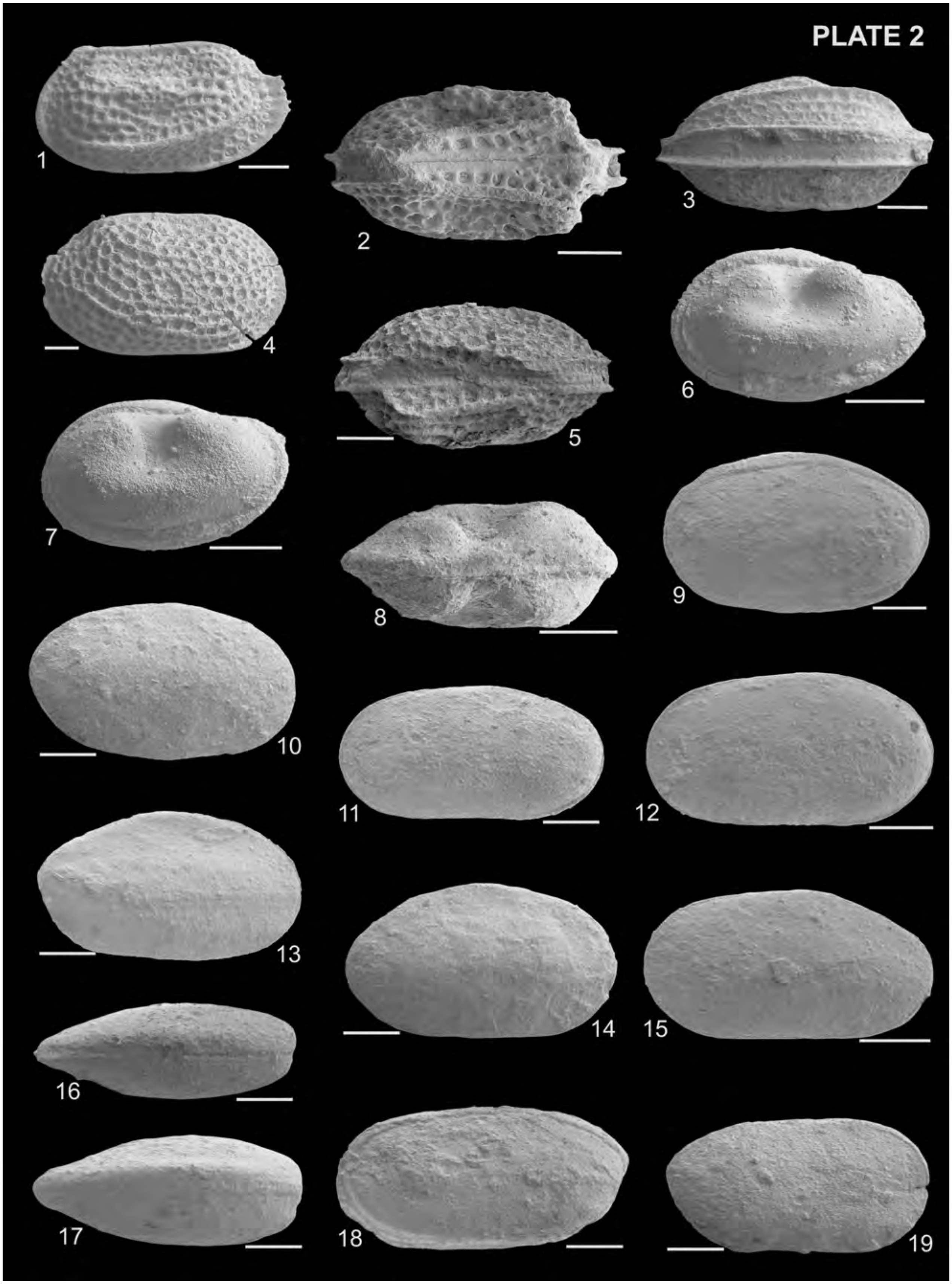


**PLATE 2**

### ***Sulcella* sp.1**

(Pl. 3, Fig. 5)

2008 *Sulcella* sp. Mette, Pl. 3, Fig. 3.

*Material.* – 280 carapaces and valves.

Dimensions (mm).– Elika Formation, sample 47, length/height/width of female carapace: 0.58/0.36/0.26; 0.54/0.34/0.28; 0.56/0.39/0.26; length/height/width of male carapace: 0.54/0.32/ 0.20; length/height of male RV: 0.56/0.36.

*Remarks*.– *Sulcella* sp.1 shows a distinct angulation of the posterior margin at 2/3rd of carapace height and a shallow subcentral sulcus ending in a pit at or just above mid-height. The most conspicuous feature of the species is a peripheral rim running around the margins. In dorsal view the species shows a distinct sexual dirmorphism in carapace outline. The female carapace has a wedge-shaped outline with greatest width at 1/4th of carapace length and the male carapace is lense-shaped with greatest width at mid-length. The weak calcification and relative small size suggests that the specimens from sample 52 are all juveniles, except the figured specimen. The specimens from sample 47 (Boundary Clay) are adults but show a poor preservation due to strong calcitic encrustation. The poorly preserved specimens of sample 47 were recorded in Mette (2008) as "*Indivisia* sp.2". In lateral outline the species resembles *Sulcella sulcata* Coryell & Rogatz but a peripheral rim was not described from the latter species.

*Stratigraphical and geographical distribution*.– *Sulcella* sp.1 is abundant in beds of the Boundary Clay (upper Dorashamian; *H. praeparvus* – *C. meishanensis* zone) and the lowermost Elika Formation (lowermost Griesbachian; *H. parvus* zone).

Suborder PODOCOPINA Sars, 1866
Superfamily BAIRDIOIDEA Sars, 1888
Family BAIRDIIDAE Sars, 1888

### **Genus *Bairdia* McCoy, 1844**

### ***Bairdia guangxiensis* Guan, 1978**

(Pl. 3, Figs. 6-7)

1978 *Bairdia guangxiensis* Guan n. sp. Guan, p.154, Pl. 38, Figs. 3,4.
1985a *Cryptobairdia bolzi* n.sp. Kozur, p. 60, Pl. 13, Figs. 6,8
2002 *Bairdia guangxiensis* Guan. Shi & Chen, p. 67, Pl. 5, Figs. 1-9, Pl. 28, Figs. 3,4.

*Material.* – 61 carapaces and valves.

*Dimensions (mm)*.– Ali Bashi Formation, sample Z39, length/height/width of carapace: 1.54/0.88/0.72; 1.48/0.86/0.72; 1.46/0.86/0.80.

*Remarks*.– According to Kozur (1985a) *Cryptobairdia bolzi* Kozur from the Middle Permian of Hungary differs slightly from the Upper Permian *B. guangxiensis* in the shape of the ventral margin. The figured specimens in Shi & Chen (2002) do not show differences between the two species and *C. bolzi* is therefore regarded as synonymous with *B. guangxiensis*.

*Stratigraphical and geographical distribution*.– *B. guangxiniensis* was first described from the Upper Permian (Wuchiapingian) of Guangxi (China). It probably also occurs in the Middle Permian of Hungary. In NW Iran the species is recorded from a sample in the middle part of the Ali Bashi Formation which is dated by conodonts as Dorashamian (*C. subcarinata* zone).

### ***Orthobairdia zaliensis* n. sp.**

(Pl. 3, Figs. 8-12)

? 1965 *Orthobairdia guadalupiana* (Hamilton 1942). Belousova, Pl. 50, Figs. 1a, 1b.

2008 *Orthobairdia* sp.1. Mette, Pl. 2, Figs. 4,5.

*Derivation of name*.– Referring to the name of the type locality (Zal).

*Holotype*.– Zal 7,4, Pl. 3, Fig.10.

*Type locality*.– Zal section, 22Km southwest of the town Jolfa at the Iran-Azerbaijan boundary, Northwest Iran.

*Material*.– 180 valves and carapaces.

*Type horizon*.– Upper Jolfa Formation (lithostratigraphical unit 3, sample 25), Dzhulfian (*Clarkina transcaucasia – C. orientalis* conodont zone).

*Occurrence*.– Jolfa Formation and Ali Bashi Formation, Dzhulfian - Dorashamian (*Clarkina leveni – C. subcarinata* conodont zones), Northwest Iran.

*Diagnosis*.– A species of *Orthobairdia* with a subovate lateral carapace outline and an anterodorsal margin which is gently convex on the left valve and weakly concave at the right valve. The species is also characterized by high intraspecific variability with regard to the carapace outline in dorsal view.

*Description*.– The left valve of the present species is characterized by gently arched dorsal and anterodorsal margins and a straight ventral margin. The anterior margin shows a maximum curvature at mid-height and gradually merges into the ventral and dorsal margins. The posterior margin is sharply angled below mid-height at 2/5th of valve height. It consists of a broadly rounded ventral part and a straight dorsal part which is inclined at 45° and angled against the dorsal margin at 2/5th of valve length.

On the right valve the dorsal margin shows a long and gently inclined straight anterior part with a weak anterodorsal concavity and a much shorter and more steeply inclined straight posterior part with a short concavity at mid-height. The middle part of the dorsal margin is almost straight and relatively short; it is gently angled against the posterior and anterior slopes and slightly inclined towards the posterior end. The ventral margin has a distinct median concavity and gradually merges into the ventral parts of the posterior and anterior margins. A maximum curvature of the anterior margin is located at mid-height and the posterior margin is pointed at 2/5th of valve height.

The left valve overlaps the right valve along all margins with a minimum at the anterior and posteroventral margins. In dorsal view the carapace shows a great variability in outline. The samples from the lower Jolfa Formation include specimens with a lens-shaped outline. In the samples from the upper Jolfa Formation and Ali Bashi Formation abundant specimens occur with a subrhomboidal outline with straight and parallel median sides and straight converging anterior and posterior parts of the sides which are angled against the middle part at 1/3rd and 2/3rd of carapace length. Maximum carapace height is located at mid-length and the lateral carapace convexity is greatest at mid-height.

*Dimensions (mm)*.– Jolfa Formation, sample Z25: length/height/width of carapace: 1.60/0.90/ 0.70; 1.64/ 0.88/0.68; length/height of LV: 1.62/0.92; length/height of RV: 1.50/0.78; 1.54/0.85; sample Z24: length/height/ width of carapace: 1.40/0.80/0.58.

*Discussion*.– *Orthobairdia zaliensis* n. sp. is somewhat similar in carapace outline to *Bairdia guadelupiana* Hamilton from the Upper Permian of Texas. The present specimens can be distinguished from the latter species by the posterior beak which is located distinctly below mid-height, the straight venter, the maximum height at mid-length, the maximum thickness at mid-height and the gently converging sides. *Bairdia beedei* Ulrich & Bassler, 1906 shows a dorsal margin with a shorter straight anterodorsal part and a longer straight median part. *Orthobairdia guadalupiana* (Hamilton, 1942) shows a similar lateral carapace outline but the figured specimens do not show intraspecific variability in dorsal carapace outline and the anterior margin is more broadly rounded. The conspecificity with *Orthobairdia zaliensis* n.sp is therefore questionable. The great intraspecific variability in dorsal carapace outline (co-occurrence of subrhomboidal and lense-shaped specimens) suggests that this feature cannot be used as a generic character in the Bairdoidea and the genus *Orthobairdia* Sohn should be critically verified.

*Stratigraphical and geographical distribution*.– The species is only known from the Upper Permian (Dzhulfian-Dorashamian) of Northwest Iran. It possibly occurs also in the Upper Permian of Azerbaijan (Belousova, 1965).

### Genus *Cryptobairdia* Sohn, 1960

### *Cryptobairdia intermedia* (Belousova, 1965)

(Pl. 3, Figs. 13-15)

1965 *Bairdia intermedia* Belousova n.sp. Belousova, p. 260, Pl. 49, Fig. 1.
1985 *Cryptobairdia intermedia* (Belousova). Kozur, Pl. 6, Fig. 5.

? 1989 *Bairdia consimilis* Gusseva. Lethiers *et al*., Pl. 3, Figs. 7,8.
2008 *Bairdia* aff. *intermedia* Belousova. Mette, Pl. 1, Figs. 16-18.

*Material*. – About 560 carapaces.

*Dimensions (mm)*.– Jolfa Formation, sample Z9: length/height/width of carapace: 1.20/0.70/0.52; sample Z10: length/height/width of carapace: 1.28/0.70/0.50; Ali Bashi Formation, sample Z31: length/height/width of carapace: 1.10/0.58/0.46; 1.04/0.58/0.42; 1.10/0.60/0.50; 1.00/0.56/0.46; sample Z41: length/height/width of carapace: 1.02/0.56/0.40.

*Remarks*.– The species is characterized by a more or less asymmetrically arched dorsal margin on the left valve which is posteriorly more strongly inclined than anteriorly and by a broadly rounded and projecting anterior margin on the right valve. A very similar species is *Bairdia consimilis* Gusseva sensu Lethiers *et al*., 1989, recorded from the Permian of Tunisia and *B. consimilis* may therefore be a junior synonym. Another similar species is *Bairdia divja* Gusseva from the Lower Permian of southern Russia (Gusseva, 1971) but this species is of much greater size and has a symmetrically arched dorsal margin on the left valve.

*Stratigraphical and geographical distribution*.– *Cryptobairdia intermedia* was first recorded from the Dzhulfian and Dorashamian of Azerbaijan (Belousova, 1965) and later also found in the Middle and Upper Permian of Hungary (Kozur, 1985b). In NW Iran *C. intermedia* is recorded from the Dzhulfian and Dorashamian (Zal section).

### Genus *Bairdiacypris* Bradfield, 1935

### *Bairdiacypris zaliensis* n. sp

(Pl. 3, Figs. 16-17)

2008 *Praezabythocypris* sp. 3. Mette, Pl. 2, Fig. 9.

*Derivation of name*.– Referring to the name of the type locality (Zal).

*Holotype*.– Zal 2,10, Pl. 3, Fig. 16.

*Type locality*.– Zal section, 22 km southwest of the town Jolfa near to the Iran-Azerbaijan boundary, Northwest Iran.

*Material*.– 19 carapaces.

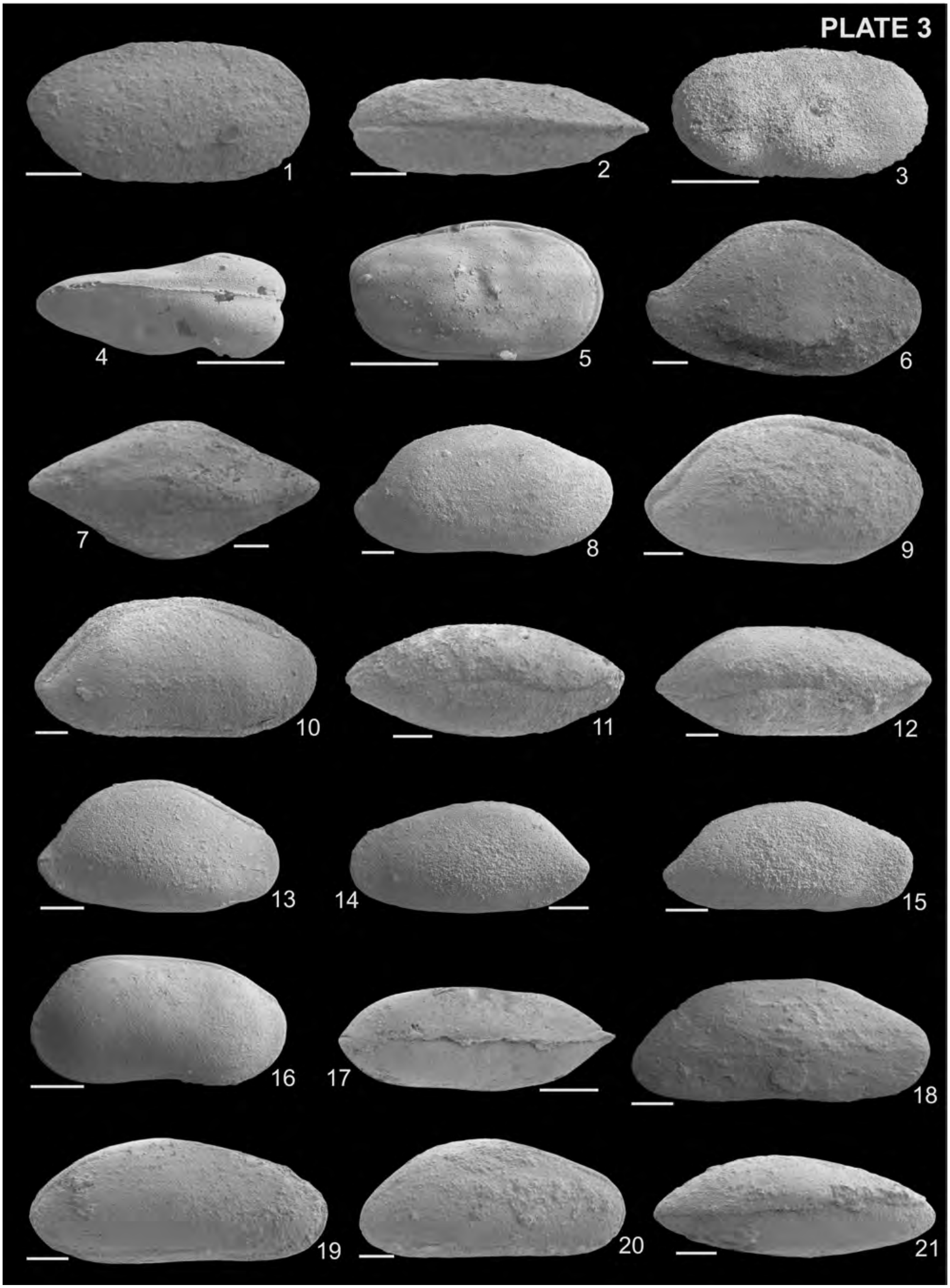
*Type horizon*.– Lower Elika Formation (shale horizon in thin-bedded micritic limestone unit, base of lithostratigraphical unit 3, sample 56), 0.7m above the base of the *Hindeodus parvus* conodont zone.

*Occurrence*.– Lower Elika Formation (samples 52, 56), Zal section, Lowermost Triassic (basal Griesbachian), Northwest Iran.

*Diagnosis*.– *Bairdiacypris zaliensis* is characterized by a distinct angulation of the posterodorsal margin and squat lateral carapace outline.

*Description*.– *Bairdiacypris zaliensis* n. sp. has a squat, subreniform lateral carapace outline and moderately convex dorsal outline with sharply tapering extremities. The anterior margin of both valves is broadly rounded with a maximum of convexity at or just below mid-height. The anterodorsal part is straight and inclined towards the anterior margin or slightly convex and gradually merging into the dorsal margin. At the posterior end the margin of both valves consists of a straight and steeply inclined posterodorsal part which is distinctly angulated against the dorsal margin and a narrowly curved posteroventral part. The dorsal margin is straight on the right valve and slightly convex on the left valve. It runs parallel to the ventral margin or is slightly inclined towards the anterior margin. At the middle part of the ventral margin a strong concavity occurs; the ventral margin gradually merges into the anterior and posterior margins. The left valve slightly overlaps

Plate 3. *1-2*: *Cavellina* aff. *longa* Kotchetkova & Gusseva. 1: right valve (sample 10); 2: carapace, dorsal view (sample 10). *3-4*: *Cavellina*? sp.. 3: carapace, right lateral view (sample 52); 4: carapace, ventral view (sample 52). *5*: *Sulcella* sp.1, male right valve (sample 52). *6-7*: *Bairdia guangxiensis* Guan. 6: carapace, right lateral view (sample 39); 7: carapace, dorsal view (sample 39). *8-12*: *Orthobairdia zaliensis* n. sp. 8: right valve (sample 25); 9: carapace, right lateral view (sample 10); 10: carapace, holotype, right lateral view (sample 25); 11: carapace, dorsal view (sample 10); 12: carapace, dorsal view (sample 25). *13-15*: *Cryptobairdia intermedia* (Belousova). 13: carapace, right lateral view (sample 33); 14: left valve (sample 28); 15: right valve (sample 28). *16-17*: *Bairdiacypris zaliensis* n. sp. 16: carapace, holotype, right lateral view (sample 56); 17: carapace, dorsal view (sample 52). 18-21: *Bairdiacypris* sp.1. 18: right valve (sample 11); 19: carapace, right lateral view (sample 6); 20: carapace, right lateral view (sample 9); 21: carapace, dorsal view (sample 6). All figures of valves are external views. Scale bar = 200µm.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the right valve along the dorsal, anterodorsal and posterodorsal margins. Maximum carapace length is located at or slightly below mid-height, maximum carapace height occurs at mid-length or at 1/3rd of carapace length and the maximum width is at mid-length. Internal features are not accessible.

*Dimensions (mm)*.– Elika Formation,sample Z52: length/height/width of carapace: 0.72/0.40/0.29; 0,84/ 0.44/0.32; 0.90/0.50/0.34; 0.88/0.50/0.35; 0.94/ 0.54/-; 0.86/0.48/0.34.

*Discussion*.– A species similar to *B. zaliensis* n.sp. is *Bairdiacypris ventralis* Chen from the Middle Permian of South China (Chen, 1958). In contrast to the latter species the present specimens show a distinct posterodorsal angulation, more sharply tapering extremities in dorsal view and the overlap of the left valve is restricted to the dorsal, anterodorsal and posterodorsal margins. *B. changxingensis* Shi, 1987 has a more elongate lateral carapace outline, a less distinct posterodorsal angulation and the extremities are more blunt in dorsal view.

*Stratigraphical and geographical distribution*.– The species is recorded from basal Triassic strata (lowermost Griesbachian) of Northwest Iran; a few centimetres to 0.4m above the Permian/Triassic boundary. This stratigraphical range suggests that the species may be a valuable biostratigraphical indicator for the basal Triassic at a regional scale.

### ***Bairdiacypris* sp.1**

(Pl. 3, Figs. 18-21)

? 2002 "*Fabalicypris gleenensis* (Harlton)". Shi & Chen, Pl. 23, Figs. 1,2.

*Material*. – 13 valves and carapaces.

*Dimensions (mm)*.– Jolfa Formation, sample Z9: length/height/width of carapace: 1.38/0.64/0.56; sample Z10: length/height/width of carapace: 1.46/0.48/0.50; sample Z11: length/height of LV: 1.26/0.60; sample Z6: length/height/width of carapace: 1.30/0.60/0.50; 1.30/ 0.58/0.48.

*Remarks*.– With regard to the lateral carapace outline the present material is somewhat similar to a species described as *Bairdiacypris jonesiana* (Kirkby) from the Permian of Russia by Ivanov (1975). The present material differs in the more rounded posterior margin, the less distinct concavity at the ventral margin and angulation of the dorsal margin at the right valve. *Bairdiacypris* sp. 1 is also comparable with the species which was described as "*Fabalicypris gleenensis*" (Harlton) from the Late Permian of China (Shi & Chen, 2002). The figured specimen however is poorly preserved and the conspecificity is therefore questionable.

*Stratigraphical and geographical distribution*.– *Bairdiacypris* sp.1 occurs in the lower Jolfa Formation, lower Dzhulfian of Northwest Iran.

## Family BAIRDIIDAE? Sars, 1888

### **Genus *Praezabythocypris* Kozur, 1985**

### ***Praezabythocypris*? *ottomanensis* (Crasquin-Soleau, 2004)**

(Pl. 4, Figs. 1-4)

2004 *Bairdiacypris ottomanensis* n.sp. Crasquin-Soleau, p. 285, Pl. 2, Figs. 13-24.
2005 *Bairdiacypris ottomanensis* Crasquin-Soleau, 2004. Crasquin-Soleau & Kershaw, Pl. 1, Figs.10-12.
2008 *Praezabythocypris* sp.1. Mette, Pl. 2, Figs. 10,11.

*Material*. – About 310 carapaces.

*Dimensions (mm)*.– Elika Formation, sample Z52: length/height/width of female carapace: 0.84/ 0.47/0.38; 0.76/0.42/0.34; 0.84/0.48/0.36; length/height/width of male carapace: 0.86/0.48/0.32; 0.72/0.40/0.32; sample Z47: length/height/width of male carapace: 0.92/0.50/ 0.40.

*Remarks*.– *Praezabythocypris pulchra* Kozur 1985 shows a more distinct dorsal overlap of the left valve which is strongly arched dorsally. *Bairdiacypris*? *caeca* Shi from the Changhsingian of Meishan section (Shi & Chen, 1987) is similar in lateral carapace outline and overlap structure. In dorsal view the present species differs in the more convex outline with more rounded extremities and the greatest width located in the posterior third. In lateral view the present species is more slender. In contrast to the material described from the early Induan of western Taurus (Crasquin-Soleau *et al.*, 2004) some specimens of the present material show a weak ornamentation of small pustulae. This feature is regarded as an ecophenotypic feature due to environmental deterioration during the P/T-crisis because it occurs only in one horizon (sample 52) located a few centimetres above the Permian-Triassic boundary (Mette, 2008). Another important characteristic of the species is the occurrence of specimens with an inflated posterior part which was mentioned by Crasquin-Soleau *et al.* (2004). Despite this observation Crasquin-Soleau assigned the species to *Bairdiacypris*. With regard to carapace outline and overlap the present species is most probably a representative of *Praezabythocypris*. Internal features including adductor muscle scars are not accessible. Since sexual dimorphism is generally not observed among representatives of Bairdioidea the systematic position of the present species is therefore questionable.

*Stratigraphical and geographical distribution*.– According to Crasquin-Soleau *et al.* (2004) *P.*? *ottomanensis* occurs in lowermost Triassic beds of the *Isarcicella isarcica* conodont zone in the Taurus (Turkey). These authors suggested a stratigraphical gap in the uppermost Changsingian and lowermost Induan. The species was also recorded from lowermost Triassic beds (*Hindeodus parvus* conodont zone) of South China (Crasquin-Soleau & Kershaw, 2005). In NW Iran *P.*? *ottomanensis* appears very abundantly in latest Permian to earliest Triassic age beds (*Clarkina meishanensis – Hindeodus praeparvus / H. parvus* zones) which suggests that this species may be a disaster species and probably a valuable biostratigraphical indicator for the P/T boundary interval in the Tethyan realm. Its stratigraphical and palaeoecological significance was also discussed in Mette (2008).

### *Praezabythocypris*? sp.2

(Pl. 4, Figs. 5-6)

2008 *Praezabythocypris* sp.2. Mette, Pl. 2, Figs. 12,13.

*Material.* – 64 carapaces.

*Dimensions (mm)*.– Elika Formation, sample Z52: length/height/width of carapace: 0.74/0.45/0.36; 0.84/ 0.50/-; 0.77/0.44/0.30; 0.80/0.50/0.35.

*Remarks*.– *Praezabythocypris*? sp.2 is probably closely related to *P.* ? *ottomanensis* (Crasquin-Soleau) but differs from the latter species in the stronger dorsal convexity and stronger overlap of the left valve. The dorsal overlap which is greatest at mid-length decreases considerably at the anterodorsal and posterodorsal slope of the right valve. In dorsal view the present species shows a similar outline to *P.*? *ottomanensis* with rounded extremities and the greatest width being located at 1/3rd of carapace length. Sexual dimorphism is not discernable at the present material. Some of the specimens which were recorded from sample 52 show a similar pustulose ornamentation (Pl. 4, Fig. 6) of the lateral surface like *P. ottomanensis* and may therefore also be due to abnormal environmental conditions. *Praezabythocypris pulchra* Kozur 1985 from the Abadehian-lower Dzhulfian of Hungary (Kozur, 1985a) shows a more regular dorsal overlap of the left valve.

*Stratigraphical and geographical distribution*.– The species occurs in earliest Triassic (Griesbachian) age beds at Zal section (*H. parvus* zone) and could therefore be an offshoot of *P.*? *ottomanensis*.

## Genus *Liuzhinia* Zheng, 1976

### *Liuzhinia* sp.1

(Pl. 4, Figs. 7-9)

? 1982 *Bairdiacypris* sp.A. Chen & Shi, Pl. 12, Figs. 27, 28.
2008 *Liuzhinia* ? sp.1. Mette, Pl. 2, Figs. 15-17.

*Material*.– 153 carapaces.

*Dimensions (mm)*.– Elika Formation, sample 56: length/height/width of carapace: 0.63/0.32/0.28; 0.64/ 0.32/0.30; 0.64/0.34/0.30; 0.68/0.34/0.34; 0.70/0.35/ 0.34.

*Remarks*.– The present species is most similar with regard to lateral and dorsal carapace outline to *Bairdiacypris* sp.A in Chen & Shi (1982) from the Upper Permian of Nantong (China) which is therefore supposed to be possibly conspecific with *Liuzhinia* sp.1. *Liuzhinia antalyaensis* Crasquin-Soleau from the Lower Induan of Taurus (Turkey) shows a dorsal margin which is more or less distinctly inclined towards the posterior margin (Crasquin-Soleau *et al.*, 2004). The present material comprises specimens with subparallel dorsal and ventral margins but also a few specimens with an inclined dorsal margin. A verification of possible conspecificity of the present material with *L. antalyaensis* would require a direct comparison of the type material and determination of intraspecific variability. *Liuzhinia parva* Wei, 1981 and *Liuzhinia subovata* Zheng, 1976 have a distinctly arched dorsal margin. Similar to *P.*? *ottomanensis* and *P.*? sp.2 the present species does also show an irregular pustulose ornamentation which is thought to be effected by environmental deterioration.

*Stratigraphical and geographical distribution*.– *Liuzhinia* sp.1 occurs in the lowermost part of the Elika Formation which is dated as lowermost Griesbachian (*H. parvus* conodont zone). Another possible occurrence is in the Upper Permian of Nantong (China).

### ***Liuzhinia* sp.2**

(Pl. 4, Fig. 10)

2008 *Liuzhinia* ? sp. 2. Mette, Pl. 2, Fig 18.

*Material*.– 10 carapaces.

*Remarks*.– *Liuzhinia* sp.2 differs from *L*. sp.1 and the other species of *Liuzhinia* in the almost symmetrically rounded anterior and posterior margins and the distinct inclination of the dorsal margin.towards the posterior margin. It is suggested to be a new species but left in open nomenclature due to insufficient and poorly preserved material for a detailed taxonomic description.

*Stratigraphical and geographical distribution*.– The present species is known from the Lower Griesbachian (*H. parvus* zone), Lower Elika Formation in Northwest Iran.

Family ACRATIIDAE Gründel, 1962

### **Genus *Paramacrocypris* Kozur, 1985**

### ***Paramacrocypris* sp.1**

(Pl. 4, Figs. 11-13)

2008 *Bairdiacypris* sp. Mette, Pl. 1, Fig. 15.

*Material*.– 29 carapaces and valves.

*Dimensions (mm)*.– Jolfa Formation, sample Z4: length/height/width of carapace: 1.00/0.40/-; 1.06/0.50/0.40; 1.10/0.46/0.38; sample Z11: length(height/width of carapace: 1.22/0.48/0.38; 1.20/0.46/-; 1.14/0.50/0.40; sample Z9: length (height/width of carapace: 1.04/0.38/0.38.

*Remarks*.– The present material is similar in carapace outline and overlap to *P. schallreuteri* from the Dzhulfian of Hungary which may therefore be closely related. In contrast to the figured specimen in Kozur (1985a,b) the maximum carapace height and width of the present species is located just behind mid-length. The specimens from Iran also show a greater maximum carapace size than the specimens from Hungary.

*Stratigraphical and geographical distribution*.– *Paramacrocypris* sp.1 is recorded from the Jolfa Formation and lower Ali Bashi Formation (Dzhulfian – lower Dorashamian) of Northwest Iran.

Superfamily BAIRDIOCYPRIDOIDEA Shaver, 1961
Family PACHYDOMELLIDAE Berdan & Sohn, 1961

### **Genus *Microcheilinella* Geis, 1933**

### ***Microcheilinella* sp.1**

(Pl. 4, Figs. 14-16)

2008 *Microcheilinella* sp. Mette, Pl. 3, Figs. 5,6.

*Material*. – 14 carapaces.

*Remarks*.– The species is characterized by a short subtriangular lateral carapace outline with the posterior extremity located in a subdorsal position. Near the posterodorsal margin of the right valve and at the posteroventral margin

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Plate 4. *1-4*: *Praezabythocypris*? *ottomanensis* (Crasquin-Soleau). 1: male (?) carapace, right view (sample 52); 2: male (?) carapace, right lateral view (sample 52); 3: female (?) carapace, dorsal view (sample 52); 4: male (?) carapace, dorsal view (sample 52). *5-6*: *Praezabythocypris*? sp.2. 5: carapace, left lateral view (sample 52); 6: carapace, right lateral view (sample 52)..*7-9*: *Liuzhinia* sp.1. 7: carapace, right lateral view (sample 52); 8: carapace, right lateral view (sample 52). 9: carapace, dorsal view (sample 52). *10*: *Liuzhinia* sp.2, carapace, left lateral view (sample 52). *11-13*: *Paramacrocypris* sp.1. 11: carapace, right lateral view (sample 4); 12: *Paramacrocypris* sp.1, right valve (sample 4); 13: carapace, dorsal view (sample 9). *14-16*: *Microcheilinella* sp.1. 14: carapace, right lateral view (sample 11); 15: carapace, dorsal view (sample 11); 16: left valve (sample 39). *17*: *Basslerella* aff. *crassa*, carapace, right lateral view (sample 39). *18*: *Permoyoungiella* sp.1, carapace, right lateral view (sample 31). *19-20*: *Permopolycope* sp.1, carapace (sample 32). All figures of valves are external views. Scale bar = 200µm.

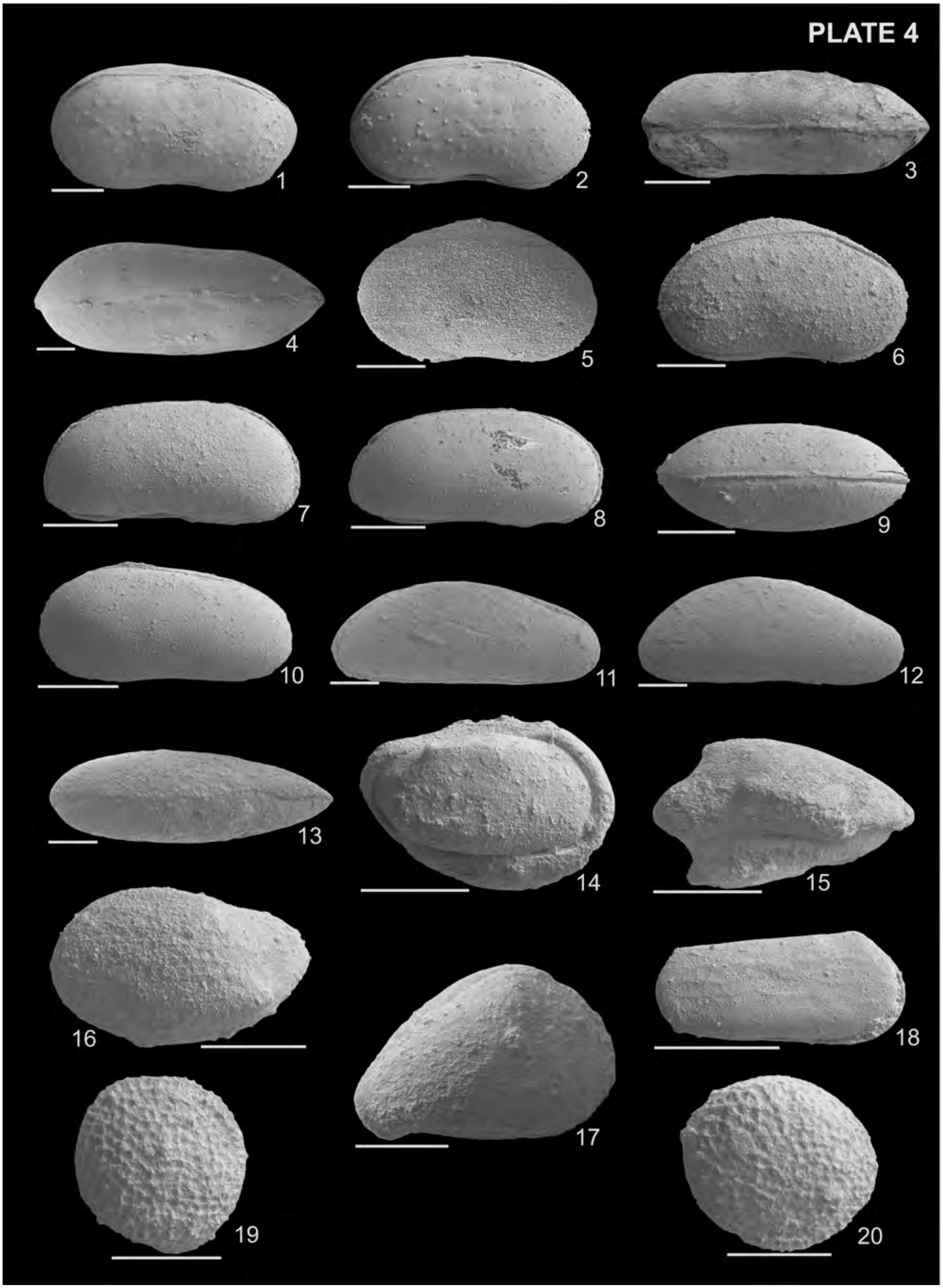
PLATE 4

of the left valve occurs a short spine. The overreach of the left valve is most strong on the ventral margin and very weak posteroventrally. In dorsal view the carapace has a short wedge-shaped outline. With respect to the carapace outline *Microcheilinella* sp.1 differs from the other known species of this genus. Because of insufficient material the species is left in open nomenclature.

*Stratigraphical and geographical distribution*. *Microcheilinella* sp.1 is distributed in the Jolfa Formation and lower-middle part of the Ali Bashi Formation (unit1), dated as Dzhulfian – Dorashamian (*C. subcarinata* –zone).

Superfamily CYTHEROIDEA Baird, 1850
Family CYTHERIDEIDAE Sars, 1925

### Genus *Basslerella* Kellett, 1935

#### *Basslerella* aff. *crassa* Kellett, 1935

(Pl. 4, Fig. 17)

? 1935 *Basslerella crassa* n. sp. Kellett, p. 156, Pl. 17, Figs.1a-c.
2008 *Basslerella* sp. Mette, Pl. 3, Fig. 8.

*Material*.– 1 carapace and 4 valves.

Remarks.– The species shows a strongly arched dorsal margin with a distinct anterodorsal angulation and a weak posterodorsal angulation. It is most similar to *Basslerella crassa* from the Lower Permian of Kansas (Kellett, 1935). Intraspecific variability cannot be determined because it is represented by only one carapace and a few valves.

*Stratigraphical and geographical distribution*.– *B*. aff. *crassa* has been found in the middle part (unit 1) of the Ali Bashi Formation (Dorashamian, *C. subcarinata* zone) at Zal section.

Family YOUNGIELLIDAE Kellett, 1933

### Genus *Permoyoungiella* Kozur, 1985

#### *Permoyoungiella* sp.1

(Pl. 4, Fig. 18)

2008 *Permoyoungiella* sp. Mette, Pl. 3, Fig. 13.

*Material*.– 1 carapace.

*Remarks*.– This species of *Permoyoungiella* is characterized by very faint longitudinal ribs and a straight ventral margin. There is no anterior or posterior peripheral bulge. It is represented by only one specimen. Species of *Permoyoungiella* comparable to the present specimen were not recorded.

*Stratigraphical and geographical distribution*.– The stratigraphic record is lower Dorashamian (*C. wangi* zone) of Northwest Iran (Zal section).

Subclass MYODOCOPA Sars, 1866
Order HALOCYPRIDA Dana, 1852
Suborder CLADOCOPINA Sars, 1866
Family PERMOPOLYCOPIDAE Kozur, 1985

### Genus *Permopolycope* Kozur, 1985

#### *Permopolycope* sp.1

(Pl. 4, Figs. 19-20)

2008 *Discoidella* cf. *suprapermiana* Kozur. Mette, Pl. 3, Figs. 9-10.

*Material*.– 6 carapaces.

*Remarks*.– A diagnostic feature of the present species is the occurrence of a long marginal rib which is separated from the free margin by a single row of fossules. The rest of the lateral surface shows an irregular reticulation. Details of the ornamentation are poorly preserved. The dorsal margin is short and the hinge margin is not incised. *Permopolycope veghae* Kozur, 1985 shows two rows of fossules between the margin rib and the free margin and in addition two inner rows of fossules running parallel to the rib.

*Stratigraphical and geographical distribution*.– The species is restricted to the lower part of the Ali Bashi Formation (unit 1) which yielded conodonts of early Dorashamian age (*C. wangi* – *C. hambastensis* zone).

## 5. ACKNOWLEDGEMENTS

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# Palynology and palynofacies of the Lower Cretaceous succession of the Matruh2-1X borehole, northwestern Egypt

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## Resumen

Se ha llevado a cabo un análisis palinológico y de palinofacies en muestras del sondeo Matruh2-1X, Desierto Noroeste, Egipto. Se realiza un análisis cronoestratigráfico detallado que señala la presencia de los pisos Barremiense-Aptiense, Aptiense, Albiense Inferior y Superior. El paleoambiente se ha interpretado a partir de las preferencias ecológicas de las plantas productoras de los distintos palinomorfos identificados. Éste fluctuó entre marginal y marino abierto de plataforma profunda o con profundidad media. Un único horizonte con profundidad de 2.170 m, podría reflejar condiciones continentales y se interpreta que tuvo lugar durante el Albiense Inferior. Un clima de tipo cálido y húmedo parece que prevaleció durante el depósito de la sección. Esto se refleja en las palinofloras por la abundancia de esporas hidrófilas de helechos y raros taxones xerofíticos. Las palmeras, un elemento importante en tierras bajas tropicales y húmedas de llanuras costeras, dominaron la vegetación terrestre asociándose con pteridofitos y otros habitantes de las tierras bajas. A partir de la recuperación de la materia orgánica palinológica se reconocen dos palinofacies. Los datos obtenidos a partir de la reflectancia teórica estimada en vitrinita, que se basan en la coloración de esporas/polen, junto con los análisis petrográficos visuales de kerógeno, se han utilizado para definir las fuentes potenciales de rocas de los sedimentos estudiados.

**Palabras clave:** Cretácico Inferior, polen y esporas, cistes de dinoflagelados, palinoestratigrafía, paleoecología, palinofacies, noroeste de Egipto.

## Abstract

Palynological and palynofacies analyses were carried out on some Lower Cretaceous samples from the Matruh2-1X well, Northern Western Desert., Egypt. A refinement of the original chronostratigraphy has been suggested and the stages Barremian-Aptian, Aptian, Early and Late Albian are recognized. The palaeoenvironment was interpreted on the basis of the palynomorphs, in the light of their ecological preferences. It was fluctuating between marginal to open (inner-middle shelf) marine. A single horizon (at depth 2170 m) might reflect a continental condition and is thought to have occurred during the Early Albian. A warm–humid climate is thought to have mostly prevailed during deposition of the section. This is reflected in the palynofloras by abundance of ferns, and other hygrophilous spores, and rare xerophytes. Palms, as an important element in tropical humid lowlands of the coastal plains, dominate the terrestrial vegetation and associate petridophytes and other lowland inhabitants. Based on the recovered palynological organic matter two palynofacies are recognized. Data gathered from the theoretically estimated vitrinite reflectances, that are based on spore/pollen colouration, and visual petrographic kerogen analysis are used to define the source rock potentialities of the studied sediments.

**Key words:** Early Cretaceous, pollen and spores, dinoflagellate cysts, palynostratigraphy, palaeoecology, palynofacies, northwestern Egypt.

# 1. INTRODUCTION

The northern part of the Western Desert, where the Matruh 2-1X borehole was drilled (Fig. 1), forms an almost featureless plain despite to its intricate buried geological history. This region was often covered by shallow seas during most of its geological history (Said, 1962). The stratigraphic succession of northern Egypt encounters several carbonate-clastic alternations that, together with the enclosed secondary transgressive-regressive cycles, constitute one of the main elements of the Mesozoic-Early Tertiary petroleum system of the Western Desert (Sestini, 1995).

The Cretaceous rocks are main targets for the oil exploration in Egypt since they are widely distributed on the surface and near the surface. The Lower and Upper Cretaceous strata in Egypt form two main facies. These are the Lower Cretaceous continental to shallow marine "Nubian" facies and the typical deep marine shale and carbonate Upper Cretaceous facies. The Cretaceous in the North Western Desert is divided into a lower unit made up primarily of clastics, which belong to the Lower Cretaceous and an upper unit made up mainly of carbonates which belong to the Upper Cretaceous.

The Lower Cretaceous sedimentation in North Western Desert exhibits a major regressive phase indicated by marginal marine sandstones and shale beds interrupted by rare carbonate streaks. These sediments were affected by synsedimentary tectonism and, to a very small degree, by subsequent geological events (Soliman & El Badry, 1970). During this time period the change from open to marginal marine conditions could be achieved by the occurrence of shales, limestones and sandstones in the Lower Cretaceous succession of Matruh 2-1X borehole and the adjacent wells such as Medeiwar-1X, Mersa Matruch-1X and Siqeifa-1X. This marine oscillation is inferred palynologically in the Matruh Basin area (Penny, 1991; Mahmoud *et al.*, 2003).

Early palynological investigations from Egypt were mostly descriptive but since the early 1960's the Western Desert stratigraphy was a subject of numerous palynological studies. From 1990 onward there was a noticeable development in the application of palynomorphs to biostratigraphic and palaeoenvironmental reconstruction. For example, in the Matruh Basin area, Penny (1986, 1988, 1991) worked intensively on angiosperm pollen assemblages, with emphasis on their morphological and taxonomical criteria. Previous results from the local records indicate that during the Albian, deltaic and nearshore sandstones and shales of the Kharita Formation, which contain the land-derived spores (see El-Beialy, 1994) were deposited in the North Western Desert. In the North Western Desert, the earliest Aptian deposits started with sandstone and shales with few interbeds of lignite, anhydrite and limestone of the Alam El Bueib Formation, in a nearshore, inner and middle shelf, marine environment (Abdel Kireem *et al.*, 1996). Deposition continued in the Alamein Dolomite (Chatelier & Slevin, 1988), followed by the Dahab and Kharita siltstones and sandstones. These sediments are deposited in a coastal shelf environment (Abdel Kireem *et al.*, 1996).The environmental fluctuations in the well section from marginal to inner and middle shelf are parallel with the regressive/transgressive cycles described from the North Western Desert (El Beialy (1994, phases III, IV). However, dissimilar conditions occur in nearby areas from the Western Desert during Aptian/Albian times (Mahmoud, 1991; Mahmoud & Moawad, 1999), which result from pre-existing mega-basement structures (i.e. Sharib-Sheiba-High, Hantar, 1990, p. 294).

The objectives of this paper are to establish palynostratigraphic, palynofacies and palaeoecological characteristics of the Lower Cretaceous succession penetrated by the Matruh2- 1X borehole, Lat. 31º 11´ 40´´ N and Long. 27º 18´ 40´´ E (Fig. 1). The aim is extended to infer possible selective degradation signature of the organic matter in the Kharita Formation, as reflected by palynomorphs and palynofacies.

# 2. STRATIGRAPHIC SETTING

The Matruh2-1X borehole rock units as recognized by Shell (1990) in the studied borehole are as follows:

## 2.1. Alam El Bueib Formation

The Alam El Bueib Formation is a sandstone unit with frequent shale and occasional limestone beds, both of which increase in abundance to the northwest. This unit was

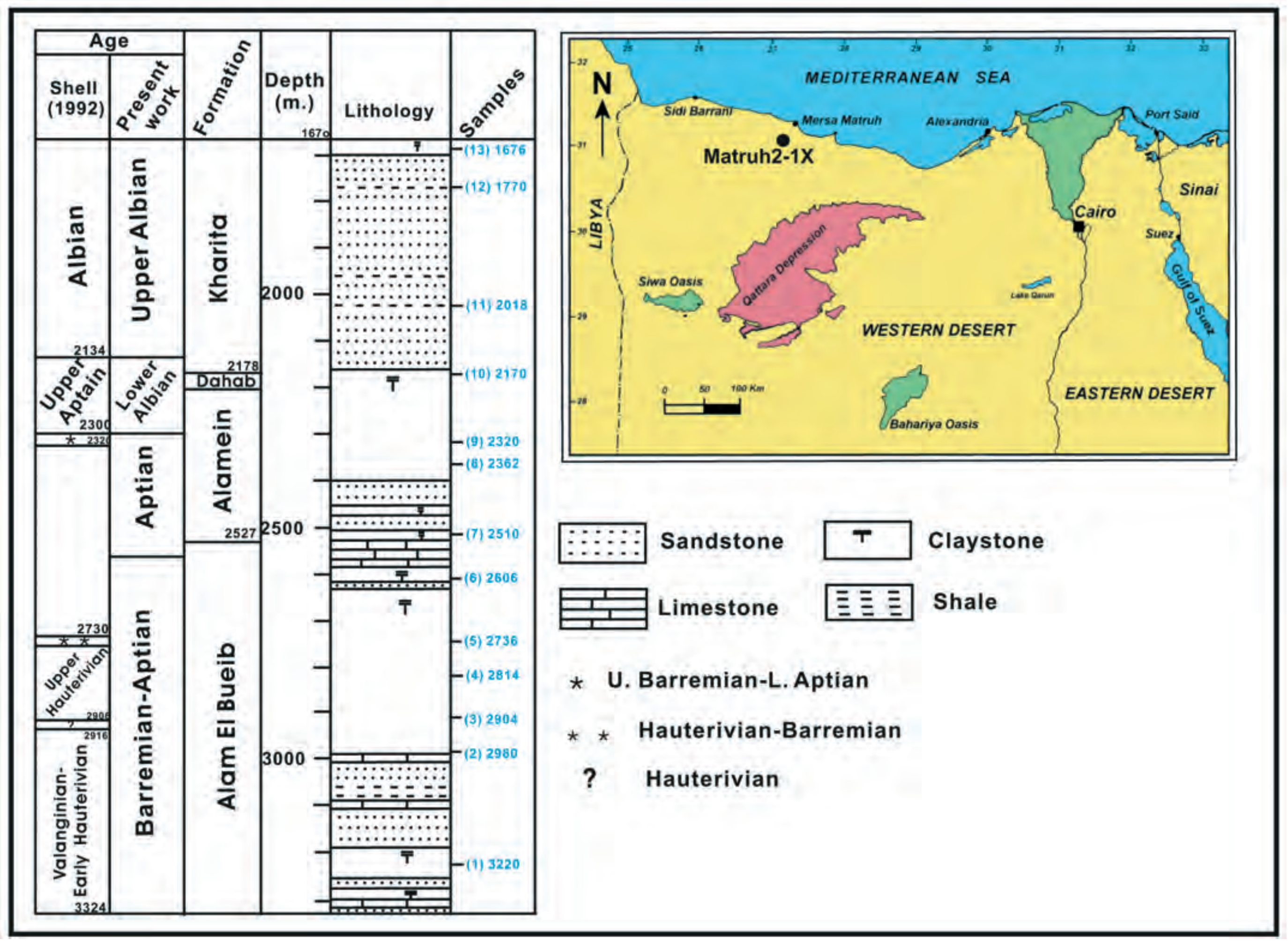

Figure 1. Location map and lithostratigraphic column of Matruh2-1X borehole (modified after Shell, 1992).

given different names by different operators such as Matruh Group, Aptian clastics, Alamein shale, Dawabis, Shaltut, Umbaraka, Mamura and operational units A, B, C, D1, D2, E, F1, and F2. The unit ranges in age from Barremian to Aptian and the environment was interpreted to be shallow marine with continental influence toward the south (Hantar, 1990). The Alam El Bueib shale probably provided the source of the gas in the Abu Gharadig field (Khaled, 1999).

## 2.2. Alamein Formation

This unit is first proposed by Norton (1967) as a member of the Burg El Arab Formation. It is made up of light brown hard microcrystalline and porous dolomite with few thin shale interbeds. The type section of this unit is the interval between 2489 to 2573 m of the Alamein-I well. The Alamein dolomite grades laterally into shales. Its thickness is in the range of 20 to 80 m over most of the area except in Kanayis-I well (up to 97 m). The age of the Alamein dolomite is Aptian/Albian in the type area and the formation as deposited in a shallow marine, low to moderate energy environment (Hantar, 1990). This unit forms hydrocarbon reservoirs in the Alamein, Razzak and Yidma fields.

## 2.3. Dahab Formation

It is a grey to greenish grey shale unit, with thin interbeds of siltstone and sandstones. The type section is in the Dahab-1 well, where the unit reaches a thickness of 174 m.

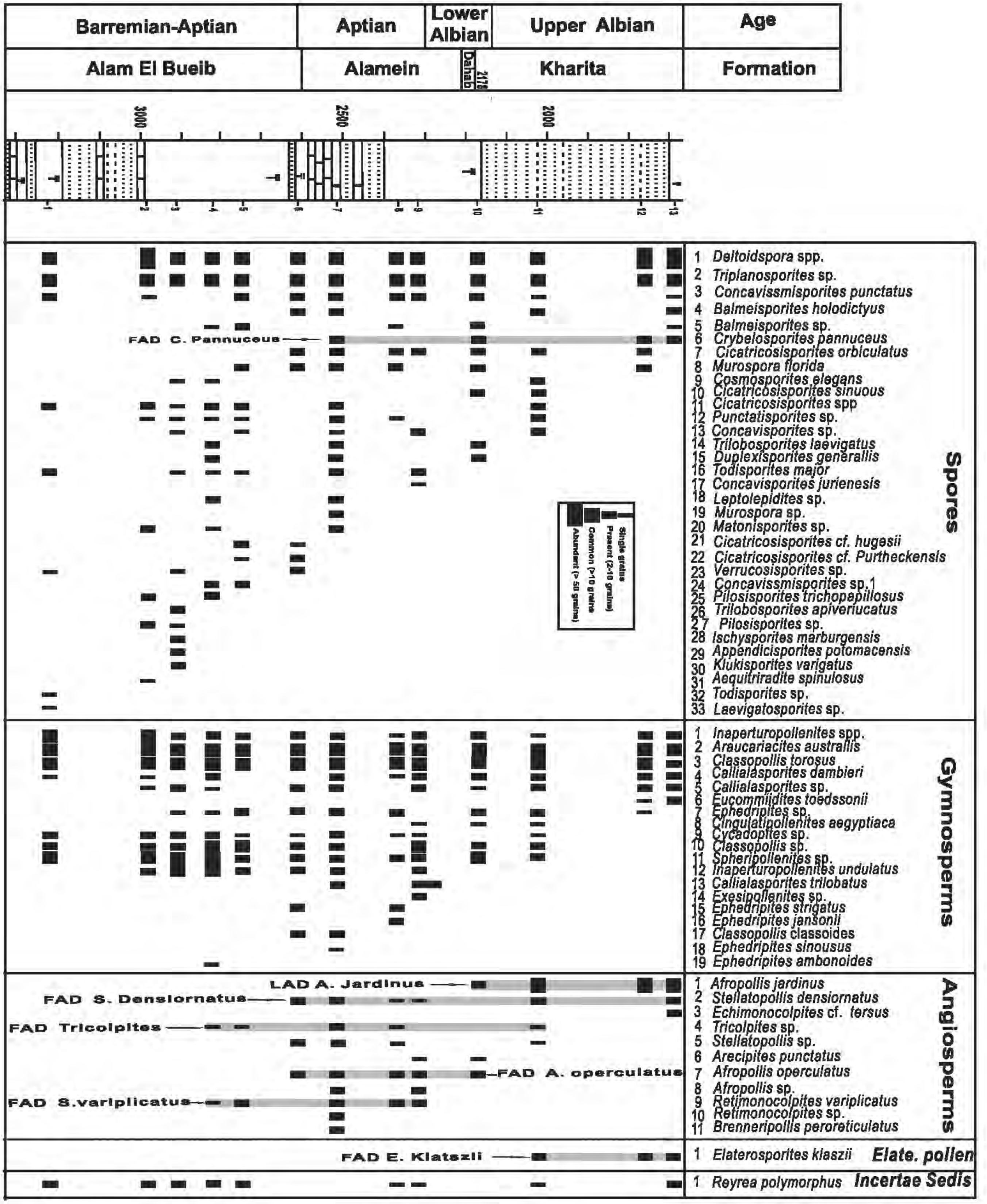

Figure 2. Selected palynomorph ranges, vertical grey bars highlight the ranges of stratigraphically significant palynomorphs taxa in the Matruh2-1X borehole. FAD=first appearance datum, LAD=last appearance datum.

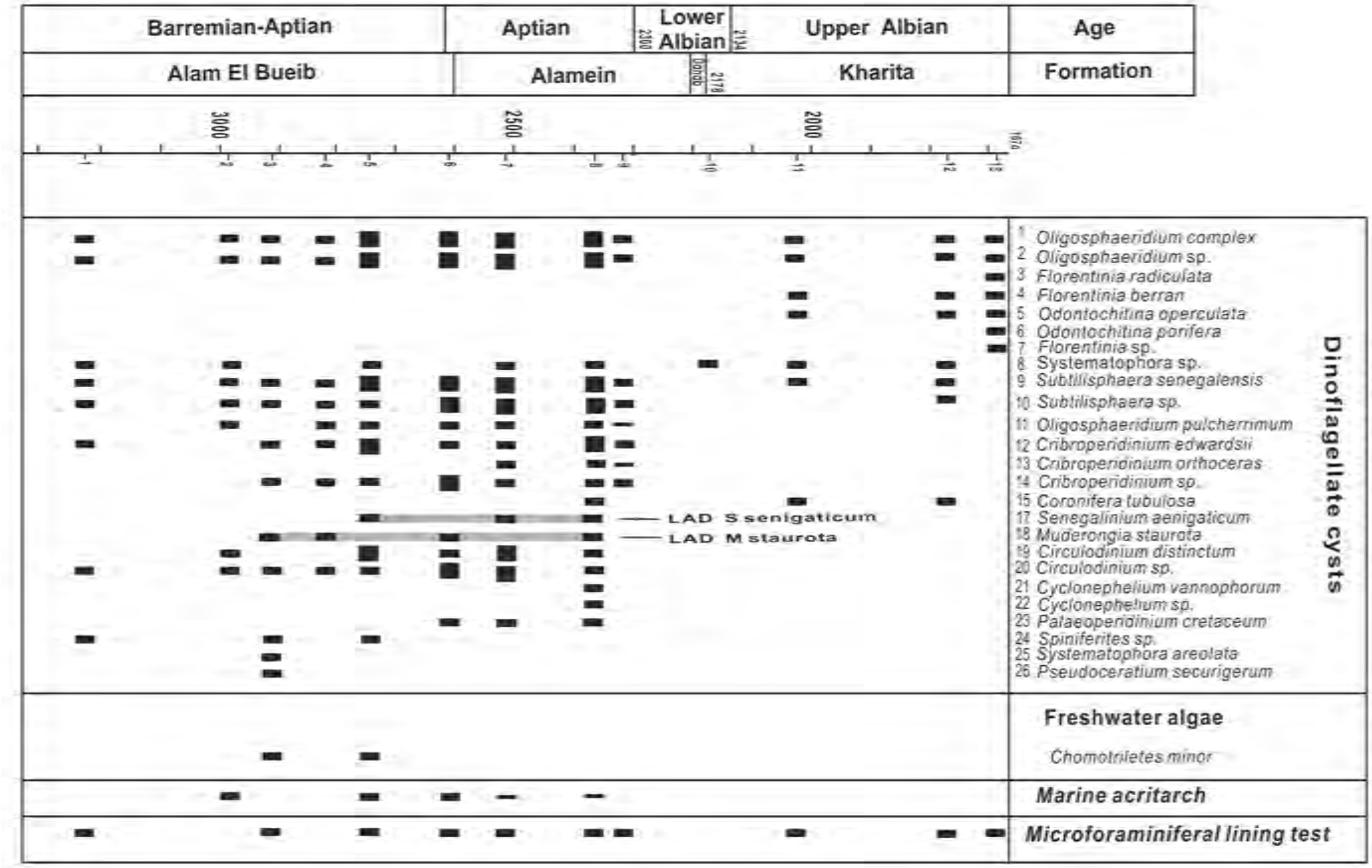

Figure 2. Continued.

## 2.4. Kharita Formation

The Kharita Formation is made up of fine to coarse grained sandstones with subordinate shale and carbonate beds. The type section is in the Kharita-1 well, at a drill interval between 2501m to 2890 m. The maximum thickness of this unit was reported from the Marsa Matruh-I well (1100m). This Aptian/Albian unit is believed to have accumulated in a local graben, in a high energy shallow marine shelf. In the extreme north the unit seems to have been deposited in deeper waters, while in the south it was deposited under the influence of continental conditions (Hantar, 1990).

## 3. MATERIAL AND METHODS

13 samples from the Matruh2-1X borehole, which was drilled in North Western Desert Egypt (Fig. 1), were found suitable for this study. Stratigraphy and position of productive samples are shown in figure 1. The material encountered includes pollen, spores, freshwater algae, fungi and dinoflagellate cysts.

10 grams of each sample are treated according to the well-known standard and routine palynological procedures. No ultrasonic or oxidation treatments were made in order to keep the organic matter for palynofacies investigations. For qualitative and quantitative study, two to five permanent slides were prepared using glycerine jelly as mounting medium. Slides were examined using an OLYMPUS CX21FS1 light microscope. For quantitative palynology a count of at least 200 grains was made for each sample.

## 4. PALYNOSTRATIGRAPHY

Age assessment in this work is based mainly on ranges of spores and pollen and partly on dinoflagellate cysts, and is as follows:

## 4.1. Barremian-Aptian (samples 1 to 9)

*Murospra florida*, *Crybelosporites pannuceus*, *Reyrea polymorphus*, *Ephedripites*, *Classopollis classoides*, *Stellatopollis, Retimonocolpites variplicatus* and *Afropollis operculatus* are sporomorphs of general Barremian-Aptian aspect. *Stellatopollis* is taken to document (late) Barremian or younger age in the Northern Gondwana Realm (Doyle *et al*., 1975, 1977, 1982; Schrank, 1992; Schrank & Mahmoud, 1998). *Retimonocolpites variplicatus* has a Barremian to Cenomanian range in the local records of Egypt and Libya (Thusu & Van der Eem, 1985; Schrank & Mahmoud, 1998). *Tricolpites* is known to enter the pollen record during early Aptian (Doyle *et al*., 1977; Penny, 1986) but is also recorded as early as Barremian (e.g. Huges & McDougall, 1990). *Afropollis operculatus* has an Aptian worldwide range (Schrank, 1983; Penny, 1986, 1991; Schrank & Mahmoud, 1998). Distinguishing Barremian from Aptian on the basis of this taxon is powerful. *Crybelosporites pannuceus* enters the palynological records during Aptian in Sudan (Kaska, 1989) and younger records are known from the Albian-Cenomanian (Schrank & Mahmoud, 1998). Dinoflagellate cysts such as *Subtilisphaera senegalensis, Cyclonephelium vannophorum, Oligosphaeridium complex* are reported from Early Cretaceous assemblages from NE Libya (e.g. Batten & Uwins, 1985) and Egypt (e.g. Mahmoud & Moawad, 2002*)*. *Subtilisphaera sengalensis* was originally described from the Aptian of Senegal (Jain & Millepied, 1973). However, it is frequently identified from lower-upper Aptian rocks in Northwest Africa (Below, 1984; Thusu & Van der Eem, 1985). Highest occurrence data of *Muderongia staurota* appear in this interval, this species is known to range from Valanginian to late Aptian (e.g. Omran *et al*., 1990; Hoedemaeker & Leereveld, 1995). According to the above discussion samples from 1 to 5 are dated Barremian-Aptian and those from 6 to 9 are dated Aptian.

## 4.2. Early Albian (sample 10)

This sample contains Last Appearance Datum (LAD) of *Afropollis operculatus*. *Afropollis jardinus* first appears in this interval, the oldest stratigraphic records of *Afropollis jardinus* according to Doyle (1999) is early Albian. Schrank & Ibrahim (1995) marked the base of the early Albian in north western Egypt from two (foraminifera-dated) sections (KRM-1 and AG-18 wells) on the basis of the lowermost occurrence level of *A. jardinus*.

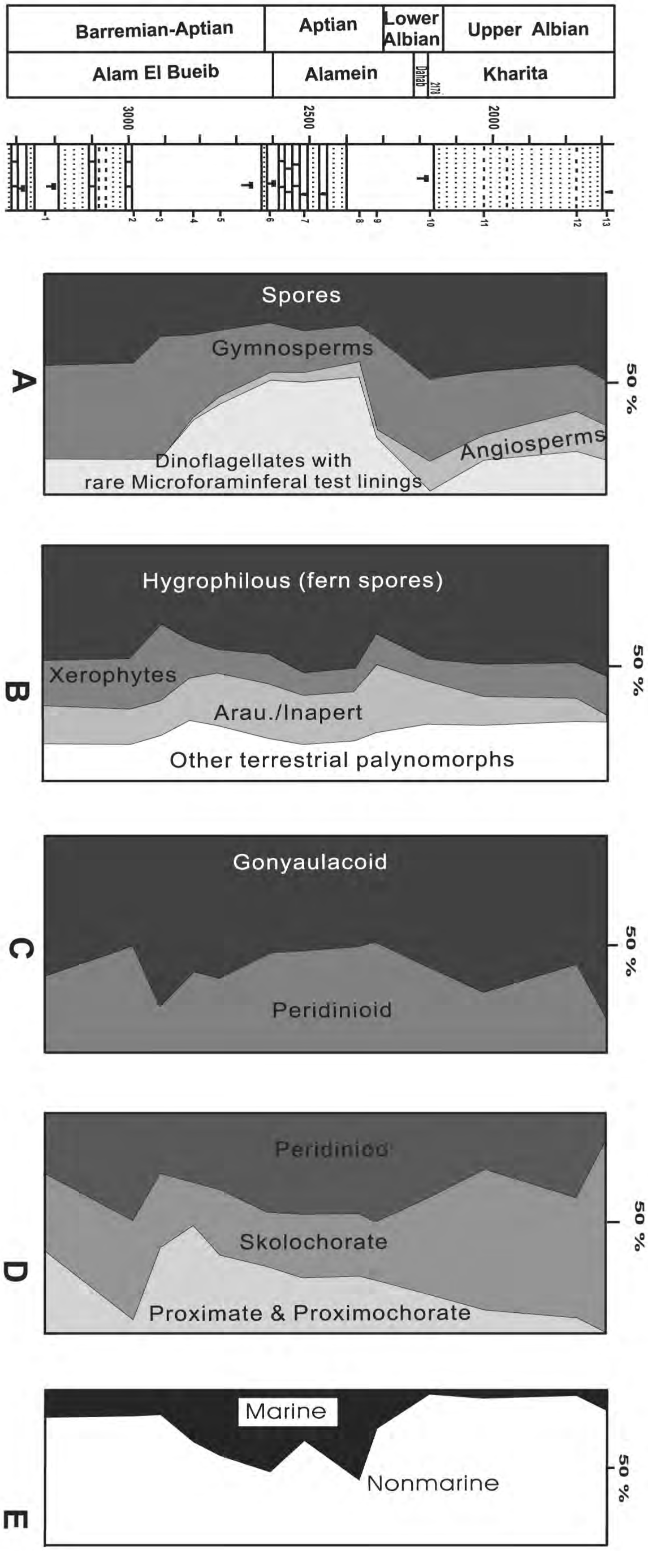

Figure 3. Compositions of palynomorph assemblages in the Matruh2-1X borehole. A: Palynomorph categories; B: Terrestrial palynomorphs categories; C: Ratio of Peridiniod versus Gonyaulacoid (excluding poor dinocysts sample 10); D: Dinoflagellate cysts categories (excluding poor dinocysts sample 10); E: Ratio of marine versus nonmarine palynomorphs.

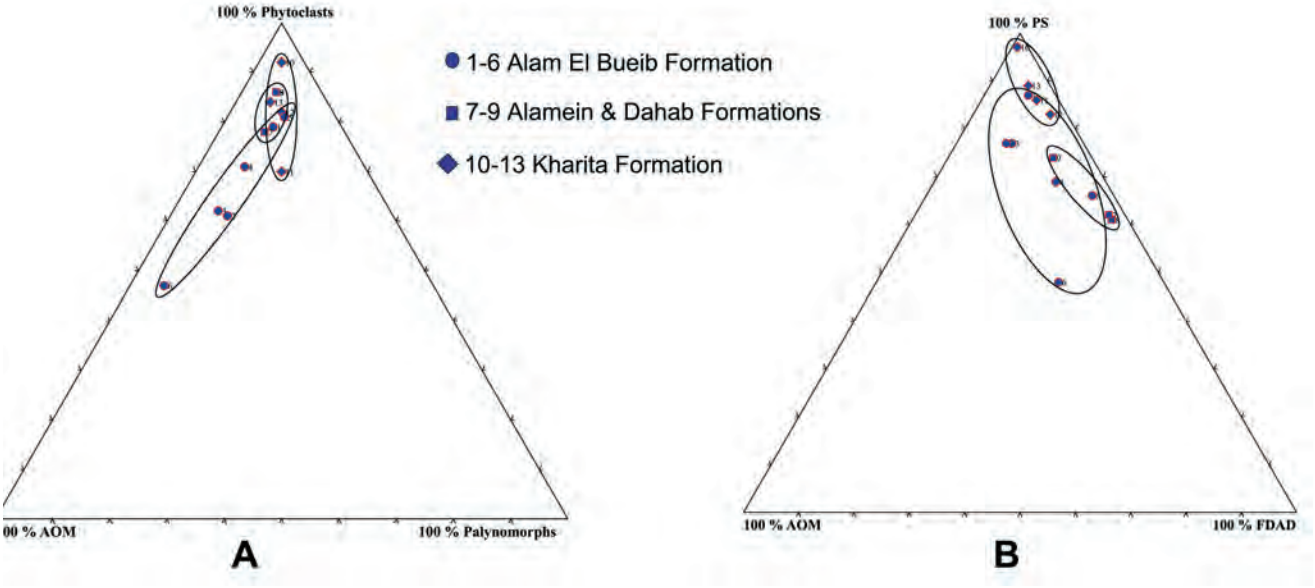

Figure 4. Ternary kerogen and palynomorph plots of the Matruh2-1X borehole. A: AOM-Phytoclast-Palynomorph plot (from Tyson, 1993); B: AOM-PS-FDAD (from Ronaglia & Kujinpers, 2006); AOM = amorphous organic matter; PS=Phytoclast & Sporomorphs; FDAD = foraminiferal lining test+dinoflagellate cysts+acritarchs.

### 4.3. Late Albian (samples 11-13)

The First Appearance Datum (FAD) of elaterates is in this interval. Batten (1996a) stated that these forms are an important element in strata of middle to late Albian and early Cenomanian age in Africa and South America. Herngreen (1998) remarked that the first occurrence of representatives of *Elaterosporites* is approximately in the middle Albian. *Elaterosporites klaszii* was reported from middle to upper Albian sediments in Senegal, Côte d´Ivoire and Gabon (Jardiné, 1967). Locally, Saad & Sultan (1987) recorded *E. klaszii* from Albian strata in northern Egypt. The presence of *Elaterosporite*s in this interval suggests a late Albian age for these samples. This age is supported by the occurrence *Reyrea polymorphus* that terminates in this interval (Herngreen, 1998).

Late Albian is supported by the occurrence of dinoflagellate cyst species *Florentinia berran*. It has been recorded previously from Late Albian-Early Cenomanian assemblages from the North Western Desert (El Beialy 1993b, 1995; Ibrahim 2002).

## 5. PALYNOFACIES CHARACTERISTICS

The use of palynofacies analysis has been steadily increased during the last decades. The technique of palynofacies analysis is widely used today as an important aid for the determination of environments of deposition and the identification of source rocks for petroleum, and also for establishment of the kerogen type. The dispersed organic matter content of sediments from the investigated interval of the Matruh 2-1X well consists of organic matter either derived from the continent (e.g. wood, cuticles, spores, pollen) or produced in the marine realm such as amorphous organic matter, microforaminiferal test linings, marine acritarchs and dinoflagellate cysts. Sediments of the Matruh 2-1X well can be classified into two palynofacies types based on the Palynological Organic Matter (POM), as follows:

### 5.1. Palynofacies A (Alam El Bueib and Alamein formations)

This palynofacies includes the Barremian-Aptian, Aptian to the lower part of the lower Albian intervals. It contains moderate to high percentages of AOM (Fig. 6). Few intervals contain relatively higher percentages of marine paly-

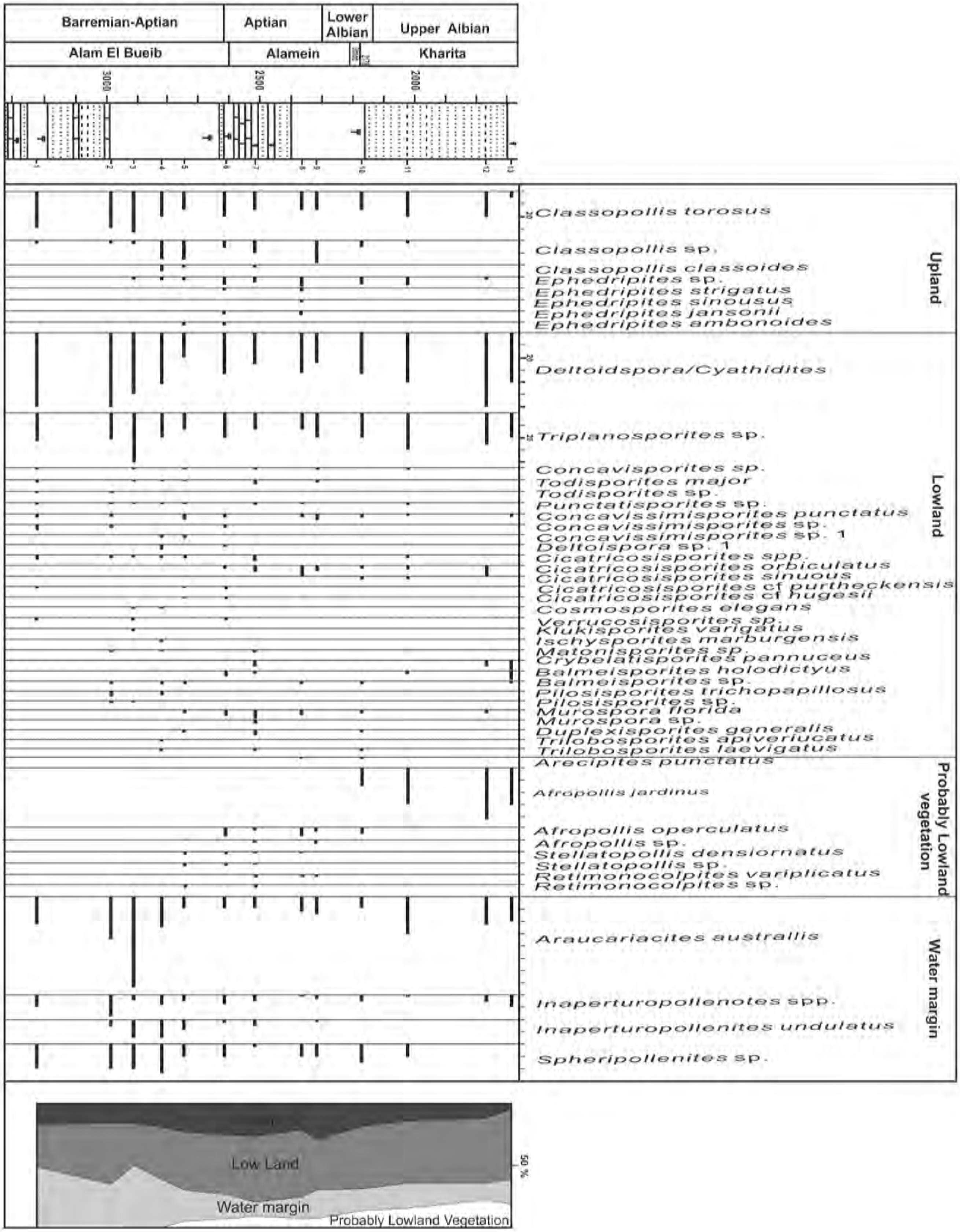

Figure 5. Terrestrial palynomorph occurrences (numbers of specimens) in the Matruh2-1X borehole, inferred habitats based on numbers of specimens recorded for each category and summarized proportion for each category.

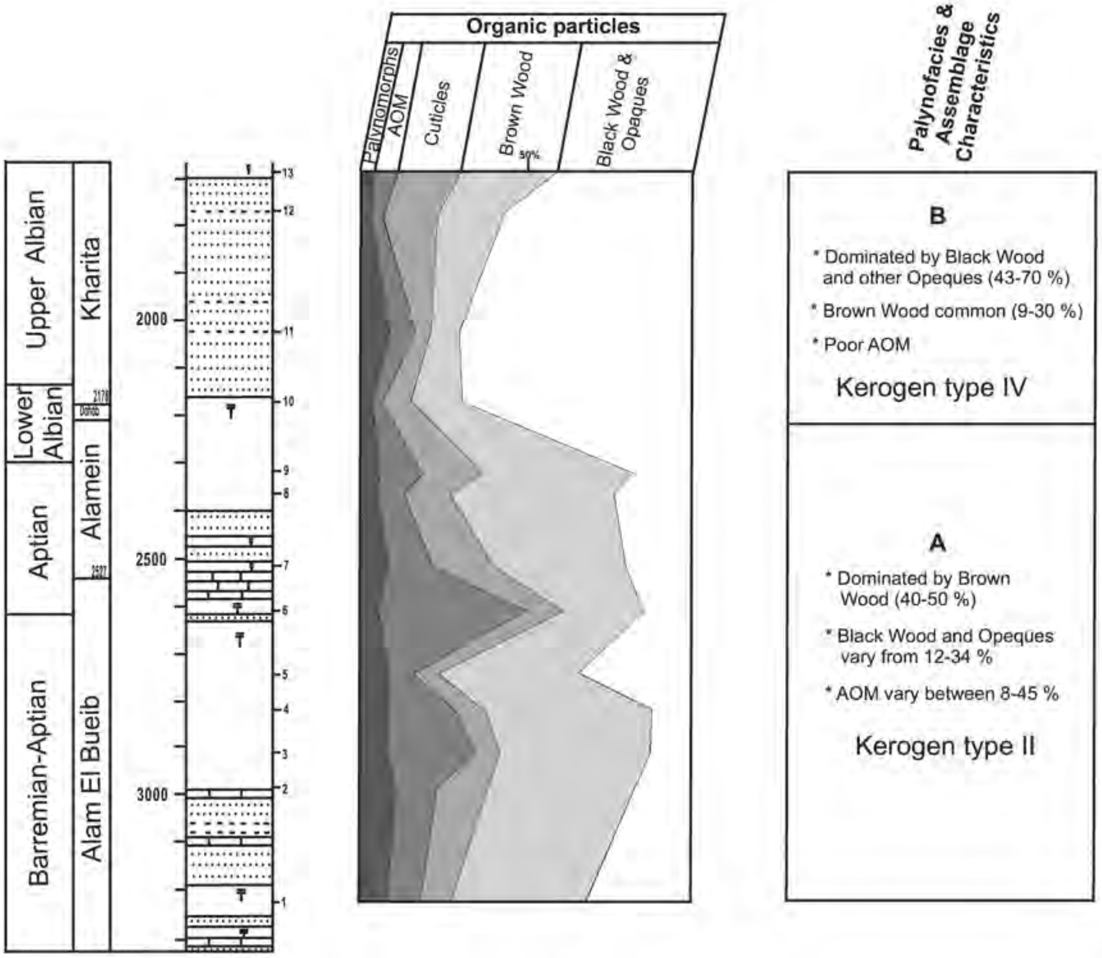

Figure 6. Percentage distribution of dispersed organic particles, palynofacies assemblages and assemblage characteristics for Matruh2-1X borehole.

nomorphs, which have values ranging from 33 to 55%. Powell *et al*. (1990) reported that high levels of AOM, coupled with the presence of rich dinoflagellate cysts and low percentage of terrestrial phytoclasts, indicate an almost exclusive marine origin. According to Tyson (1995) AOM is the dominant organic component in dysoxic to anoxic environments which increases with increasing nutrient availability and decreasing oxygen in the waters. Terrigenous brown wood influence is high (23-50 %) whereas sporomorphs, cuticles and resinous matter are few. Black wood and opaques are common (13 to 34%).

## 5.2. Palynofacies B (Dahab and Kharita formations)

This palynofacies is inferred from the Albian interval and is characterized by an unusual high input of black wood and opaque which have values ranging from (up to 70%). Based on the state of preservation and the degree of thermal maturation, wood is classified into black and brown wood (Batten, 1973). The high percentage of black debris may indicate that oxidation occurred prior the deposition; and may have resulted from higher oxidation at the source of the phytoclasts (Oboh-Ikuenobe & De Villiers, 2003). Tracheids and cuticles show regular to sub-regular rectangular cell outline, moderately preserved with internal structures which may indicate a gymnospermous origin (Tyson, 1995). AOM is generally rare (less than 8%) and marine palynomorphs are scarce. AOM has darker colours and includes fine and undifferentiated particles that can be derived from the degradation of land derived organic debris (Batten, 1996a).

## 6. PALAEOECOLOGY

Changes in palynofacies types and composition of palynomorph assemblages may provide information regarding the interpretation of depositional environments (e.g. Wall *et al*., 1977; Lister & Batten, 1988; Harker & Sarjeant, 1990; Tyson, 1993, 1995; Batten, 1996a). Palynomorphs from the lower part of the Barremian-Aptian interval (depth from 3220 m to 2980 m) suggest deposition in marginal marine (deltaic) environment. This is interpreted by the occurrence of proximate dinoflagellate cysts such as *Systematophora* and *Subtilisphaera* and large influx of terrestrial palynomorphs along with palynofacies. The AOM-Phytoclast-Palynomorph ternary plot of Tyson (1993) (Fig. 4A) as well as the ternary plot (Fig. 4B) of Roncaglia & Kuijpers (2006) suggest deposition in a marginal dysoxic-anoxic basin. A transgressive, open marine phase is followed (depth 2904 m to 2320 m) and continued during the Aptian because skolochorate dinocysts such as *Oligosphaeridium* increase (33% to 55% of total palynomorphs). On a global scale, the Aptian was a time of a major marine transgression (Haq *et al*., 1987). A global drop in sea level took place at the end of the Aptian (Murris, 1980). The above mentioned ternary plots suggest that the upper parts of the Alam El Bueib and the Alamein formations are deposited in a proximal suboxic-anoxic shelf. A second regressive phase with deposition in a marginal marine environment took place during deposition of the Albian interval (upper part of Alamein, Dahab and Kharita formations, depth from 2018 m to 1676 m) and a marginal dysoxic-anoxic basin was again developed. AOM is abundant in the dysoxic to anoxic depositional environment and increases with increasing nutrient availability and decreasing oxygen in the waters. A single horizon at depth 2170 m might reflect continental conditions because terrestrial palynomorphs are abundant and marine palynomorphs are completely missing. The abundance and diversity of the dinoflagellate cysts in the lower part of the studied section (Fig. 3) implies deposition in a normal marine environment and rich nutrients which support their population (Uwins & Batten, 1988). However, the diversity of the dinocysts and the increase in number of the gonyaulacoid over peridinoid cysts (Fig. 3) suggests a coastal to inner-shelf environment during depositions of the Kharita Formation. In addition, data available from nearby wells indicate that the Kharita Formation was deposited in a high energy nearshore to shallow marine shelf environment (Penny, 1988; Hantar, 1990; El-Beialy, 1993a). Although in the Kharita Formation the gonyaulacoid cysts percentages are obviously greater than those of the peridinioid cysts, this cannot be used to infer more open marine environment of the formation. This is most probably an inverse picture due to expected selective preservation during deposition (see part 8), which might overprint the original primary productivity of peridinioids. The peridinioid cysts are sensitive to aerobic decay (see Zonneveld *et al*., 2009). In this interval black wood dominates and reflects the effect of oxidation. These dark fragments indicate that oxidation occurred prior to the deposition (Oboh Ikuenobe *et al*., 2003).

The abundance of hygrophilous palynomorphs (mainly fern spores) such as *Deltoidospora, Cicatricosisporites* and *Concavissimisporites* in most samples probably reflects the local pteridophyte vegetation and wetlands (Playford, 1971; Schrank & Mahmoud, 1998; Atta-Peters & Salami, 2006), while the abundant araucariacean pollen reflect a conifer vegetation on relatively dry hinterlands (Schrank & Mahmoud, 1998; Schrank, 2001; Mahmoud & Moawad, 2002). The occurrence of *Classopollis* and ephedroids, both of which are commonly interpreted as xerophytic elements (Schrank & Nesterove, 1993; Schrank & Ibrahim, 1995; Schrank & Mahmoud, 1998), does not imply general dry conditions because they are not as abundant as ferns. *Crybelosporites*, a water fern, at the top of the studied sec-

Plate 1. Spores (1-19) and Gymnosperm (20) of Barremian-Aptian (1-3, 5-9, 12, 14, 16, 18-19), Aptian (4, 10, 15, 20), Lower Albian (17), Upper Albian (11), Mat2-1X= Matruch2-1X well. All figures x 400.

1- *Todisporites major,* Mat2-1X, 3220 m, Diameter 68 µm; 2- *Punctatisporites* sp., Mat2-1X, 2980 m, Diameter 70 µm; 3, 4- *Concavissimisporites punctatus*, 3. Mat2-1X, 3220 m, Diameter 58 µm, 4. Mat2-1X, 2320 m, Diameter 57 m; 5- *Trilobosporites apiverrucatus*, Mat2-1X, 2814 m, Diameter 55 µm; 6- *Duplexisporites generalis,* Mat2-1X, 2736 m, Diameter 68 µm; 7- *Murospora florida*, Mat2-1X, 2510 m, Diameter 94 µm;8- *Verrucosisporites* sp., Mat2-1X, 2814 m, Diameter 55 µm; 9- *Pilosisporites trichopapillosus*, Mat2-1X, 2510 m, Diameter 57 µm; 10- *Cyathidites australlis*, Mat2-1X, 2320 m, Diameter 62 µm; 11- *Crybelosporites pannuceus,* Mat2-1X, 1770 m, Diameter 64 µm; 12- *Balmeisporites holodictyus,* Mat2-1X, 2736 m, Diameter 60 µm; 13- *Cicatricosisporites sinuosus,* Mat2-1X, 2170 m, Diameter 56 µm; 14- *Cicatricosisporites* cf. *hughesii*, Mat2-1X, 2510 m, Diameter 58 µm; 15- *Cicatricosisporites orbiculatus,* Mat2-1X, 2320 m, Diameter 58 µm; 16- *Leptolepidites* sp., Mat2-1X, 2606m, Diameter 54 µm; 17- *Trilobosporites laevigatus*, Mat2-1X, 2170 m, Diameter 60 µm; 18- *Appendicisporites potomacensis*, Mat2-1X, 2904 m, Diameter 62 µm; 19- *Aequitriradites spinulosus,* Mat2-1X, 2904 m, Diameter 64 µm; 20- *Cingulatipollenites aegyptiaca,*Mat2-1X, 2320 m, Diameter 54 µm.

## Plate 1


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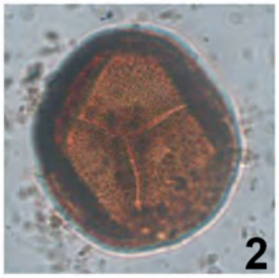
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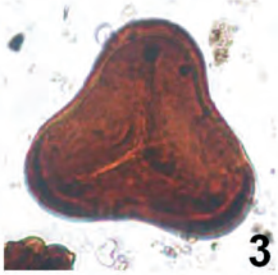
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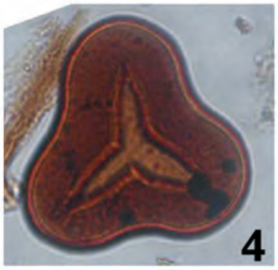
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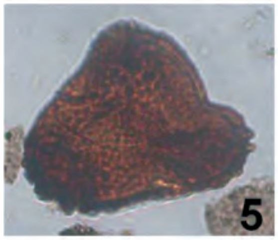
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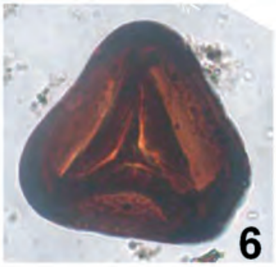
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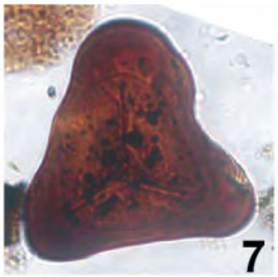
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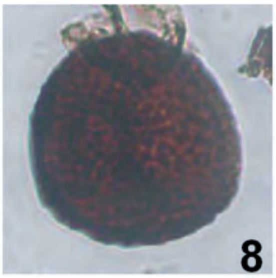
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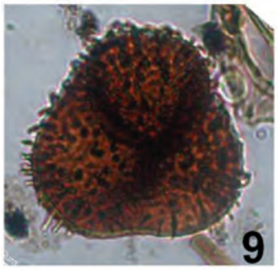
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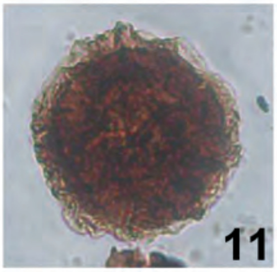
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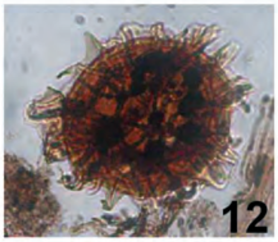
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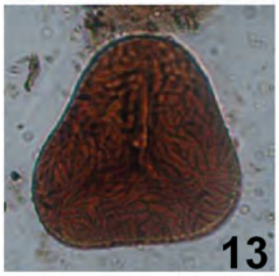
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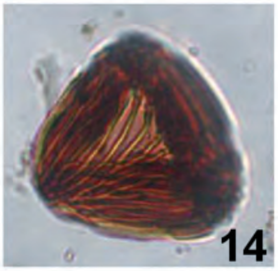
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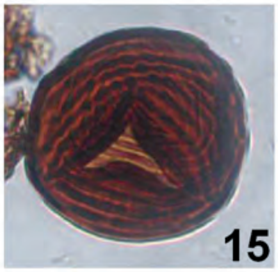
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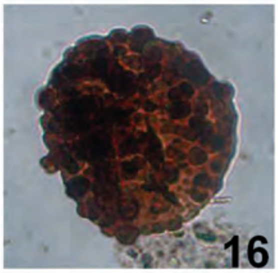
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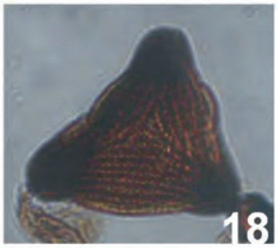
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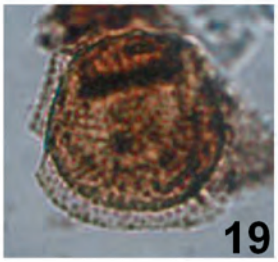
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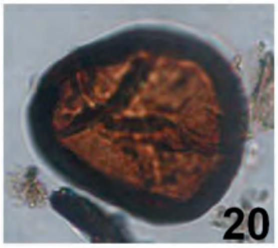
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**Magnifications are 600X**

**50 μm**

tion, suggests occurrence of freshwater bodies (lakes and ponds) (see Schrank & Mahmoud, 1998; Mahmoud & Moawad, 2002). Such a lowland freshwater environment is supported by the occurrence of probable lowland indicators such as the fern spores *Deltoidospora/ Cythidites* and *Verrucosisporites* (Fig. 5). The occurrence of *Afropollis* in appreciable amounts in the upper part of the section indicates more local temporary short term coastal humidity condition (Schrank, 2001). The occurrence of *Classopollis/ Ephedripites* could reflect derivation from conifers in upland areas far removed from the site of deposition (Yi *et al.*, 2003). Pollen of palms (e.g. *Arecipites punctatus*) is an important element of the terrestrial palynoflora of the studied well. Palms may have been abundant in tropical humid lowlands of the coastal plain where they were associated with pteridophytes and other plants that inhabited lowland sites (Mahmoud & Schrank, 2007).

## 7. VISUAL ASSESSMENT OF ORGANIC THERMAL MATURATION

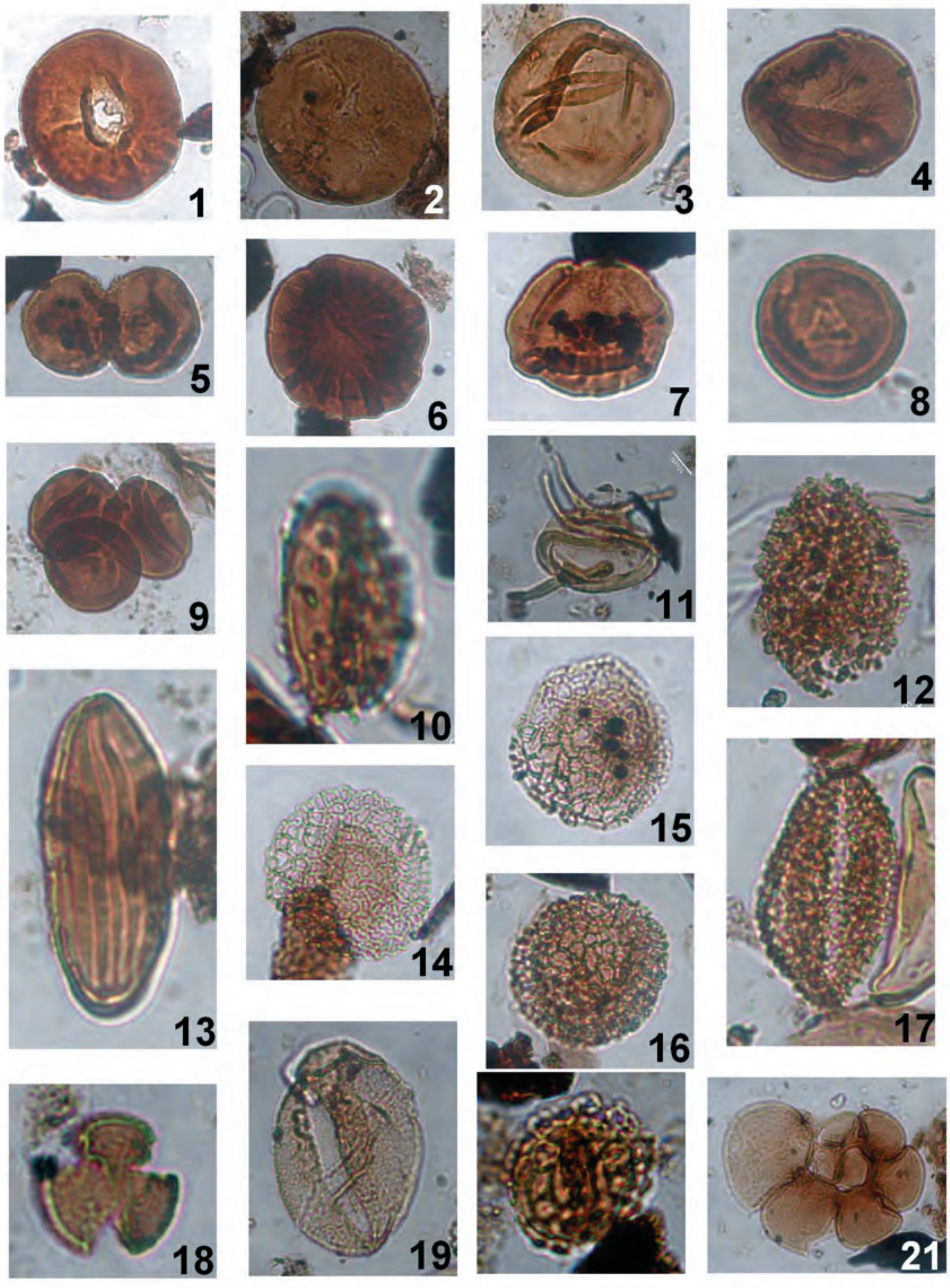
Maturation is the process by which plants and other algal material deposited in sediments are thermally decomposed to yield oil, natural gas and other products. It is governed by both time and temperature, in which the same degree of maturation can be attained at a low temperature for a long period of time as at a high temperature for a short period of time (Oehler, 1983). Source rocks are naturally capable of generating and releasing hydrocarbons in amounts to form commercial accumulations (Hunt, 1979). Several numerical scales, based on palynomorph colour, linked with phases of organic maturation and petroleum generation were erected in the late 1960s by Correia (1967), Staplin (1969), Pearson (1984) and Firth (1993). This change in colour mirrors the thermal and burial history of organic matter (OM).

Source rock potential of hydrocarbons in the North Western Desert of Egypt was studied by many authors such as Parker (1982) and Younes (2002). In this study palynomorph exine colours were investigated using the Pearson (1984) colour chart to suggest tentative thermal alteration index (TAI) and vitrinite reflectance (Ro %) in terms of organic thermal maturity colour chart. Younes (2005) stated that the Alam El-Bueib Member from Shushan Basin is located within the early to mid-mature stages of the oil generation window between vitrinite reflectance (Ro%) 0.5 to 1.0 Ro%, TOC varies from 1.85 to 2.40 wt. %. Samples from the Alam El Bueib and Alamein formations are characterized by large influx of AOM associated with thermally mature palynomorphs of orange to brown colours, suggesting a thermal alteration index (TAI) between +2 and -3 and vitrinite reflectance (Ro%) values between 0.5 to 0.9, according to the spore/pollen colour chart of Pearson (1984). However, the palynofacies A and B contain palynomorphs of the Kerogen types II and IV respectively. Kerogen type II material in the Alam El Bueib and Alamein formations produces oil and gas (Table, 1). However, accurate evaluation of source rock potentialities implies measuring TOC % and carrying out rock-eval pyrolysis. According to Younes (op. cit.) the Kharita Formation from Abu Gharadig-5 indicates a low source potential for hydrocarbon accumulation. This formation (with its underlying Dahab Formation) is dominanted by opaque (inert) material, hence the type IV kerogen composition (see Ibrahim, 2002) and cannot produce hydrocarbons. This contradicts results on the same rock unit, designated by Zobaa (2006) as "Late Albian Kharita Member", who counted high numbers of AOM. However, because AOM is not particulate organic matter (POM), this controversy between both results occurred.The palynofacies of the

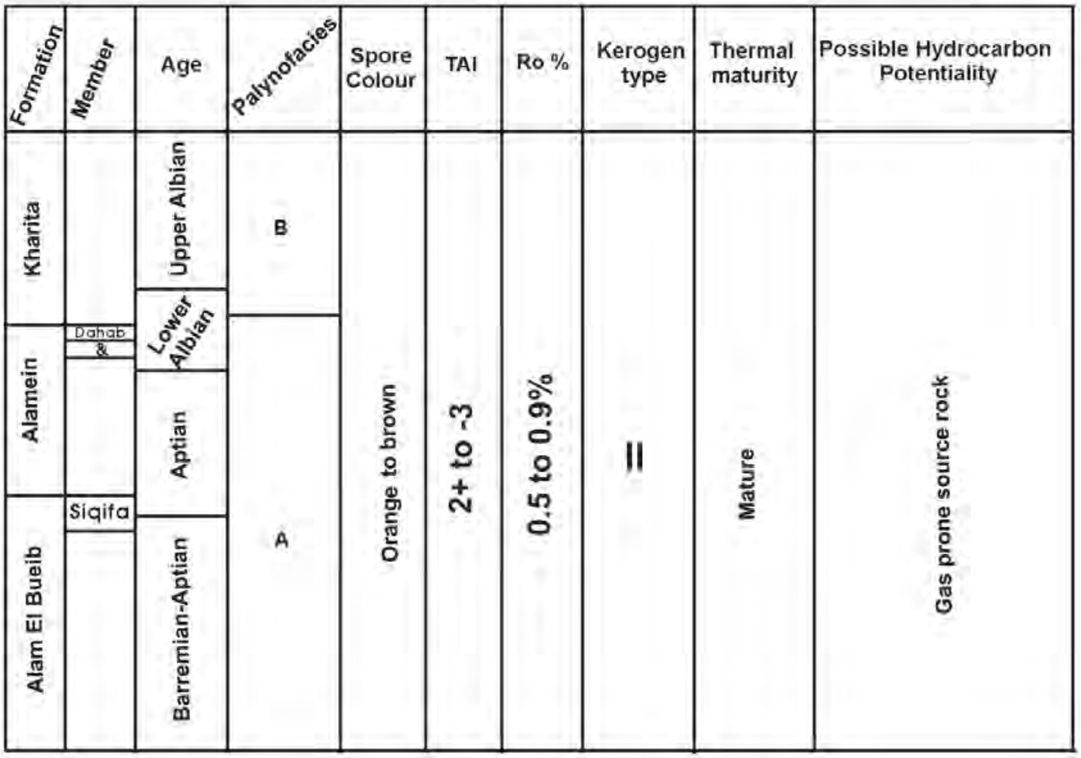
Plate 2. Gymnosperms (1-9, 13), Angiospermous pollen grains (10-12, 14-20) and microforaminiferal lining test (21) of Barremian-Aptian2, 4-5, 8-9, 12-13, 17-21), Aptian (1, 3, 7, 16), Lower Albian (6, 14), Upper Albian (10-11, 15), Mat2-1X= Matruch2-1X well. All figures x 400 unless otherwise stated.

1- *Inaperturopollenites undulates,* Mat2-1X, 2320 m, Diameter 70 µm; 2-*Inaperturopollenites* spp., Mat2-1X, 2814 m, Diameter 76 µm; 3- *Araucariacites australis*, Mat2-1X, 2320 m, Diameter 65 µm; 4- *Araucariacites* sp., Mat2-1X, 2980 m, Diameter 64 µm; 5- *Spheripollenites* sp., Mat2-1X, 2814 m, Diameter 23 µm; 6- *Callialasporites dampieri*, Mat2-1X, 2170 m, Diameter 56 µm; 7- *Callialasporites trilobatus*, Mat2-1X, 2320 m, Diameter 48µm; 8- *Classopollis torosus*, Mat2-1X, 2980 m, Diameter 36 µm; 9- *Classopollis classoides*, Mat2-1X, 2606 m, Diameter 34 µm; 10- *Echimonocolpites* cf. *tarsus,* Mat2-1X, 1676 m, Diameter 46 µm; 11- *Elaterosporites klaszii*, Mat2-1X, 1676 m, Diameter 46 µm; 12- *Stellatopollis densiornatus*, Mat2-1X, 2736 m, Diameter 46 µm; 13- *Ephedripites* sp., Mat2-1X, 2736 m, Diameter 70 µm; 14, 15- *Afropollis jardinus,* 14-Mat2-1X, 2170 m, Diameter 34 µm, 15- Mat2-1X, 2018 m, Diameter 36 µm; 16- *Afropollis operculatus*, Mat2-1X, 2320 m, Diameter 38 µm; 17- *Stellatopollis* sp., Mat2-1X, 2510 m, Diameter 46 µm, 18- *Tricolpites* sp., Mat2-1X, 2510 m, x1000, Diameter 34 µm; 19- *Retimonocolpites variplicatus,* Mat2-1X, 2510 m, Diameter 74 µm; 20- *Brenneripollis peroreticulatus,*Mat2-1X, 2510 m, Diameter 34 µm; 21- Microforaminiferal test lining, Mat2-1X, 2980 m.

**Plate 2**



Magnifications are 600X (1-17, 19-21); 1000X (18)



| Formation | Member | Age | Palynofacies | Spore Colour | TAI | Ro % | Kerogen type | Thermal maturity | Possible Hydrocarbon Potentiality |
|---|---|---|---|---|---|---|---|---|---|
| Kharita | | Upper Albian | B | Orange to brown | 2+ to -3 | 0.5 to 0.9% | II | Mature | Gas prone source rock |
| Alamein | Dahab<br>& | Lower Albian | A | | | | | | |
| | | Aptian | | | | | | | |
| Alam El Bueib | Siqifa | Barremian-Aptian | | | | | | | |

Table 1. Summary of palynofacies, kerogen type, spore/pollen colour, TAI, Vitrinite reflectance (Ro %), thermal maturation and source rock potentiality of Matruh2-1X borehole.

studied samples suggest production of gas rather than oil, since land derived pollen/spores and phytoclasts are the main components. This is in agreement with available information.

## 8. PRESERVATION IN THE KHARITA FORMATION

"Selective degradation" is nowadays a growing aspect in palynological research that is of the organic matter and its influence on changing primary productivity signal of palynofloral assemblages. One of the main factors influencing dinoflagellate cyst degradation rate is the bottom water oxygen concentration (e.g. Zonneveld *et al.*, 2008). This is apart from other factors such as the exposure time of palynomorphs to oxygen, such as sedimentation rates. Selective degradation could be observed by studying recent microfossils such as dinoflagellate cysts from bottom sediments of modern oceans and seas. Recently, the environmental significance of dinoflagellate cysts has been establish from the study of the proximal part of the Po-river discharge plume at the Eastern Mediterranean (Zonneveld *et al.*, 2009). This study established that dinoflagellate cyst association reflects both upper and bottom water circulation; certain species display high relative abundances in sites where bottom waters are low in oxygen and decrease remarkably in sites where bottom waters are relatively high in oxygen.

The distribution patterns of our preserved organic remains contain abundant black phytoclasts in the Kharita Formation sediments (Fig. 6), extremely higher than in the underlying and the overlying formations, implying that pre-depositional oxidation might played a role in the preservation of the formation organic matter. In this interval (samples 10 to 13) dinoflagellate cysts such as *Oligosphaeridium pulcherrimum, Cribroperidinium edwardsii, C. orthoceras, Cyclonephelium distinctum, C. vannophorum, Palaeoperidinium cretaceum, Systematophora areolata* and *Pseudoceratium securigerum* are missing. That these cysts were probably living during deposition of the Kharita Formation sediments but had undergone decay during early digenetic stages is greatly

**Plate 3**

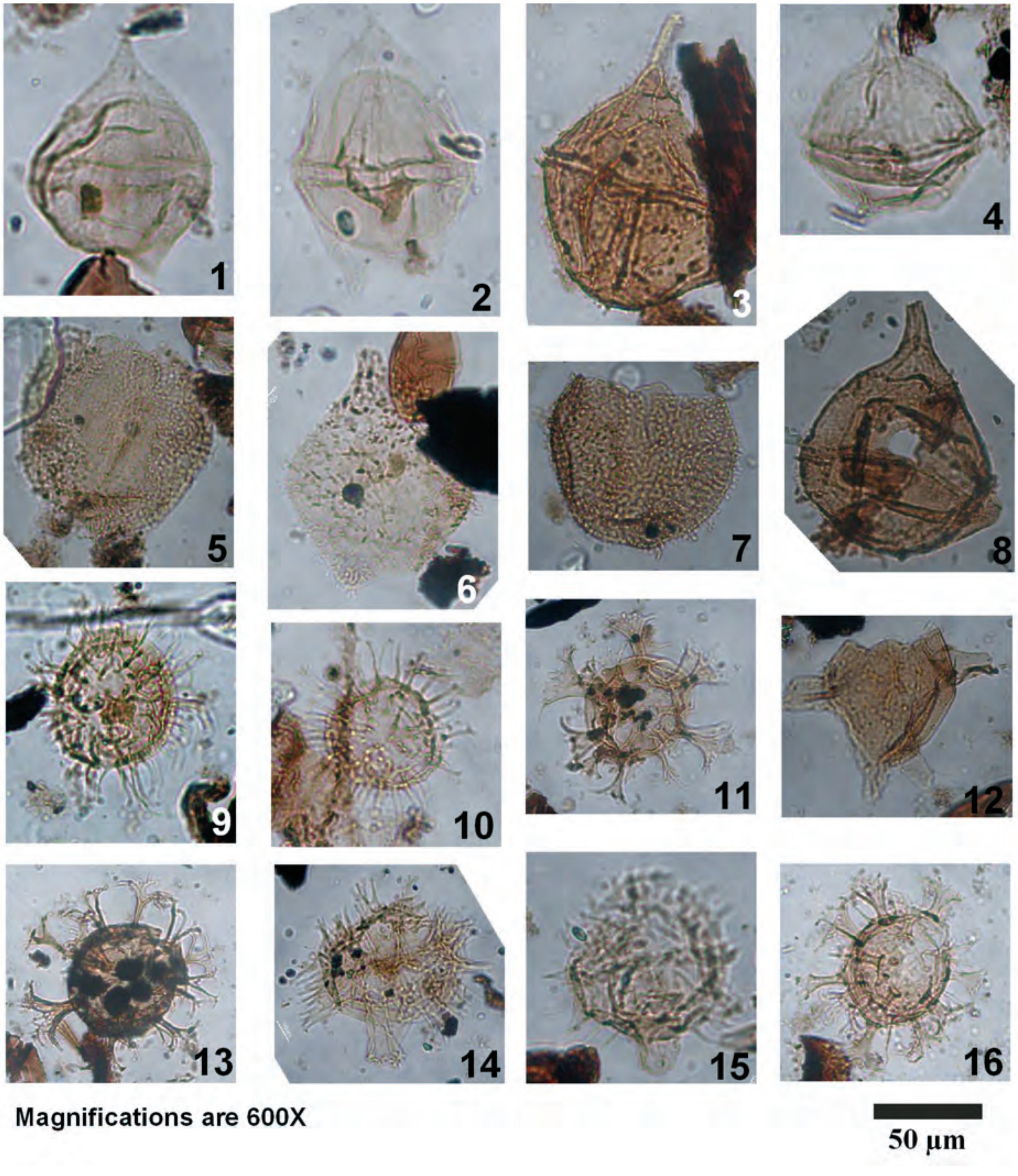


Plate 3. Gonyaulacoid (3, 7-11, 13-14, 16) and Peridinioid (1-2, 4-6, 12, 15). Dinoflagellate cysts of Barremian-Aptian (1-13, 16), Upper Albian (14-15), Mat2-1X= Matruch2-1X well. All figures x 400. 1- *Subtilisphaera senegalensis*, Mat2-1X, 2814 m, Length 58 µm; 2- *Palaeoperidinium cretaceum,* Mat2-1X, 2980 m, Length 72 µm, breadth 68 µm; 3- *Cribroperidinium edwardsii,* Mat2-1X, 2980 m, Overal Length 74 µm; 4- *Senegalinium aenigmaticum*, Mat2-1X, 2606 m, Overal Length 64 µm; 5- *Pseudoceratium securigerum,* Mat2-1X, 2904 m, Length 64 µm; 6- *Cyclonephelium vannophorum,* Mat2-1X, 2510 m, Length 60 µm; 7- *Circulodinium distinctum,* Mat2-1X, 2904 m, Length 58 µm; 8- *Cribroperidinium orthoceras,* Mat2-1X, 2904 m, Overal Length 74 µm; 9- *Systematophora* sp., Mat2-1X, 3220 m, Diameter 48 µm; 10- *Systematophora areolata,* Mat2-1X, 2606 m, Diameter 48 µm; 11- *Oligosphaeridium* sp., Mat2-1X, 2814 m, Diameter of body 36 µm, Length of processes 26 µm; 12- *Muderongia staurota,* Mat2-1X, 2904 m, Diameter of body 36 µm; 13- *Oligosphaeridium complex*, Mat2-1X, 2980 m, Diameter of body 46 µm, Length of processes 26µm; 14- *Florentinia berran,* Mat2-1X, 1676 m, Diameter of body 36 µm, Length of processes 26 µm; 15- *Coronifera tubulosa*, Mat2-1X, 2360 m, Overal Length 40 µm, Length of processes 10 µm; 16- *Oligosphaeridium pulcherrimum,* Mat2-1X, 2980 m, Diameter of body 36 µm, Length of processes 26 µm.

suggested. It is worthy noting that these cyst types are recovered frequently from similar Kharita (Albian) clay/shale interbeds in the local record (e.g. Omran *et al*., 1990; Deaf, 2010). We also argue in favor that *Subtilisphaera senegalensis* in this interval is resistant to aerobic degradation because it occurs abundantly with black phytoclasts. These ideas ought to be tested in future studies by studying intervals where aerobic decay or, for example, early diagenesis, is thought to have affected the original organic matter. However, inference of bottom water oxygen in material as old as Cretaceous and recognition of probable sensitive/resistant dinoflagellate cyst taxa may be established by using present-day signature in the light of the taxonomic uniformitarian approach.

## 9. CONCLUSIONS

1. Ninety two species of Early Cretaceous palynofloras were recovered from the Alam El Beuib, Alamein and Kharita formations encountered in the Matruh2-1X borehole.

2. The Barremian-Aptian interval is interpreted according to the presence of *Stellatopollis* and *Retimonocolpites variplicatus*. The Aptian stage is inferred by the first occurrence of *Duplexisporites generalis, Murospora florida, Afropollis operculatus* and tricolpate pollen. *Afropollis jardinus* marks the Early Albian stage.

3. A marginal marine environment is suggested for the lower part of the Barremian-Aptian interval in the well (lower part of Alam El Bueib Formation). Open marine (inner to middle shelf) environment terminates this setting during Barremian-Aptian and Aptian times (Alam El Bueib Formation). A transgressive, open marine phase is followed and continued during the Aptian (upper part of Alam ElBueib and Alamein formations). A second regressive phase and marginal marine environment took place during the Albian interval (upper part of Alamein, Dahab and Kharita formations). This environmental fluctuation reflects global and local transgressive/regressive episodes.

4. A warm-humid condition probably prevailed during deposition of the sediments. This is reflected by abundance of the ferns and other hygrophilous spores (e.g. *Deltoidospora, Cicatricosisporites* and *Triplanosporites*) and the scarcity of xerophytes. This contradicts the known well established warm-arid palaeoclimate in the majority of the Early Cretaceous and early Late Cretaceous within the pre -Albian West Africa-South American Province (WASA) of and mid-Cretaceous African-South American Province (ASA), which are characterized by dominance of gymnospermous pollen such as *Classopollis, Ephedripites* and *Araucariacites/Inaperturopollenites*. Our interpretation is supported by the coastal palaeogeographic position of Egypt during mid-Cretaceous times.

5. Based on the POM groups, two palynofacies are recognized. The lower part of the Alam el Bueib Formation is characterized by dominant terrigenous land-derived elements (pollen, spores, woody phytoclasts, cuticle sheets) and poor marine dinoflagellate cysts. Increasing terrestrial components suggests marginal near land deposition. Most of the interval of the Alam el Bueib with the overlying Alamein Formation is characterized by increasing marine elements and amorphous organic matter (AOM). This indicates deposition in more open marine conditions. The palynofacies recovered from Dahab and Kharita formations are dominated by terrestrial elements and rare marine dinoflagellate cysts. Black and opaque fragments could have resulted from oxidation before deposition.

6. Exine colours of thin-walled psilate palynomorphs using the Pearson (1984) colour chart may suggest a possible source for hydrocarbons.

## 10. ACKNOWLEDGEMENTS

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## Plate 4

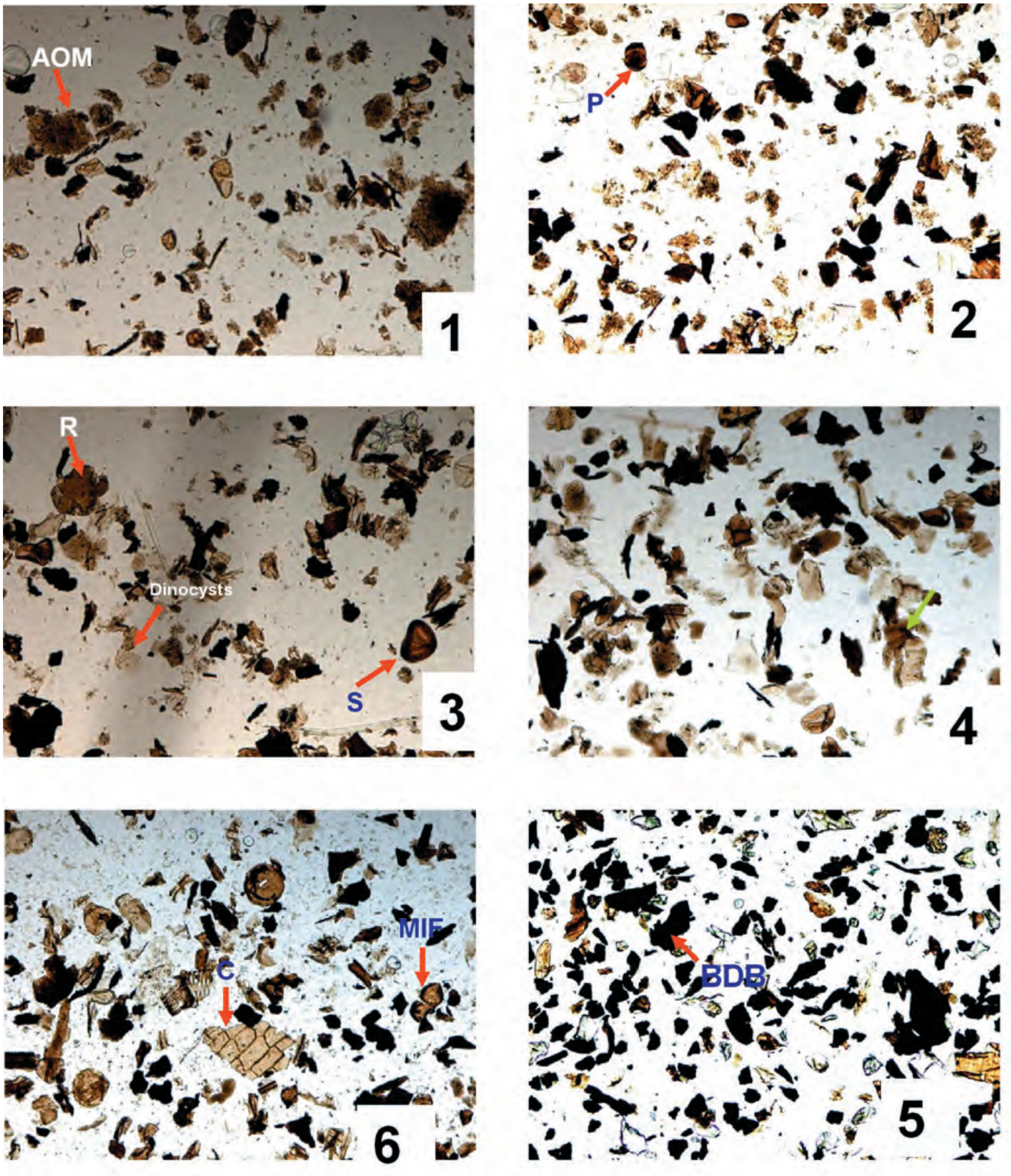

Plate 4. Photomicrographs of representative samples of the two palynofacies assemblages. 1, 2- Palynofacies A, sample 2904. 3- Palynofacies A, sample 2510. 4- Paynofacies A, sample 2320. 5- Palynofacies A, sample 2980. 6- Palynofacies B, 1770. Abbreviations for phytoclasts and palynomorphs: AOM: amorphous organic matter, P: pollen, R: Resin, S: Spores, W: Brown Wood, C: Cuticles, MIF: microforaminifera test linings, BDB: black debris

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# APPENDIX

List of species

**Spores and Pollen**

*Aequitriradites spinulosus* (Cookson & Dettmann) Cookson & Dettmann 1961
*Afropollis jardinus* (Brenner) Doyle *et al*., 1982
*Afropollis operculatus* Doyle et *al*., 1982
*Afropollis* sp.
*Appendicisporites potomacensis* Brenner, 1963
*Araucariacites australis* Cookson ex Couper, 1953
*Araucariacites* sp.
*Arecipites punctatus* Wodehlouse, 1933
*Balmeisporites holodictyus* Cookson & Dettmann, 1958
*Balmeisporites* sp.
*Brenneripollis peroreticulatus,* (Brenner) Juhász & Góczan, 1985
*Callialasporites dampieri* (Balme) Sukh Dev, 1961
*Callialasporites trilobatus* (Balme) Sukh Dev, 1961
*Callialasporites* sp.
*Cicatricosisporites orbiculatus* Singh, 1964
*Cicatricosisporites sinuosus* Hunt, 1985
*Cicatricosisporites* cf. *hughesii* Detman, 1963
*Cicatricosisporites* cf. *purbeckensis* Norris, 1969
*Cicatricosisporites* spp.
*Cingulatipollenites aegyptiaca,* Saad & Ghazaly, 1976
*Classopollis classoides* Pflug, 1953
*Classopollis torosus* (Reissinger) Couper, 1958
*Classopollis* sp.
*Concavissimisporites punctatus* (Delcourt & Sprumont) Brenner, 1963.
*Concavissimisporites* sp.1
*Cosmosporites elegans* Nilsson, 1958
*Concavisporites* sp.
*Crybelosporites pannuceus* (Brenner) Strivastava, 1977
*Cycadopites* sp.
*Deltoidospora/Cythidites* spp.
*Duplexisporites generalis* Deák, 1962
*Echimonocolpites* cf. *tersus* Ward, 1986
*Elaterosporites klaszii* (Jardiné & Magloire) Jardiné, 1967
*Ephedripites striatus* Brenner, 1968
*Ephedripites jansonii* (Pocock) Muller, 1986
*Ephedripites* sp.
*Exesipollenites* sp.
*Eucommiidites troedssonii* (Erdtmann) Potonié, 1958
*Eucommiidites* sp.
*Klukisporites variegat* Couper, 1958
*Inaperturopollenites* spp.
*Inaperturopollenites undulatus* Weyland & Greifeld, 1953
*Ischyosporites marburgensis* Jersey, 1963
*Laevigatosporites* sp.
*Leptolepidites* sp.
*Matonisporites* spp.
*Murospora florida* (Balme) Pocock, 1961
*Murospora* sp.
*Pilosisporites trichopapillosus* (Thiergart) Delcourt & Sprumont, 1955
*Pilosisporites* sp.
*Punctatisporites* sp.
*Trilobosporites laevigatus* El-Beialy, 1994
*Trilobosporites apiverucatus* Couper, 1964
*Trilobosporites* sp.
*Tricolpites* sp.
*Triplanosporites* sp.
*Todisporites major* Couper, 1958
*Todisporites* sp.
*Spheripollenites* sp.
*Stellatopollis densiornatus* (De Lima) De Lima, 1989
*Stellatopollis* sp.
*Retimonocolpites variplicatus* Schrank & Mahmoud, 1998
*Retimonocolpites* sp.
*Verrucosisporites* sp.

**Dinoflagellate cysts**

*Circulodinium distinctum* (Deflandre & Cookson) Jansonius, 1986
*Circulodinium* sp.
*Cleistophaeridium* sp.
*Coronifera tubulosa* Cookson & Eisenack, 1974
*Coronifera* sp.
*Cribroperidinium edwardsii* (Cookson & Eisenack) Davey, 1969
*Cribroperidinium orthoceras* (Eisenack) Davey, 1969
*Cribroperidinium* sp.
*Cyclonephelium vannophorum* Davey, 1969
*Cyclonephelium* sp.
*Florentinia radiculata* (Davey & Williams) Davey & Verdier, 1973
*Florentinia berran* Below, 1982

*Florentinia* sp.
*Muderongia staurota* Sarjeant, 1966
*Odontochitina operculata* (O. Wetzel) Deflandre & Cookson, 1955
*Odontochitina porifera* Cookson, 1956
*Oligosphaeridium complex* (White) Davey & Williams, 1966
*Oligosphaeridium pulcherrimum* (Deflandre & Cookson) Davey & Williams, 1966
*Oligosphaeridium* sp.
*Palaeoperidinium cretaceum* Poccok, 1962
*Pseudoceratium securigerum* (Davey & Verdier) Bint, 1986
*Senegalinium aenigmaticum* (Boltenhagen) Lentin & Williams, 1981
*Spiniferites* sp.
*Subtilisphaera senegalensis* Jain & Millepied, 1973
*Subtilisphaera* sp.
*Systematophora areolata* Klement, 1960
*Systematophora* sp.

**Freshwater algae**
*Chomotriletes minor* (Kedves) Pocock, 1970

**Incertae Sedis**
*Reyrea polymorphus* Herngreen, 1973

**Microforaminferal test lining**

**Marine acritarch**

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# Origin, taxonomic revision and evolutionary classification of the late Coniacian-early Campanian (Late Cretaceous) planktic foraminifera with multichamber growth in the adult stage

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## Resumen

Una revisión taxonómica y una clasificación evolutiva de foraminíferos planctónicos del Coniaciense tardío-Campaniense temprano ha puesto de manifiesto que el estado adulto con crecimiento de multicámaras se desarrolló independientemente en tres linajes direccionales: *Texasina* – nuevo (Coniaciense tardío-Campaniense temprano), *Sigalia* Reiss, 1957 – enmendado (Santoniense), *Proliferania* – nuevo (Santoniense) y un clado del linaje, es decir, *Ventilabrella* Cushman, 1928 – enmendado (Santoniense- Campaniense temprano). Aparentemente, *Texatina* evolucionó a partir del grupo de especies que engloba *"Heterohelix" globulosa* (Ehrenberg, 1840). Los otros tres linajes evolucionaron divergentemente a partir de *Planulitella* – nuevo, un descendiente de *Planoheterohelix* Georgescu & Huber, 2009.

**Palabras clave:** Foraminíferos planctónicos, Cretácico Superior, clasificación evolutiva, nuevos linajes direccionales, nuevos clados de linajes, nuevas especies.

## Abstract

Taxonomic revision and evolutionary classification of the late Coniacian-early Campanian planktic foraminifera reveals that the adult stage with multichamber growth developed independently in three directional lineages: *Texasina* – new (late Coniacian-early Campanian), *Sigalia* Reiss, 1957 – emended (Santonian), *Proliferania* – new (Santonian) and a branched lineage, namely *Ventilabrella* Cushman, 1928 – emended (Santonian-early Campanian). *Texasina* apparently evolved from the *"Heterohelix" globulosa* (Ehrenberg, 1840) group of species. The other three divergently evolved from the branched lineage *Planulitella* – new, a descendant from *Planoheterohelix* Georgescu & Huber, 2009.

**Key words:** Planktic foraminifera, Late Cretaceous, evolutionary classification, new directional lineages, new branched lineages, new species.

## 1. INTRODUCTION

Cretaceous planktic foraminifera with serial chamber arrangement evolved in the late Albian from benthic ancestors (Georgescu, 2009a) and therefore, their basic architectural plan consists of a proloculus followed by chambers alternately added with respect to the test growth axis resulting in a biserial arrangement. This fundamental architectural plan has been modified as result of evolutionary changes undergone by the group until its extinction at the Cretaceous/Tertiary boundary event. Probably the most evident change is the increase in number of chambers in the adult stage. The adult stage of such tests is characterized by addition of new chambers in sets, rather than one by one as in the earlier stage with biserial arrangement. There are two stratigraphical intervals in which representatives of the heterohelicid group developed adult stages with multichamber growth: late Coniacian-earliest Campanian and late Campanian-Maastrichtian. The highest diversity and frequency of the tests with a multichamber growth stage are known from the late Santonian and Maastrichtian respectively. Noteworthy, although rare, tests with incipient multichamber growth in the adult stage are also known from other stratigraphical intervals, such as the late Turonian and middle Campanian (Cushman, 1938; Aliyulla, 1977; Georgescu, 2009b).

The late Coniacian-earliest Campanian tests with multichamber growth in the adult stage were traditionally assigned to two genera: *Ventilabrella* Cushman, 1928 and *Sigalia* Reiss, 1957. The separation between the two is defined by the presence or absence of the raised sutures (Reiss, 1957; Loeblich & Tappan, 1987; Nederbragt, 1991), which are developed only in the latter. Their classification is based on typological principles, without taking into consideration the convergent and iterative pattern of the planktic foraminiferal evolutionary process (Steineck & Fleisher, 1978). These taxa are particularly interesting due to their relatively short stratigraphic ranges, which make them potential markers for the biozones of this stratigraphical interval (Masters, 1976, 1977; Weidich, 1984; Reiss *et al.*, 1985; Honigstein *et al.*, 1987; Nederbragt, 1991). Nederbragt (1990) provided the first and only biostratigraphic framework for the Cretaceous based on heterohelicids. This framework shows the highest resolution (four biozones based on species of *Sigalia* and *Ventilabrella*) is in the Santonian-early Campanian interval.

The phylogenetic relationships between these taxa are relatively poorly understood despite their frequency in the fossil record, interesting test morphology and biostratigraphical significance. Aliyulla (1965, p. 220-221) recognized that the development of raised sutures and adult stages with multichamber growth successively occurred in this group during the Coniacian-Santonian.

A new taxonomic framework is proposed for the late Coniacian-earliest Campanian heterohelicid planktic foraminifera that developed an adult stage with multichamber growth. High resolution, scanning electron microscope (SEM) based morphological observations made in biostratigraphic context show that the chamber proliferation in the adult stage developed independently in four directional or branched lineages. The evolutionary changes in the gross test architecture (e.g., transition from biserial tests to tests with chamber proliferation in the adult, etc.) are supported by changes in the test ultrastructure, ornamentation and porosity. Extensive use of the SEM revealed for the first time the presence of an evolutionary continuum in the case of these foraminifera. One of the most interesting outcomes of this study is that it demonstrates that species can be grouped either into directional lineages or branched lineages, both taxonomic units with significance in evolutionary classification.

Three directional lineages (*Texasina* – new, *Sigalia* Reiss, 1957 – emended and *Proliferania* – new) and two branched lineages (*Planulitella* – new and *Ventilabrella* Cushman, 1928 – emended) are recognized. *Texasina* evolved from the "*Heterohelix*" *globulosa* (Ehrenberg, 1840) group of species. *Planulitella* probably evolved from *Planoheterohelix* Georgescu & Huber (2009) and is the ancestral group for *Sigalia*, *Proliferania* and *Ventilabrella*.

## 2. NEW TEST STRUCTURES AND TERMINOLOGY

The terminology of the heterohelicid test is refined as result of increased observation resolution due to the extensive use of the SEM and x-rays, in order to accommodate the newly observed morphological structures. Some gross heterohelicid test architecture terms are reviewed in order to be consistent with the growth patterns.

### 2.1. Growth stages

The tests with an adult flaring stage were traditionally referred to as "multiserial" or "with multiserial growth". A different terminology based on growth characteristics of the various stages is proposed in order to better describe the growth processes and their outcomes. For example, the earlier stage often described as "biserial" is in fact formed through the alternate addition of chambers with respect to the test axis of growth. As a result, the biserial chamber arrangement is only the result of the growth strategy, the term "biserial" having a rather descriptive meaning. The adult stage begins with the first biaperturate chamber, which is known as a progressive chamber (van Hinte, 1965, p. 61) and continues with sets of two or more chambers, the number of chambers in each set increasing during ontogeny (Fig. 1). Multiserial chamber arrangement can be rarely achieved and the gerontic portions of the test, which are characterized by significant chamber proliferation, completely lack this feature (Fig. 1: C). Consequently, the expression "multichamber growth" appears to better describe the growth pattern of the adult flaring stage and is preferred over the more imprecise "multiserial".

## 2.2. Sutural ridges

The raised calcitic structures developed over the sutures, were often described as "raised sutures". These structures occur in three Upper Cretaceous heterohelicid taxa: *Sigalia* Reiss, 1957 (Santonian), *Proliferania* – new directional lineage (Santonian) and *Lipsonia* Georgescu & Abramovich, 2008a (upper Maastrichtian). High resolution SEM microphotographs study of the sutural ridges in the two Santonian directional lineages, namely *Sigalia* and *Proliferania* (Fig. 2), resulted in the recognition of two stages: calyptoridges and phaneroridges.

*Calyptoridges* (Fig. 2: 1-2) represent the early stage of development of the sutural ridges and are known only in the oldest species of *Sigalia* and *Proliferania*, namely *S. incipiens* – new species and *P. initialis* – new species. This term is derived by adding the Greek prefix *calypto-* (=hidden) to the root-word *ridge*; the name emphasizes the difficulty to observing this feature under the optical stereomicroscope.

*Phaneroridges* (Fig. 2: 3-4) are fully developed sutural ridges, elevated calcitic structures over the sutures, often retaining the original costate ornamentation, which are easily visible under the optical stereomicroscope. Phaneroridges result from the gradual thickening of the calyptoridges. The term is derived from the root-word *ridge* to which the Greek prefix *phanero-* (=visible, obvious) is added. The Santonian species with phaneroridges are: *Sigalia deflaensis* (Sigal, 1952), *S. proliferans* – new species, *Proliferania carpatica* (Salaj & Samuel, 1963) and *P. decoratissima* (de Klasz, 1953).

## 2.3. Periapertural flanges

The paramount taxonomic role of the periapertural structures in the heterohelicid taxonomy was emphasized by Georgescu (2009a) and Georgescu & Huber (2009), who demonstrated that the earliest (late Albian-early Turonian) heterohelicids of the genus *Protoheterohelix* Georgescu &

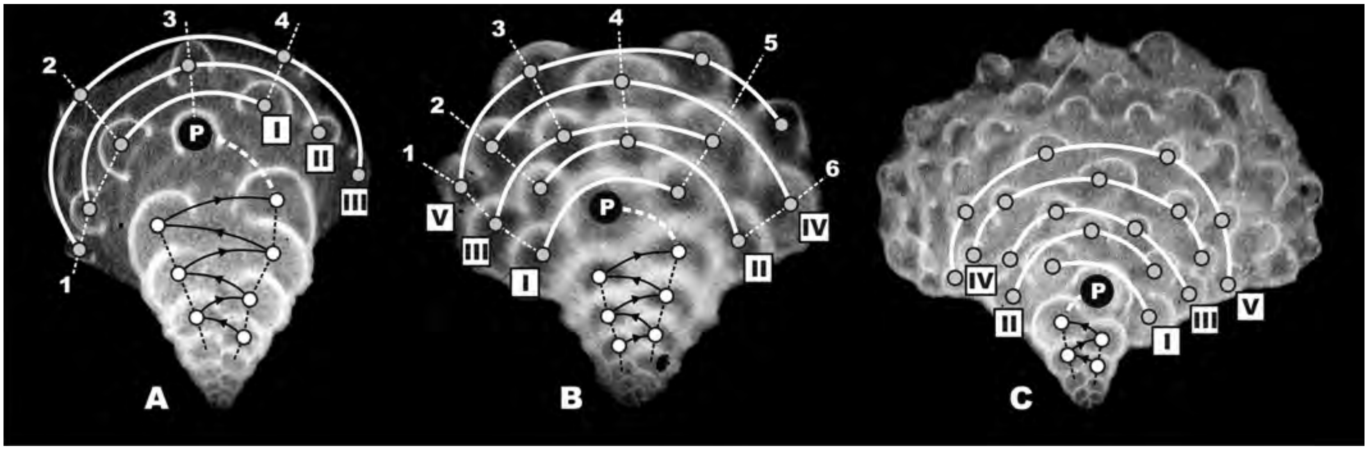


Figure 1. Adult flaring stage with multichamber growth illustrated with x-ray micrographs of three specimens: A-*Praegublerina robusta* (de Klasz, 1953), B-*Proliferania decoratissima* and C-"*Planoglobulina*" sp. The chambers of the early stage with alternate addition of chamber with respect to the test growth axis are marked with white circles; P – progressive chamber; chambers of the adult stage with multiserial stage are marked with grey circles. Chamber sets of the adult stages are labeled with Roman numerals. Lines legend: continuous black lines with arrowhead – pattern of chamber addition in the biserial stages, dashed black lines – biserial rows in the earlier stages, continuous white lines – chamber sets of the adult stages and white dashed lines – inferred "multiserial" chamber pattern in the adult stages showing the subjective nature of this term.

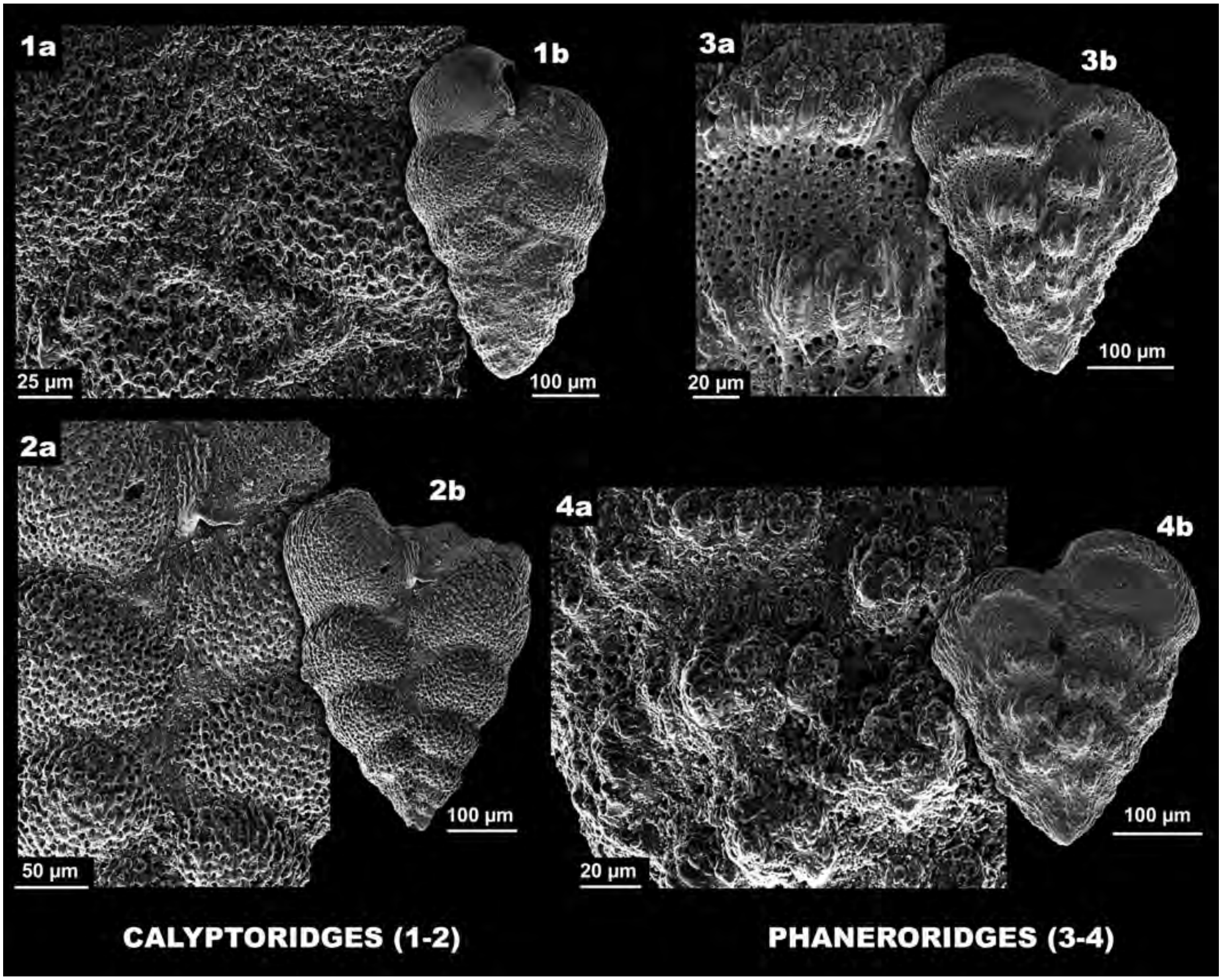


Figure 2. Examples of calyptoridges in *Proliferania initialis* (1-2) and phaneroridges in *P. carpatica* (3-4).

Huber, 2009 have asymmetrical periapertural structures and the first symmetrical such structures occurred in *Planoheterohelix moremani* (Cushman, 1938), a species that has first occurrence in the middle Cenomanian (lower part of the *Thalmanninella reicheli* Biozone). The earliest heterohelicids species, *Protoheterohelix washitensis* (Tappan, 1940) exhibits asymmetrical periapertural structures consisting of an imperforate lip on one side and a ridge on the other (Georgescu, 2009a; Georgescu & Huber, 2009). The next type of periapertural structure that developed in the heterohelicid group during the middle Cenomanian are the flanges, which are thin, commonly perforate lamellae bordering the aperture. A four-fold classification of the flanges based on their asymmetry/symmetry and morphology is proposed herein (Fig. 3)

*Archeoflanges* (Fig. 3: 1) occur only in *Protoheterohelix obscura* Georgescu & Huber, 2009 (late Albian-early Turonian) and are asymmetrically developed and non-rimmed. They can be observed best in the specimens illustrated in both lateral and edge views. The name is derived by adding the Greek prefix *archeo-* (=old) to the root-word *flange*.

*Orthoflanges* (Fig. 3: 2) first occurred in middle Cenomanian, in *P. moremani*. This type of flange differs from the archeoflange by being symmetrically developed on the two sides of the aperture. Orthoflanges are the first symmetrical periapertural structures in the heterohelicids group. For this reason their name is formed adding the Greek prefix *ortho-* (=good, well, true) to the root-word *flange*. Orthoflanges are typically developed in *Laeviheterohelix pulchra* (Brotzen, 1936).

*Metaflanges* (Fig. 3: 3) exhibit a strong resemblance to orthoflanges from which they evolved. The only difference is that the metaflanges have an imperforate rim at the distal edge. The first occurrence of metaflanges in the heterohelicid record is from the early Turonian. Most of the heterohelicids of the Turonian-Maastrichtian have metaflanges. The name is derived from the Greek prefix *meta*- (=after, beyond), which added to the root-word *flange*. Metaflanges are typically developed in *Planoheterohelix planata* (Cushman, 1938).

*Leptoflanges* (Fig. 3: 4) are thin, symmetrical periapertural structures, which are rimmed on both anterior and posterior sides. They are known only from *Braunella brauni* Georgescu, 2007 of the late Campanian-Maastrichtian. The name is derived by adding the Greek prefix *lepto*- (=thin) to the root-word *flange*.

## 2.4. Costae

Earliest heterohelicids have a smooth chamber surface and apparently ornamentation is a gradually acquired feature and the first ornamented species are known from in the late Cenomanian (Georgescu, 2009a; Georgescu & Huber, 2009). The earliest ornamentation is the costate one, which remained the only type during the late Cenomanian-late Campanian. Incipiently reticulate ornamentation occurred in the *Braunella* Georgescu, 2007 and *Praegublerina* Georgescu, Saupe & Huber, 2009 lineages of the late Campanian-Maastrichtian interval. A practical terminology is proposed herein to subdivide the costae

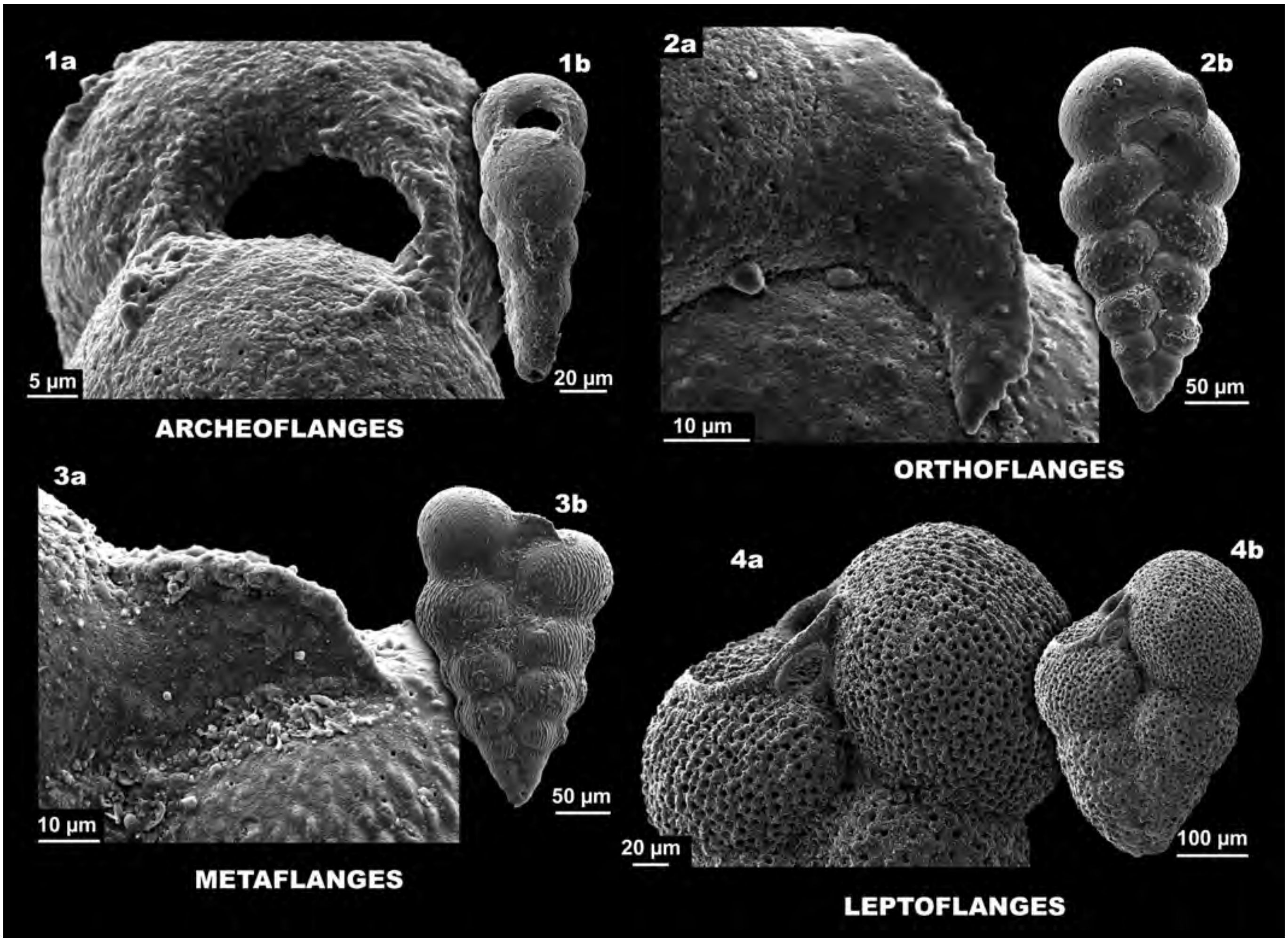


Figure 3. Flange types in Cretaceous heterohelicids illustrated with four specimens of *Protoheterohelix obscura* (1), *Laeviheterohelix pulchra* (2), *Planoheterohelix planata* (3) and *Braunella brauni* (4). The two lateral views of specimens of the *Laeviheterohelix* directional lineage were figured by Georgescu (2009b, figs. 7.2 and 8.4), demonstrating the symmetrically developed metaflanges.

into two categories, leptocostae and pycnocostae (Fig. 4), which cannot preclude the usage of the more general term of costae. Tests with ornamentation parameters between the two kinds occur frequently; a classification consisting of sharply defined categories and based only on the costae characteristics appears impossible due to the iterative and convergent pattern in heterohelicid ornamentation evolution.

*Leptocostae* (Fig. 4: 1-2) represent the dominant kind of costae in the heterohelicid group. It is the only one during the late Cenomanian-early Santonian and for this reason it can be referred to as primitive. The leptocostae are thin, discontinuous and with straight or irregular sides; pores generally occur between the leptocostae, rarely interrupting them. The name is derived by adding the Greek prefix *lepto-* (=thin) to the root-word *costae*. Leptocostae are typically developed in *P. planata*, *"H." globulosa* and *T. papula*.

*Pycnocostae* (Fig. 4: 3-4) are stronger developed than the leptocostae, often longer and with straight, parallel sides resulting in a robust appearance. Pores do not penetrate through the pycnocostae. The term is derived by adding the Greek prefix *pycno-* (=thick) to the root-word *costae*. *Pseudoguembelina excolata* (Cushman, 1926), *"Heterohelix" striata* (Ehrenberg, 1840) are two examples of species completely ornamented with pycnocostae; other

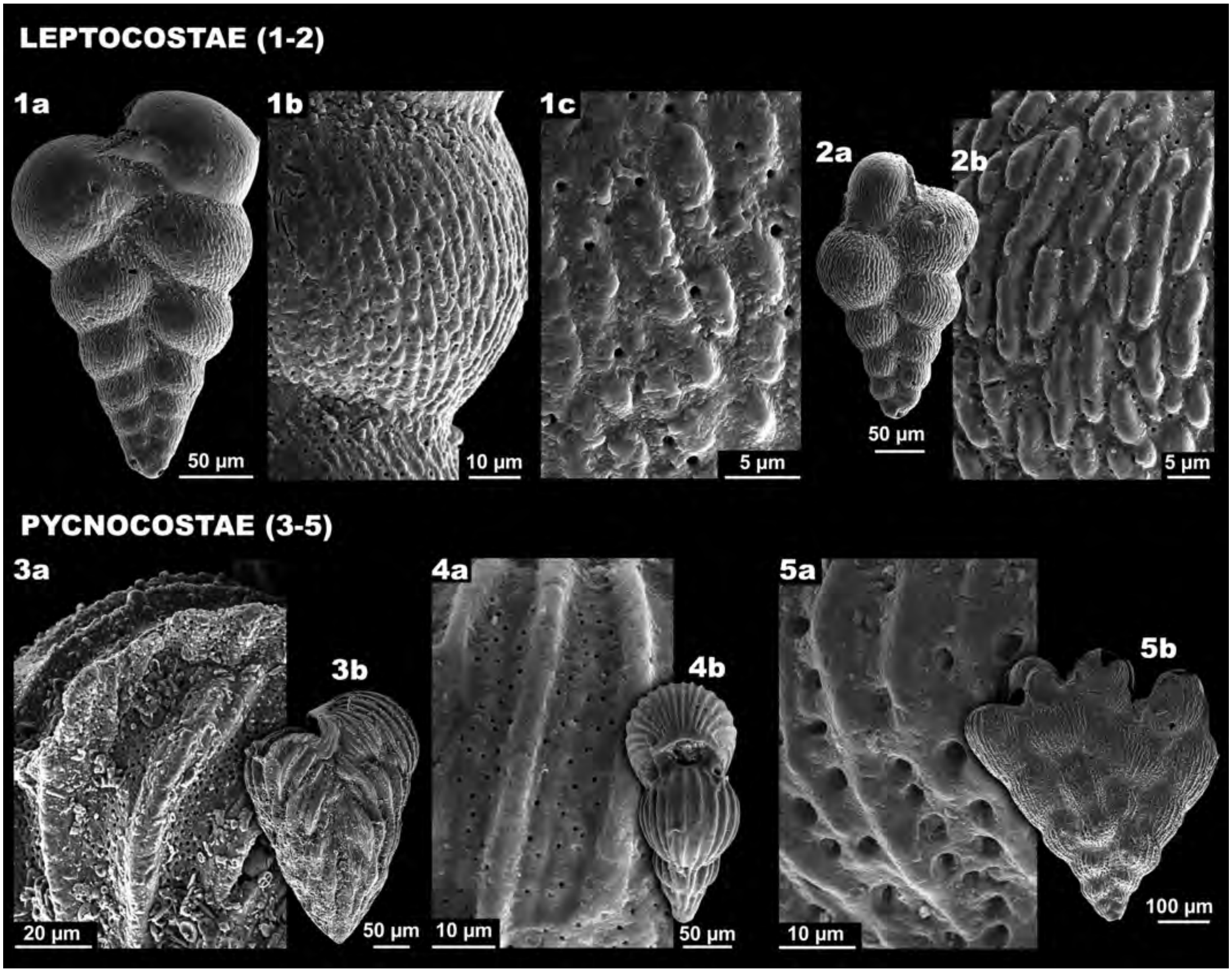


Figure 4. Costae types in the heterohelicid group of lineages. Leptocostae illustrated in *Planoheterohelix planata* (1) and *Texasina papula* (2); pycnocostae illustrated in *Pseudoguembelina excolata* (3), "Heterohelix" *striata* (4) and *Ventilabrella glabrata* (5).

species, such as *V. glabrata* develop pycnocostae only in the early portion of the test through addition of successive layers of calcite.

## 2.5. Pore shape

The pioneer work by Banner & Desai (1988) firmly established the use of test porosity in Cretaceous planktic foraminiferal taxonomy. Subsequent studies showed that pore size fluctuates along a lineage and their gradual change can be used to characterize the lineage evolution (Georgescu, 2009a, 2009b, 2009c, 2010). However, the use of SEM observations further complicated the problem and resulted in identifying different pore shapes among the representatives of the heterohelicid group (Fig. 5). A three fold classification of the pore shape is proposed herein.

*Simple pores* (Fig. 5: 1) are circular to subcircular, rarely elliptical openings that penetrate through the test wall. It is the most frequent pore shape among the heterohelicids.

*Scalaropores* (Fig. 5: 2) are crater-like with stepped walls and are reported in both heterohelicid and hedbergellid groups (Georgescu, 2008; Georgescu & Abramovich, 2008b, 2009). A new term, scalaropores, is proposed to accommodate this kind of pore. The name is derived by adding the Latin prefix *scalaro-* (=stepped) to the rootword *pores*. Scalaropores are known only in the Campanian and Maastrichtian heterohelicids.

*Vuggy pores* (Fig. 5:3-4) are known only from two Cretaceous heterohelicids, namely *Sigalia decoratissima* and *Lipsonia lipsonae* of the Santonian and late Maastrichtian respectively. They are irregular in shape and form in the earlier and median portions of the test through the addition of successive layers of calcite and the formation of wide irregular depressions; each of these vuggy pores include a variable number of regular pores.

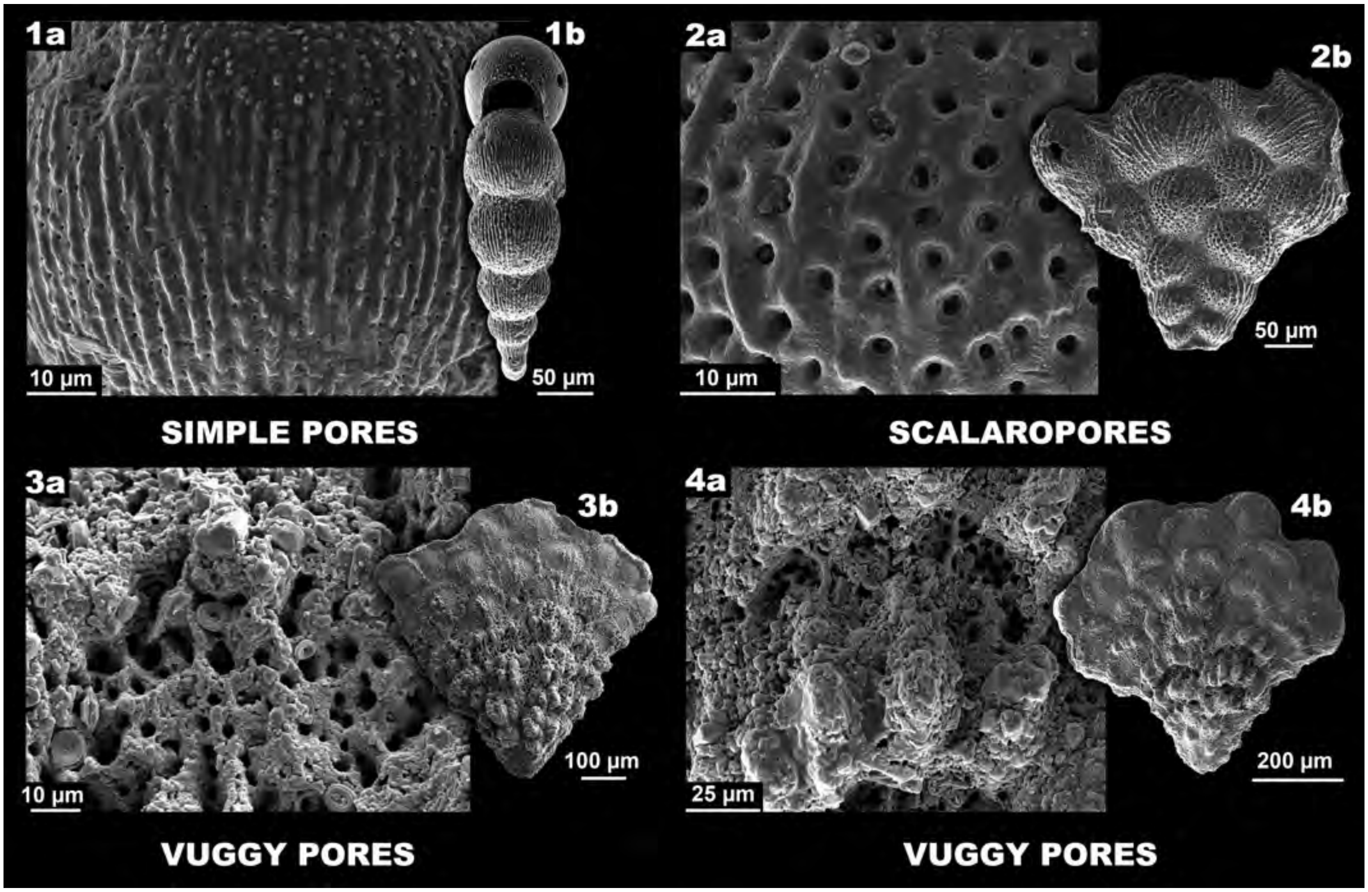


Figure 5. Pore types in the heterohelicid group of lineages illustrated in *Planoheterohelix planata* (1), *Ventilabrella. glabrata* (2), *Lipsonia lipsonae* (3) and *Proliferania decoratissima* (4).

## 3. MATERIAL AND METHODS

The analyzed material is extensive and includes not only the late Coniacian-early Campanian taxa that developed multichamber growth in the adult stage and their ancestors with biserial chamber arrangement throughout, but also comparison material from throughout the heterohelicids stratigraphic range (upper Albian-Maastrichtian). It includes both collection and newly acquired material from a number of wells drilled in the Atlantic Ocean, Caribbean region and Gulf of Mexico.

A preliminary study of the material was made in the Ocean Micropaleontology Collection (OMC) at the National Museum of Natural History, Washington, D.C. (NMNH). Attention was focused initially on three wells drilled under the auspices of the Deep Sea Drilling Project, namely Site 95 (Yucatan outer shelf, off Mexico), Site 356 (São Paolo Plateau, off Brazil) and Site 357 (Rio Grande Rise, off Brazil). This examination revealed that the richest and best preserved fossil material could be collected from Site 95, which was therefore selected for use in this study. In contrast, the planktic foraminifera at Sites 356 and 357 are often affected by diagenesis, making observations on the test ultrastructure, ornamentation and porosity extremely difficult; this material will be studied in more detail in a forthcoming article, which will focus on the newly proposed taxonomic framework applications in biostratigraphy.

Sample labeling follows the system used at various sites. The DSDP and ODP (Ocean Drilling Program) samples are labeled as follows: leg-site-core-section, sample depth given in centimetres. The only exception is represented by the ODP Leg 174AX, Bass River Site, where the sample depth is given in meters below surface (mbsf). The samples from the Gulf of Mexico Eureka well 67-128 are labeled as depth from the sea level (mbsl). Maintaining the original sample labeling system has the advantage of making the new data of this study easily comparable to those of the previously published ones.

The fossil material was first investigated under the classical optical stereomicroscope followed by approximately 1,100 SEM micrographs taken mostly on well preserved specimens. Additional investigation was carried out on 15 x-ray micrographs of well-preserved specimens, which were taken on SO-253 High Speed Holographic Film, developed with D-19 developer and fixed in F-5 fixing bath; 12 of them were used to reconstruct the ontogenetic trajectories and study in detail the chamber addition patterns in the adult stage with multichamber growth. The measurements used to reconstruct the ontogenetic trajectories were made using the ImageJ program.

### 3.1. DSDP Site 95

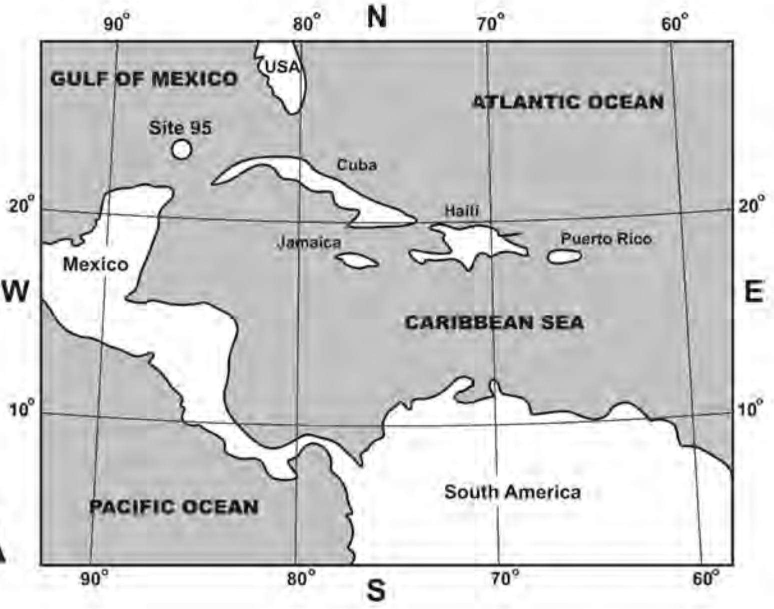
DSDP Site 95 was drilled offshore Mexico in the Yucatan outer shelf (Fig. 6A). McNeely (1973, p. 683-684) recognized the occurrence of Santonian and lower Campanian sediments in the interval between cores 18 and 13. The age dating was reviewed by Nederbragt (1991, p. 334) who considered that the interval between cores 17 and 13 is Santonian. This interval is thoroughly analyzed in this study and assigned to the late Turonian-early Campanian (Fig. 6B).

Twenty five samples were investigated, four of them being deposited in the Ocean Micropaleontology Collection (NMNH) and 21 from resampling of the stratigraphic succession. Four planktic foraminiferal biozones are recognized: upper part of the *Marginotruncana sigali* Biozone (late Turonian), *Dicarinella concavata* Biozone (latest Turonian-early Santonian), *D. asymetrica* Biozone (middle-late Santonian) and lowermost part of *Globotruncanita elevata* Biozone (earliest Campanian). A detailed biostratigraphic study will be the topic of a forthcoming article. An earlier version of this framework was published by Georgescu & Huber (2009). Planktic foraminiferal assemblages were collected from soft limestones accumulated under distal shelf environments and contain an extremely rich and diverse foraminiferal assemblage in most of the samples. All the species of *Planulitella*, *Sigalia*, *Proliferania* and *Ventilabrella* occur at Site 95 (Fig. 6B) and the good to very good preservation allowed excellent observations on the test morphology, although test fragmentation and dissolution is evident in some samples.

### 3.2. ODP Leg174AX at Bass River Site

The ODP Leg 174AX was drilled at the Bass River Sire in the New Jersey coastal plain (Fig. 7A). The Santonian-Campanian succession consists of sediments accumulated under inner to outer shelf environments (Georgescu,

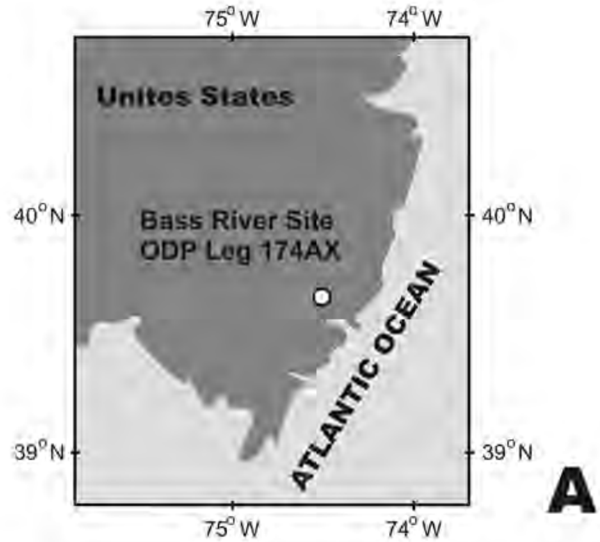
**A**



**B**

| SAMPLES | STAGES | Planktic foraminiferal biozonation after Georgescu and Huber (2009), with modificatons | *Planulitella sphenoides* | *P. stenopos* | *P. malocaucasica* | *Sigalia incipiens* | *S. deflaensis* | *S. proliferans* | *Proliferania initialis* | *P. carpatica* | *P. decoratissima* | *Ventilabrella eggeri* | *V. alpina* | *V. glabrata* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Selected planktic foraminiferal species | | | | | | | | | | | |
| 13-1, 101.5-103 cm | CAMPANIAN | *G. elevata* | | | | | | | | | | | R | R |
| 13-2, 101.5-102.5 cm | SANTONIAN | *D. asymetrica* | | | | | R | R | | | | | R | R |
| 13-3, 78-92 cm | | | | | | | C | F | C | R | | C | F | F |
| 13-3, 100-102 cm | | | R | | C | | A | F | C | C | | C | C | C |
| 13-4, 100-101 cm | | | R | R | R | R | F | C | F | F | | | R | R |
| 14-1, 99-112 cm | | | F | R | C | C | A | F | C | R | | R | | |
| 14-1, 102-105 cm | | | F | R | F | C | A | A | F | | | F | R | |
| 15-1, 97-100 cm | | | A | F | R | R | F | | A | | | R | | |
| 15-2, 73-87 cm | | | F | C | R | F | | | A | A | R | | | |
| 15-2, 100.5-101.5 cm | | | A | C | R | R | | | R | R | A | R | | |
| 15-3, 101.5-102.5 cm | | | A | C | | C | | | F | F | A | R | | |
| 15-4, 99.5-100.5 cm | | | C | R | | R | | | R | F | F | | | |
| 15-6, 104-118 cm | | | F | R | | F | | | R | F | | | | |
| 16-1, 99.5-101 cm | | | R | | | R | | | R | | | | | |
| 16-2, 100.5-102.5 cm | | *D. concavata* | R | | | | | | | | | | | |
| 16-3, 97.5-99 cm | | | | | | | | | | | | | | |
| 16-4, 100.5-101.5 cm | CONIACIAN | | | | | | | | | | | | | |
| 16-5, 100.5-102 cm | | | | | | | | | | | | | | |
| 16-6, 99-100 cm | | | | | | | | | | | | | | |
| 17-1, 99.5-100.5 cm | | | | | | | | | | | | | | |
| 17-2, 101.5-102.5 cm | | | | | | | | | | | | | | |
| 17-3, 100-101 cm | upper TURONIAN | | | | | | | | | | | | | |
| 17-4, 102-103.5 cm | | *M. sigali* | | | | | | | | | | | | |
| 17-5, 99.5-100.5 cm | | | | | | | | | | | | | | |
| 17-6, 100-101 cm | | | | | | | | | | | | | | |

Figure 6. Geographic position of DSDP Site 95 (Yucatan outer shelf, offshore Mexico) (A) and stratigraphic distribution and relative abundance of selected planktic foraminiferal species in the upper Turonian-lowermost Campanian sediments at this site (B). Foraminiferal species relative abundances: R – rare (< 5 specimens/sample), C – common (6-10 specimens/sample), F – frequent (11-25 specimens/sample) and A – abundant (over 26 specimens/sample). Samples deposited in the OMC, NMNH are given with grey background.



**B**

| SAMPLES | STAGES | Planktic foraminiferal biozonation after Georgescu (2006) | Selected planktic foraminiferal species | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | *"Heterohelix" globulosa* | *Hendersonites carinata* | *Planoheterohelix planata* | *Texasina papula* | *Laeviheterohelix pulchra* | *Ventilabrella eggeri* | *V. glabrata* |
| 493.16 - 19 mbsf | lowermost CAMPANIAN | *G. arca* | F | R | | | | | |
| 493.47 - .50 mbsf | | | F | | R | | | | |
| 493.77 - 80 mbsf | | | C | R | R | | C | | |
| 494.08 - 11 mbsf | | | F | | | | F | | R |
| 494.38 - 41 mbsf | | | F | | R | | | | R |
| 494.81 - 84 mbsf | | | C | R | R | | F | | |
| 495.30 - 33 mbsf | | | A | R | R | | R | | R |
| 496.82 - 85 mbsf | | | A | | R | | | | R |
| 498.34 - 37 mbsf | | | A | R | | R | C | | R |
| 499.84 - 87 mbsf | | | A | | | | R | | |
| 501.39 - 42 mbsf | | | A | | | R | C | R | R |
| 504.44 - 47 mbsf | upper SANTONIAN | | A | | C | R | R | | R |
| 505.05 - 08 mbsf | | | A | | R | | C | R | C |
| 505.35 -38 mbsf | | | A | R | C | R | F | R | R |
| 505.63 - 66 mbsf | | | A | | R | | F | R | R |
| 505.93 - 96 mbsf | | | A | | | R | C | R | |
| 506.27 - 30 mbsf | | *D. concavata* | A | R | R | R | F | R | R |
| 506.57 - 60 mbsf | | | A | R | R | R | C | | |
| 506.88 - 91 mbsf | | | A | | R | | | | |
| 507.49 - 52 mbsf | | | F | | | R | R | | |
| 509.01 - 04 mbsf | | | F | | | | R | | |
| 510.54 - 57 mbsf | | not zoned | R | | | | | | |

Figure 7. Geographic position (A) and stratigraphic distribution and relative abundances of selected planktic foraminiferal species in the upper Santonian-lowermost Campanian sediments of the ODP Leg 174AX at Bass River Site (New Jersey coastal plain, USA) (B).

2006). Planktic foraminifera are abundant and well-preserved in the transgressive systems tracts Merchantville Formation (late Santonian) and Marshalltown Formation (late Campanian). A five-fold biostratigraphic framework for the late Santonian-Campanian based on planktic foraminifera was given by Georgescu (2006). Four heterohelicid species of interest for this study occur in this section in the sediments below the Santonian/Campanian boundary: *Texasina papula* (Belford,1960), *Ventilabrella eggeri* Cushman, 1928, *V. alpina* (de Klasz, 1953) and *V. glabrata* Cushman, 1928 (Fig. 7B).

### 3.3. DSDP Sites 356 and 357

The DSDP Sites 356 and 357 (western South Atlantic Ocean) were drilled in the São Paolo Plateau and Rio Grande Rise respectively (Fig. 8A). The sediments are dominantly carbonates and accumulated under outer shelf-upper bathyal environments. Preservation is poor to rarely good at these sites, with specimens frequently being affected by diagenesis (Fig. 8B) and for this reason this material was not considered suitable for a highly detailed taxonomic study. Planktic foraminiferal assemblages that were collected from a total of eight spot samples from the OMC (NMNH) are rich and diverse. Seven species with relevance for this study are identified: *Texasina austinana* (Cushman, 1938), *Planulitella sphenoides* (Masters, 1976), *P. stenopos* (Masters, 1976), *P. malocaucasica* (Aliyulla in Geodakchan & Aliyulla, 1959), *Sigalia incipiens* – new species, *V. eggeri* and *V. glabrata* (Fig. 8C). Nederbragt (1991) provided a planktic foraminiferal zonation for both sites and this framework is followed herein.

### 3.4. DSDP Site 511

DSDP Site 511 was drilled in the Falkland Plateau (South Atlantic Ocean) (Fig. 9A) and it intersected thick Cretaceous (Aptian-Campanian) shallow water sediments (Krasheninnikov & Basov, 1983; Huber *et al.*, 1995) accumulated under middle and outer shelf environments. Foraminiferal assemblages are generally well-preserved, which makes them ideal for the study of the test ultrastructure, ornamentation and porosity. Heterohelicid taxonomy and stratigraphical distribution was reviewed by Georgescu (2008, p. 159). *Texasina papula* is recorded from upper Santonian-lowermost Campanian sediments (Fig. 9B) of the *M. marginata* Biozone in the zonation by Huber (1992) and Huber *et al.* (1995).

### 3.5. Eureka 67-128 well

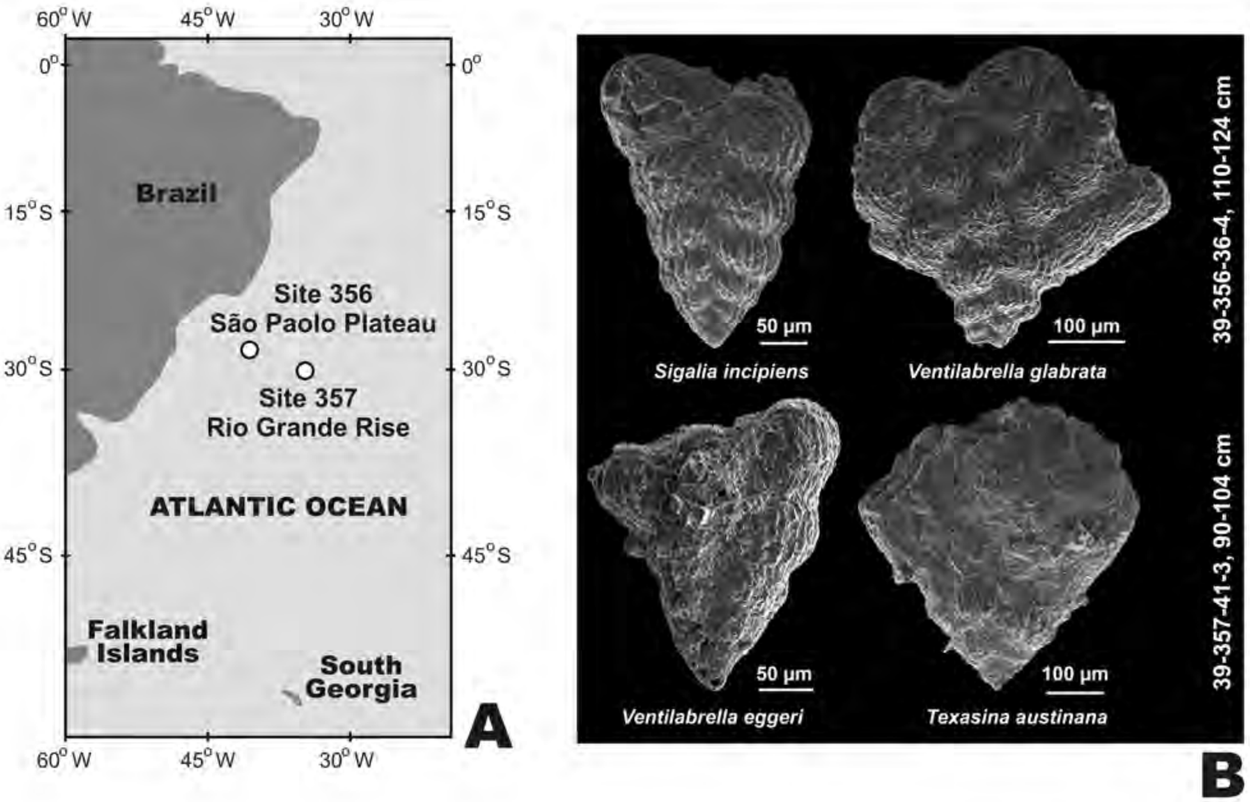
Eureka 67-128 well was drilled in the Gulf of Mexico (Fig. 10A), namely in the De Soto Canyon, at approximately 480 km from Tampa (Florida). Cretaceous stratigraphy was presented in detail by Dowsett (1984, p. 129-130) and is followed herein. Spot samples from the Santonian sediments were studied in the Van Morkhoven Collection (NMNH). Planktic foraminiferal assemblages preservation is good and very good. Fossil material was collected from six spot samples of late Santonian sediments (*D. asymetrica* Biozone). Nine species with relevance for this study were identified and studied with the aid of the SEM: *Planulitella sphenoides*, *P. stenopos*, *P. malocaucasica*, *Sigalia incipiens*, *S. deflaensis*, *S. proliferans* – new species, *Proliferania initialis*, *P. carpatica* and *P. decoratissima* (Fig. 10B).

### 3.6. Additional collection material

Additional collection material improved the database for this study. Topotype material of *Texasina papula*, from the lower Santonian sediments of northwest Australia, was put at my disposal by Dr Brian T. Huber (NMNH). The type material (holotype and paratypes) of *T. austinana*, *P. sphenoides*, *P. stenopos* and a paratype of *Proliferania decoratissima*, which are deposited in the Cushman Collection (NMNH), were analyzed and photographed under the ESEM. Very well preserved hypotypes of *T. austinana* from the Santonian Nanaimo Group from Denman Island, British Columbia, Canada, deposited in the McGugan Foraminifera Collection (University of Calgary, Calgary, Alberta, Canada) allowed detailed observations on the test ultrastructure of this species.

## 4. LINEAGE ARCHITECTURE

Evolutionary classification involves species grouping into lineages, based on the inferred direct ancestor-descendent relationships. Species grouping is based on both morphological resemblances and differences, the former being the result of ancestry relationships between them and the lat-

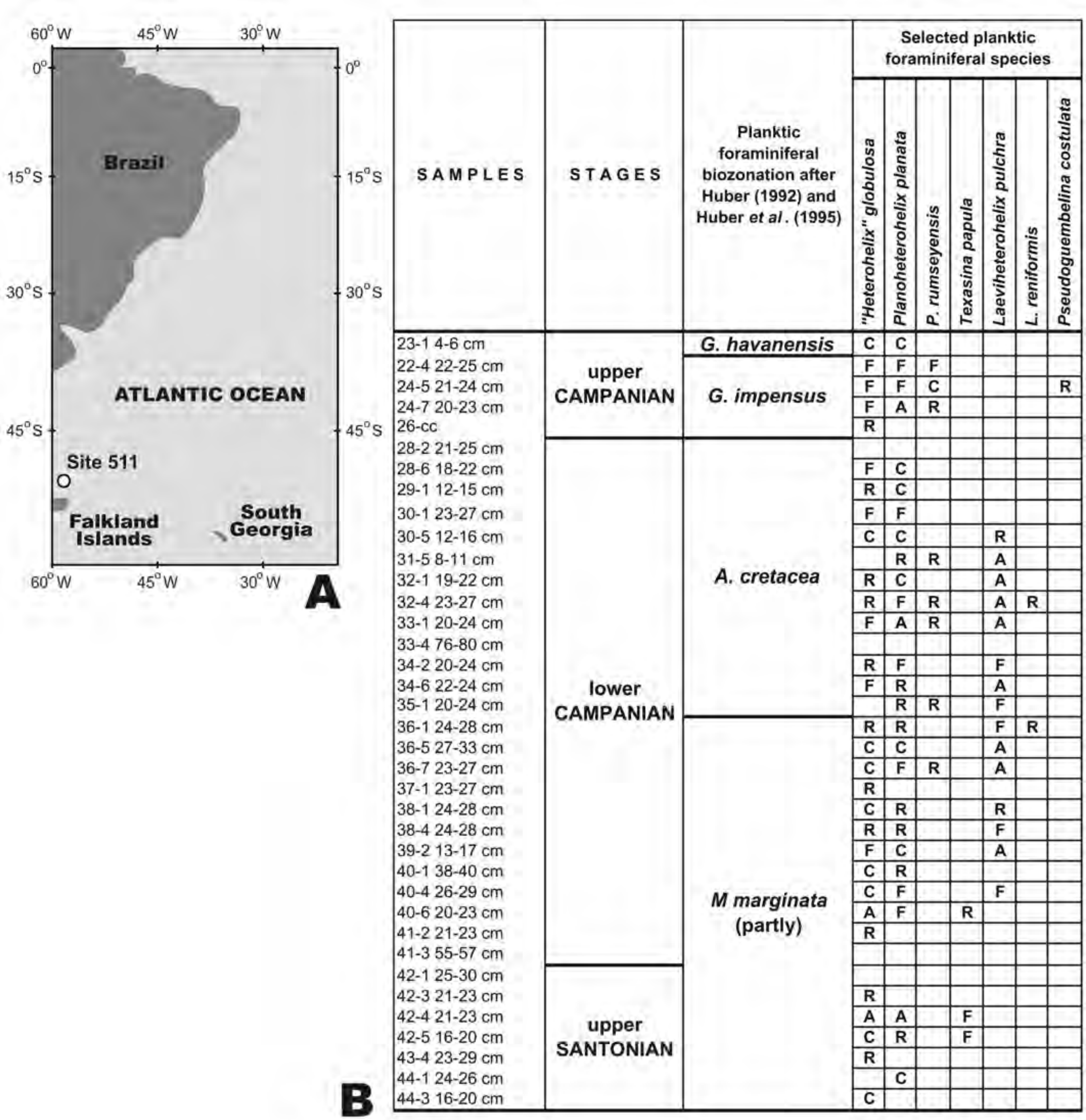


**C**

| SAMPLES | STAGE | Planktic foraminiferal biozonation after Nederbragt (1991) | Selected planktic foraminiferal species | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **DSDP Site 356** | | | *Planulitella sphenoides* | *P. stenopos* | *P. malocaucasica* | *Sigalia incipiens* | *Ventilabrella eggeri* | *V. alpina* | *V. glabrata* | *Texasina austinana* |
| 35-2, 130-144 cm | upper SANTONIAN | *D. asymetrica* | | | | | x | | | |
| 36-4, 110-124 cm | | | x | x | | x | x | | x | x |
| 36-5, 102-116 cm | | | x | | | x | x | | x | |
| 37-1, 82-96 cm | | | x | x | x | x | x | | | x |
| 37-5, 15-29 cm | | | x | | | | | | | |
| 39-5, 94-108 cm | | | x | | | | | | | |
| **DSDP Site 357** | | | | | | | | | | |
| 41-3, 98-114 cm | upper SANTONIAN | *D. asymetrica* | | | | | x | | | x |
| 43-4, 90-104 cm | | | | | | | x | | | |

Figure 8. Geographic position (A), preservation examples (B) and stratigraphic distribution and relative abundances of selected planktic foraminiferal species in the spot samples from the upper Santonian sediments of the DSDP Sites 356 and 357 (São Paolo Plateau and Rio Grande Rise) considered in this study (C).

ter by the changes resulted in the course of the evolutionary process. The lineage was defined as taxonomic in evolutionary classification by Georgescu (2009d) as follows: "…a taxonomic unit with significance in evolutionary classification, situated immediately above the species level, representing a grouping of species based on the monophyletic phylogenetical relationships between them, having a distinct evolutionary history in space and time that can be reconstructed from the fossil and stratigraphic record and separated by morphological gaps from other



| SAMPLES | STAGES | Planktic foraminiferal biozonation after Huber (1992) and Huber *et al*. (1995) | Selected planktic foraminiferal species | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | *"Heterohelix" globulosa* | *Planoheterohelix planata* | *P. rumseyensis* | *Texasina papula* | *Laeviheterohelix pulchra* | *L. reniformis* | *Pseudoguembelina costulata* |
| 23-1 4-6 cm | upper CAMPANIAN | *G. havanensis* | C | C | | | | | |
| 22-4 22-25 cm | | *G. impensus* | F | F | F | | | | |
| 24-5 21-24 cm | | | F | F | C | | | | R |
| 24-7 20-23 cm | | | F | A | R | | | | |
| 26-cc | | | R | | | | | | |
| 28-2 21-25 cm | lower CAMPANIAN | *A. cretacea* | | | | | | | |
| 28-6 18-22 cm | | | F | C | | | | | |
| 29-1 12-15 cm | | | R | C | | | | | |
| 30-1 23-27 cm | | | F | F | | | | | |
| 30-5 12-16 cm | | | C | C | | | R | | |
| 31-5 8-11 cm | | | | R | R | | A | | |
| 32-1 19-22 cm | | | R | C | | | A | | |
| 32-4 23-27 cm | | | R | F | R | | A | R | |
| 33-1 20-24 cm | | | F | A | R | | A | | |
| 33-4 76-80 cm | | | | | | | | | |
| 34-2 20-24 cm | | | R | F | | | F | | |
| 34-6 22-24 cm | | | F | R | | | A | | |
| 35-1 20-24 cm | | | | R | R | | F | | |
| 36-1 24-28 cm | | *M marginata* (partly) | R | R | | | F | R | |
| 36-5 27-33 cm | | | C | C | | | A | | |
| 36-7 23-27 cm | | | C | F | R | | A | | |
| 37-1 23-27 cm | | | R | | | | | | |
| 38-1 24-28 cm | | | C | R | | | R | | |
| 38-4 24-28 cm | | | R | R | | | F | | |
| 39-2 13-17 cm | | | F | C | | | A | | |
| 40-1 38-40 cm | | | C | R | | | | | |
| 40-4 26-29 cm | | | C | F | | | F | | |
| 40-6 20-23 cm | | | A | F | | R | | | |
| 41-2 21-23 cm | | | R | | | | | | |
| 41-3 55-57 cm | | | | | | | | | |
| 42-1 25-30 cm | upper SANTONIAN | | | | | | | | |
| 42-3 21-23 cm | | | R | | | | | | |
| 42-4 21-23 cm | | | A | A | | F | | | |
| 42-5 16-20 cm | | | C | R | | F | | | |
| 43-4 23-29 cm | | | R | | | | | | |
| 44-1 24-26 cm | | | | C | | | | | |
| 44-3 16-20 cm | | | C | | | | | | |

Figure 9. Geographic position (A) and stratigraphic distribution and relative abundances of selected planktic foraminiferal species in the upper Santonian-Campanian sediments of the DSDP Site 510 (Falkland Plateau) (B).

**B**

| SAMPLES (top samples only) | STAGES | Planktic foraminiferal biozonation | Selected planktic foraminiferal species | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *Planulitella sphenoides* | *P. stenopos* | *P. malocaucasina* | *Sigalia incipiens* | *S. deflaensis* | *S. proliferans* | *Proliferania initialis* | *P. carpatica* | *P. decoratissima* |
| 1658.11 mbsl | upper SANTONIAN | *D. asymetrica* | x | | | | | | | | |
| 1658.42 mbsl | | | x | | | | x | | | | |
| 1659.03 mbsl | | | x | x | | x | x | x | x | x | |
| 1659.94 mbsl | | | | | | x | | | | | |
| 1661.16 mbsl | | | x | | | x | | | | | |
| 1662.23 mbsl | | | | | | | | | | x | x |

Figure 10. Geographic position (A) and stratigraphic distribution and relative abundances of selected planktic foraminiferal species in the upper Santonian sediments of Eureka 67-128 well (Gulf of Mexico) (B).

similar units." Species grouping into lineages is a method that characterizes the evolutionary classification. It contrasts to the typological approach in classification, where species are grouped into genera based on their resemblances.

One of the major outcomes of this study is that it shows the situation is more complex and lineages can present different architecture. Two kinds of lineages are recognized according to the general relationship patterns between species: directional and branched (Fig. 11). Directional lineages (DL) and branched lineages (BL) are taxonomic units above the species level with significance in evolutionary classification, which details the more general category of lineage (Georgescu, 2009c). A directional lineage is characterized by the continuous evolution of two or more features in one direction and in a monophyletic-linear succession of species. In contrast, at least one feature shows divergent evolution in a branched lineage, resulting in a monophyletic-branched succession of species. The directional and branched lineages are units at the same taxonomic level in the evolutionary classification. General architecture pattern is herein included in the formal usage of the lineage (e.g., directional lineage, branched lineage). However, the term of *lineage* can retain its informal sense.

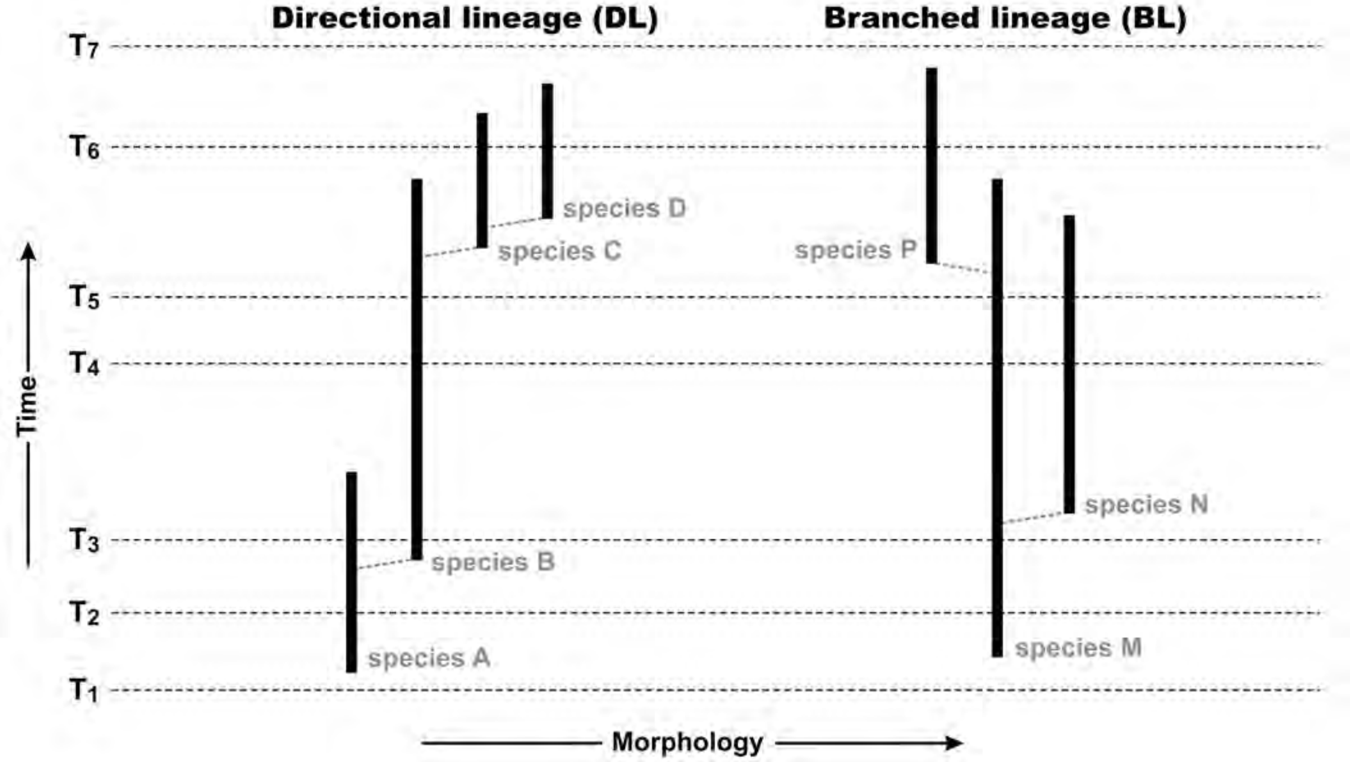


Figure 11. Diagram showing the directional and branched lineages architecture in the evolutionary continuum (morphology-time coordinates).

Species grouping in evolutionary classification strongly contrasts to that in the typological one (Fig. 12). The existence of two categories of supraspecific units at the same level is characteristic for the evolutionary classification. Additional kinds of lineages can be recognized as the process of development of the evolutionary classification framework advances. All these developments demonstrate that the differences between the evolutionary and typological classification are more than just semantic as considered by some authors (Loeblich & Tappan, 1974, p. 2).

## 5. SYSTEMATIC CLASSIFICATON

Higher systematic units are after Loeblich & Tappan (1987); these typological categories are given as no evolutionary classification framework above the directional lineage/branched lineage level is as yet developed. Lineages are presented in stratigraphic-evolutionary order. The concept of composite paleontological species developed by Georgescu & Huber (2007, 2009) is used throughout.

### Superfamily HETEROHELICACEA Cushman, 1927

### Family HETEROHELICIDAE Cushman, 1927

### Directional lineage ***Texasina*** – new

Type species: *Ventilabrella austinana* Cushman 1938, p. 26, pl. 4, fig. 19 (original designation).

*Description*.– Test consisting of chambers that are alternately added with respect to the test axis of growth resulting in biserial arrangement in the primitive species and with adult stage with multichamber growth in the evolved one. The adult stage begins with the biaperturate progressive chamber, which is followed by two to three sets of two chambers. Chambers are globular to subglobular, overlapping at various rates. Sutures are distinct and depressed between all the chambers of the test. Periphery is rounded and simple, without peripheral structures. Aperture is a medium high arch at the base of the last formed chamber, simple in the completely biserial tests and multiple in those with the adult flaring stage. Chambers ornamented with longitudinal leptocostae. Test wall calcitic, hyaline and perforate.

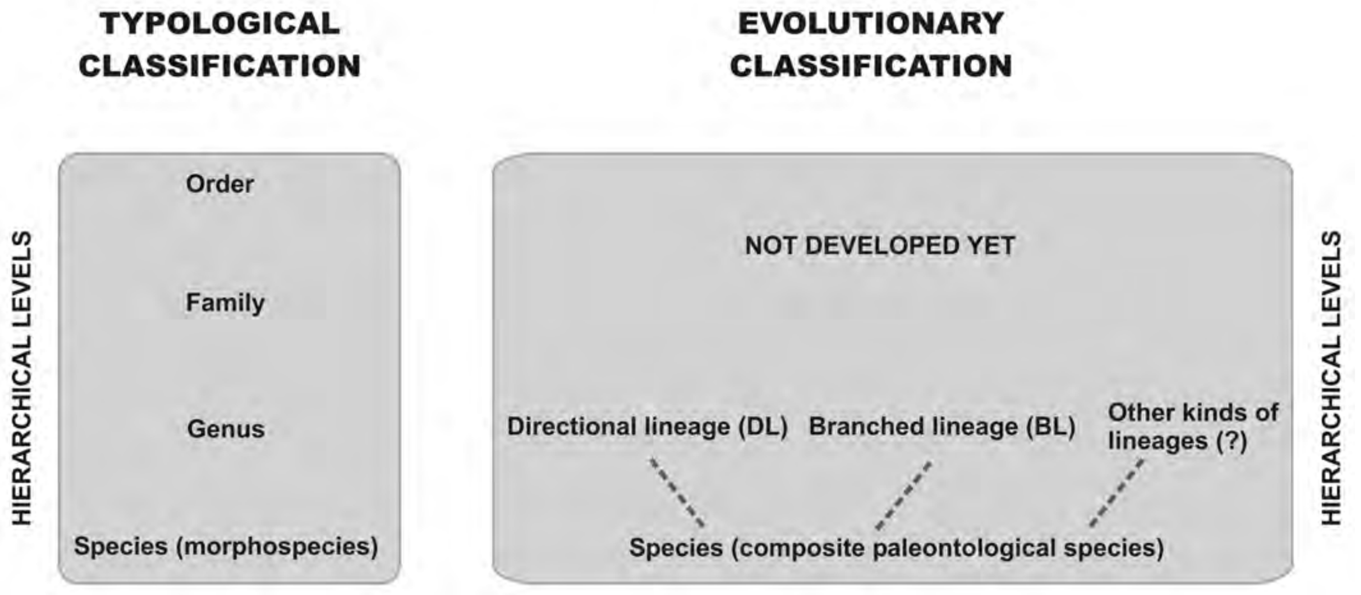


Figure 12. Diagram presenting the conceptual differences in taxa hierarchy between typological and evolutionary classifications. Note that species are grouped into units of a single kind (i.e., genera) in the former and in two (i.e., directional lineages, branched lineages) or possibly more in the latter.

*Remarks*.– *Texasina* accommodates a directional lineage in the Coniacian-early Campanian, which develops a multichamber growth adult stage. It differs from *Sigalia* and *Proliferania* mainly by (i) lacking sutures lined with calyptoridges and phaneroridges, (ii) having a simple periphery, without transverse keels and (iii) fewer chambers in the adult stage with multichamber growth when compared to the end members of either of the two directional lineages. *Texasina* evolved from the *"H." globulosa* group of species, as suggested by the (i) globular to subglobular chambers, (ii) periapertural structures consisting of narrow metaflanges and (iii) leptocostate ornamentation.

*Species included*.– *Texasina papula* (Belford, 1960) and *T. austinana* (Cushman, 1938).

*Etymology*.– Directional lineage named after the State of Texas (USA) where the type species was first reported.

*Stratigraphic range*.– Coniacian-early Campanian (from the *D. concavata* Biozone to the *G. elevata* Biozone).

*Geographic distribution*.– USA (Texas, Wyoming, Kansas, Nebraska, South Dakota, New Jersey), Canada (British Columbia), Europe (Germany), Central Asia (Azerbaijan), Australia, South Atlantic Ocean (Falkland Plateau) and East Indian Ocean (Exmouth Plateau) (Fig. 13).

### ***Texasina papula* (Belford, 1960)**

(Plate 1, Figures 1-8)

1960 *Gümbelina papula* Belford, p. 57, pl. 15, figs. 6-8, text-fig. 3:1-6.
1983 *Heterohelix papula* (Belford) – Belford, p. 15, pl. 5, figs. 20-21.
1983 *Heterohelix globulosa* (Ehrenberg). – Krasheninnikov & Basov, p. 807, pl. 12, fig. 12.
1983 *Heterohelix rumseyensis* Douglas. – Krasheninnikov & Basov, p. 807, pl. 12, figs. 4-5.
2000 *Heterohelix papula* (Belford). – Petrizzo, p. 498, fig. 11:4.
2001 *Heterohelix papula* (Belford). – Petrizzo, fig. 10:7.
2006 *Heterohelix papula* (Belford). – Georgescu, fig. 1:4.

*Material*.– Circa 100 specimens.

*Description*.– Test consists of 13-17 globular to subglobular chambers that are alternately added with respect to the test growth axis, resulting in biserial arrangement throughout and overlap at various rates; a biaperturate chamber can follow the biserial stage. Chambers increase gradually in size. Sutures distinct and depressed, straight to slightly curved and oblique to the test growth axis. Periphery broadly rounded, without peripheral structures (Pl. 1,

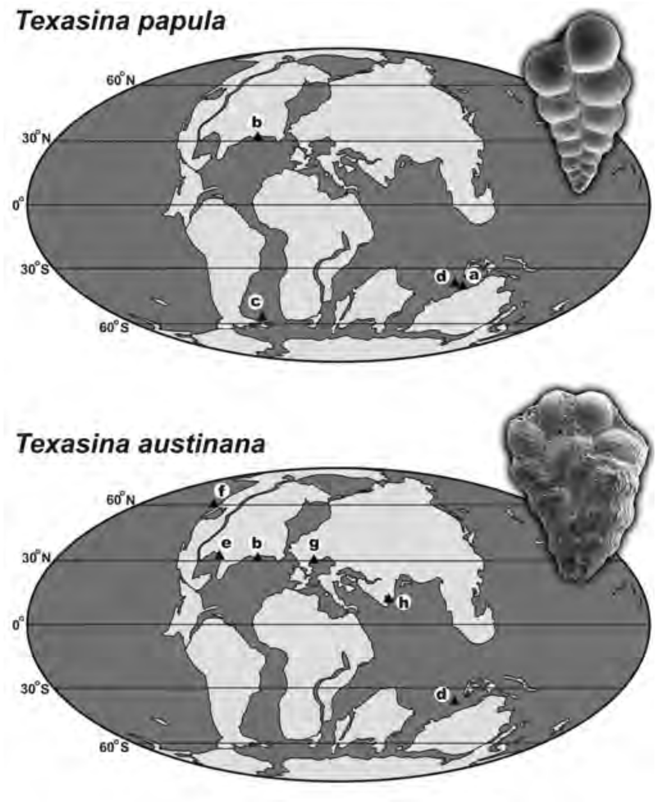


Figure 13. Paleobiogeographical distribution and occurrences of the species included in the new directional lineage *Texasina*. Letter significance: a – northwest Australia (Belford, 1960, 1983; this study), b – New Jersey coastal plain (Georgescu, 2006; this study), c – Falkland Plateau (Krasheninnikov & Basov, 1983; this study), d – Exmouth Plateau (Petrizzo, 2000, 2001), e – combined USA occurrences from Texas, Arkansas, Wyoming, Kansas, Nebraska, Missisippi and South Dakota (Carman, 1929; Loetterle, 1937; Cushman, 1938, 1946; Martin, 1972; Masters, 1977; Frerichs & Dring, 1981), f – British Columbia (this study), g – south Germany (Weidich, 1984) and h – Azerbaijan (Aliyulla, 1965). Base map after Hay *et al.* (1999), with modifications.

Figs. 1, 5, 7). Aperture is simple, a medium high arch at the base of the last formed chamber (Pl. 1, Figs. 1, 5, 7); two symmetrically developed narrow metaflanges border the aperture (Pl. 1, Figs. 2, 6). Chambers ornamented with fine (3.0-3.6 µm) and discontinuous leptocostae (Pl. 1, Figs. 3, 8). Test wall calcitic, hyaline and perforate (0.3-0.9 µm); pores simple, circular, situated in the space between the costae or, more rarely, penetrate through them (Pl. 1, Figs. 3, 8).

*Remarks*.– *Texasina papula* differs from *Planoheterohelix rumseyensis* (Douglas, 1969) by having (i) globular to subglobular chambers overlapping at various rates rather than subglobular to reniform chambers, (ii) higher rate of chamber increase in size and (iii) narrower metaflanges bordering the aperture. It differs from *Pseudotextularia nuttalli* (Voorwijk, 1937) mainly by having globular chambers rather than deeper than wide. Test gross morphology (i.e., globular chambers), ornamentation (i.e., fine and discontinuous costae) and test wall porosity characteristics (i.e., small sized pores with diameter of 0.3-0.9 µm) indicate that *T. papula* is phylogenetically related to "*H.*" *globulosa* group of species.

*Stratigraphic range*.– Coniacian-early Campanian (from the *D. concavata* Biozone to the *G. elevata* Biozone).

*Geographic distribution*.– Australia, USA (New Jersey), South Atlantic Ocean (Falkland Plateau) and East Indian Ocean (Exmouth Plateau) (Fig. 13).

### ***Texasina austinana* (Cushman, 1938)** – emended
(Plate 1, Figures 9-13)

1929 *Ventilabrella eggeri* (Cushman). – Carman, p. 314, pl. 34, fig. 7.
1937 *Ventilabrella eggeri* (Cushman). – Loetterle, p. 35, pl. 5, fig. 5.
1938 *Ventilabrella austinana* Cushman, p. 26, pl. 4, fig. 19.
1946 *Ventilabrella austinana* (Cushman). – Cushman, p. 111, pl. 47, fig. 16.
1965 *Planoglobulina transcaucasica* Aliyulla, p. 26, pl. 1, figs. 9-10.
1972 *Ventilabrella* (?) *austinana* (Cushman). – Martin, p. 84, pl. 1, figs. 1-2.
1977 *Ventilabrella austinana* (Cushman). – Masters, p. 389, pl. 6, fig. 5.
1981 *Ventilabrella austinana* (Cushman). – Frerichs & Dring, p. 68, pl. 1, figs. 15-16.
1984 *Ventilabrella* (?) *austinana* (Cushman). – Weidich, p. 80, pl. 1, fig. 19.
2000 *Ventilabrella eggeri* (Cushman). – Petrizzo, fig. 11:10.

*Material*.– 7 specimens.

*Description*.– Test with two distinct growth stages; earlier stage subtriangular, consists of 12-14 globular to subglobular chambers, which increase gradually in size and are alternately added with respect to the test growth axis; adult flaring stage with multichamber growth initiates with the biaperturate progressive chamber, which is followed by two to three sets of two chambers (Pl. 1, Figs. 9, 11). Sutures are distinct and depressed, straight to slightly curved; central suture in the biserial stage with well-developed indentations. Periphery is broadly rounded, without peripheral structures (Pl. 1, Figs. 10, 13). Aperture is simple in the early stage, a medium high arch at the base of the last formed chamber; multiple apertures occur in the adult stage. Two symmetrically developed metaflanges border the aperture. Chambers ornamented with fine (3.0-6.9 µm), discontinuous longitudinal leptocostae, which ocassionally are more prominent over the chambers of the earlier portion of the test. Test wall calcitic, hyaline and perforate (pore diameter 1.2-2.9 µm); pores simple, circular, situated between the leptocostae, ocassionally interrupting them.

*Remarks*.– *Texasina austinana* differs from its ancestor, *T. papula*, by having (i) an adult stage with multichamber growth, (ii) larger pores (1.2-2.9 µm rather than 0.3-0.9 µm) and (iii) wider leptocostae (3.0-6.9 µm rather than 3.0-3.6 µm). *Planoglobulina transcaucasica* (Aliyulla, 1965, p. 26) from the lower Coniacian of the Great Caucasus (Azerbaijan) exhibits strong morphological similarities to *T. austinana* in (i) shape and large-size of the biserial stage, (ii) adult stage with incipient multichamber growth and (iii) weak and uniformly distributed ornamentation.

*Stratigraphic range*.– Coniacian-Santonian (from the *D. concavata* Biozone to *D. asymetrica* Biozone).

*Geographic distribution*.– USA (Texas, Arkansas, Wyoming, Kansas, Nebraska, Missisippi, South Dakota, ? New Jersey), Canada (British Columbia), Europe (Germany), Central Asia (Azerbaijan) and East Indian Ocean (Exmouth Plateau) (Fig. 13).

### Branched lineage ***Planulitella*** – new

Type species: *Heterohelix sphenoides* Masters, 1976, p. 318, pl. 1, figs. 1-3 (original designation).

*Description*.– Test with chambers added alternately with respect to the test groth axis resulting in a biserial arrangement. Earlier chambers are globular, those of the adult stage petaloid, subrectangular or with antero-posterior elongation. Sutures are distinct and depressed, often hardly visible between earlier chambers of the test. Test compressed in edge view; periphery is simple, without peripheral structures. Aperture is a subcircular to subogival arch at the base of the last formed chamber. Chamber ornamentation consists of leptocostae; well-developed periapertural pustulose area. Test wall calcitic, hyaline and perforate.

*Remarks*.– *Planulitella* differs from *Protoheterohelix* Georgescu and Huber, 2009 (late Albian-early Turonian) mainly by having symmetrical tests and periapertural structures. It differs from *Planoheterohelix* (middle Cenomanian-lower Maastrichtian) by having compressed tests in edge view, larger pores (1.1-4.4 µm rather than 0.5-0.9 µm) and chambers ornamented with thicker leptocostae, which can be coarser over the earlier portion of the test. *Heterohelix* Ehrenberg, 1843 (early Turonian-Santonian) also presents slightly compressed tests but differs from *Planulitella* by having lateral tubulospine-like projections, smooth or finely striate tests and finer pores (0.4-0.8 µm rather than 1.1-4.4 µm).

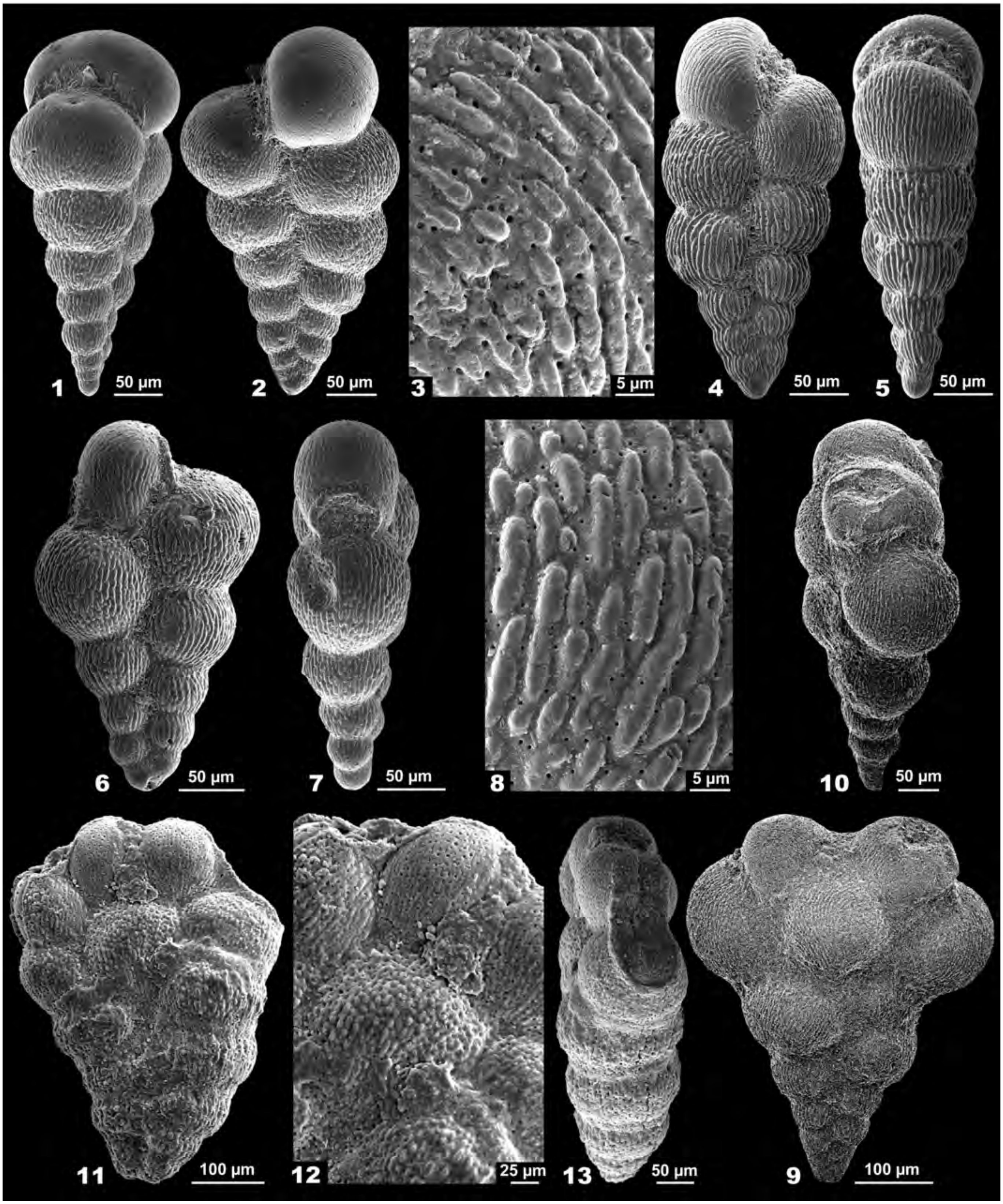
*Species included*.– *Planulitella sphenoides* (Masters, 1976), *P. stenopos* (Masters, 1976) and *P. malocaucasica* (Aliyulla in Geodakchan & Aliyulla, 1959).

*Etymology*.– Branched lineage name derived from the Latin prefix *plano*- (= plane) to which the suffix -*itella* is added; the reference is to the compressed tests in lateral view.

*Stratigraphic range*.– Santonian (from the uppermost part of *D. concavata* Biozone to *D. asymetrica* Biozone).

Plate 1. Specimens of *Texasina papula* (Belford, 1960) and *T. austinana* (Cushman, 1938). 1-3, Hypotype of *T. papula* from the upper Santonian (*Globotruncana arca* Biozone) sediments of ODP Leg 174AX at Bass River Site (New Jersey coastal plain), Sample 505.35-505.38 mbsf. 4-5, Hypotype of *T. papula* from the upper Santonian (*G. arca* Biozone) sediments of ODP Leg 174AX at Bass River Site (New Jersey coastal plain), Sample 505.35-505.38 mbsf. 6-8, Hypotype of *T. papula* from the upper Santonian (*G. arca* Biozone) sediments of ODP Leg 174AX at Bass River Site (New Jersey coastal plain), Sample 505.05-505.08 mbsf. 9-10, Holotype of *T. austinana* from the Gober Chalk of (Fannin County, Texas), originally figured by Cushman (1938, pl. 4, fig. 19) as *Ventilabrella austinana*; specimen deposited in the Cushman Collection (NMNH, USNM 24409). 11-13, Hypotype of *T. austinana* from the undivided Santonian sediments of the Nanaimo Group (British Columbia, Western Canada); specimen from the McGugan Collection (University of Calgary, Canada).

**Plate 1**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*Geographic distribution*.– Central Asia (Azerbaijan), USA (Alabama, Texas), Gulf of Mexico, Caribbean region (Yucatan outer shelf), western South Atlantic Ocean (São Paolo Plateau, Rio Grande Rise) and Africa (Nigeria, Tunisia) (Fig. 14).

### ***Planulitella sphenoides*** **(Masters, 1976)** – emended
(Plate 2, Figures 1-11)

1959 *Gümbelina conjakica* Geodakchan in Geodakchan & Aliyulla, p. 58, pl. 1, fig. 8 (only).
1976 *Heterohelix sphenoides* Masters, p. 318, pl. 1, figs. 1-3.
1977 *Heterohelix sphenoides* Masters. – Masters, p. 354, pl. 2, fig. 6, pl. 3, fig. 1.
1982 *Heterohelix calabarflanki* Oláníyí Odébòdé, p. 238, pl. 1, figs. 1-5.
(?) 1988 *Heterohelix conjakica* Geodakchan. – Aliyulla in Ali-Zade *et al.*, p. 127, pl. 24, fig. 4.
1991 *Heterohelix sphenoides* Masters. – Nederbragt, p. 248, pl. 4, fig. 6 (only).
1993 *Heterohelix sphenoides* Masters. – Nederbragt, pl. 1, figs. 3-5.
2006 *Heterohelix sphenoides* Masters. – Georgescu, fig. 4:15.

*Material*.– Circa 200 specimens.

*Emended description*.– Test with subtriangular outline, consisting of 10-13 chambers, which are alternately added with respect to the test growth axis resulting in a biserial arrangement and increase gradually in size at high rate; earlier chambers are globular, whereas those of the adult stage are petaloid. Sutures are depressed and oblique to the test growth axis, straight in the early portion of the test, often curved between the last formed chambers (Pl. 2, Figs. 3, 5, 8, 11); the central suture is almost straight in the early portion of the test and with shallow indentations in the adult part (Pl. 2, Figs. 2, 3, 5, 8, 11). Test shape is variable: earlier portion with inflated appearance, the adult one distinctly compressed (Pl. 2, Figs. 1, 7, 10). Aperture is a medium to high arch at the base of the last formed chamber. Two symmetrical metaflanges border the main aperture; ocassionally they can form a small accessory aperture on the previous chamber (Pl. 2, Figs. 2, 5, 6). Chamber surface ornamented with leptocostae, which are finer (3.1-4.8 μm) on the chamber sides and stronger (6.3-7.9 μm) in the peripheral region of the earlier portion of the test; well-developed periapertural pustulose area (Pl. 2, Figs. 1, 4, 7, 10). Test wall calcitic, hyaline and perforate; pores simple, with variable diameter (1.9-4.4 μm), situated between the leptocostae.

*Remarks*.– *Planulitella sphenoides* differs from *Planoheterohelix planata* (Cushman, 1938) by having (i) test composed of more chambers, (ii) higher rate of chamber size increase, (iii) compressed adult portion of the test in edge view, (iv) higher main aperture, (iv) an occasional accessory aperture in the adult portion of the test, (v) thicker costae and (vi) larger pores. It differs from *Planoheterohelix postmoremani* Georgescu & Huber, 2009 mainly by having (i) compressed tests, (ii) higher rate of chamber increase in size, (iii) periapertural structures consisting of metaflanges rather than orthoflanges, (iv) occasional occurrence of an accessory aperture in the proximity of the central suture in the adult portion of the test, (v) chamber ornamentation consisting of leptocostae rather than costae consisting of rows of pustules and (vi) coarsely perforate test wall. It is possible that *Guembelina conjakica* Geodakchan in Geodakchan & Aliyulla (1959) includes *P. sphenoides*. The two originally figured specimens of *G. conjakica* (op. cit., pl. 1, figs. 7, 8) are morphologically different and probably are not even congeneric and the lack of ornamentation details in the original description and illustration prevents a clear assignment to either *Planoheterohelix* Georgescu & Huber, 2009 or *Planulitella*. Moreover, there are contradictory data in the original report on the holotype, which is given as No. 404 in the text and No. 405 in the plate caption, which makes reassessment of the species taxonomic status impossible. *Heterohelix calabarflanki* Oláníyí Odébòdé, 1982 is morphologically identical to *P. sphenoides* and for this reason is considered the latter's junior synonym.

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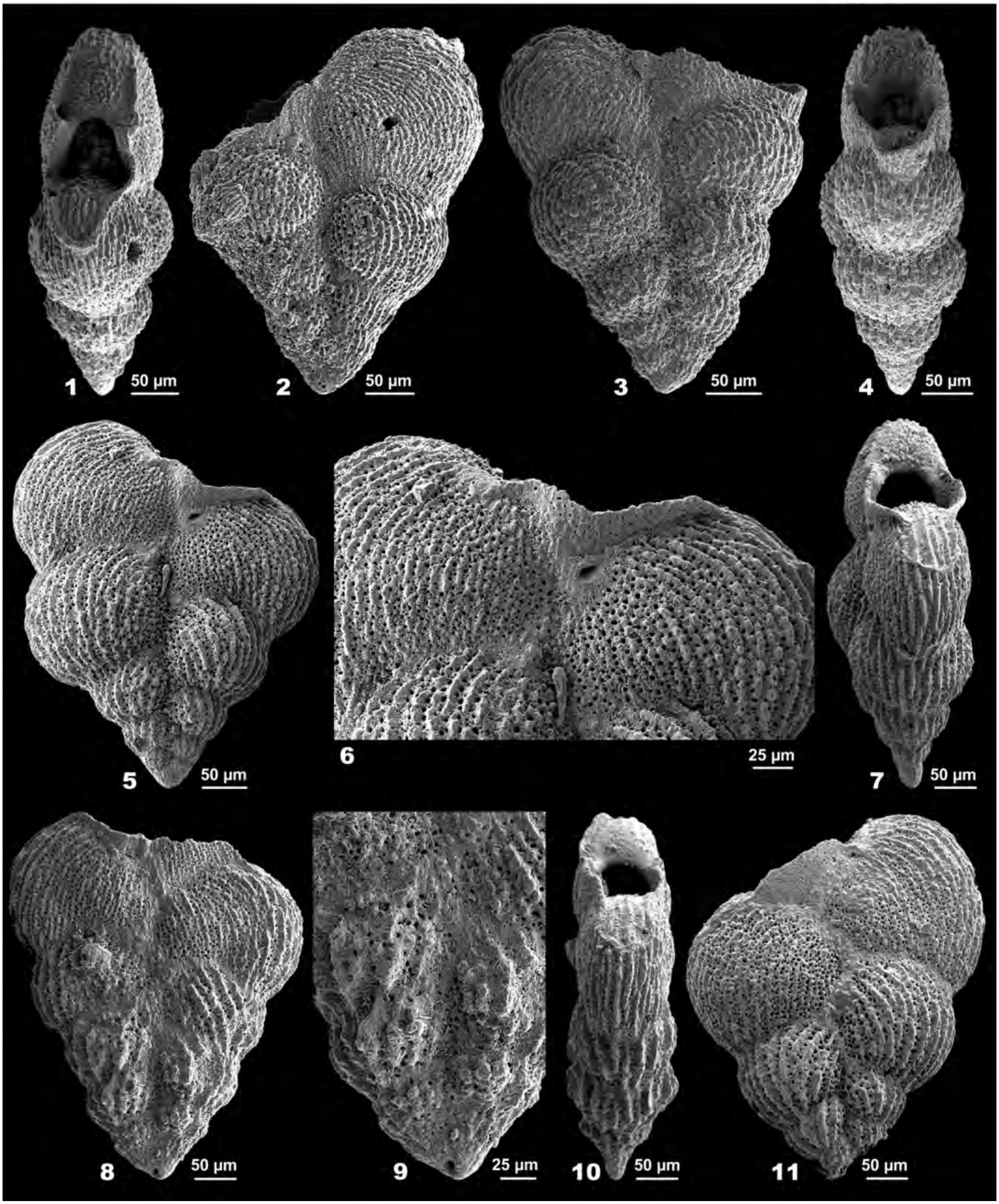
Plate 2. Specimens of *Planulitella sphenoides* (Masters, 1976). 1-2, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 99-112 cm. 3-4 Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 99-112 cm. 5-7, Specimen from the upper Santonian (*D. asymetrica* Biozone) sediments of the Eureka 67-128 well (Gulf of Mexico), Sample top 1659.03 mbsl. 8-10, Specimen from the upper Santonian (*D. asymetrica* Biozone) sediments of the Eureka 67-128 well (Gulf of Mexico), Sample top 1659.03 mbsl. 11, Specimen from the upper Santonian (*D. asymetrica* Biozone) sediments of the Eureka 67-128 well (Gulf of Mexico), Sample top at 1659.03 mbsl.

**Plate 2**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*Stratigraphic range*.– Santonian (from the uppermost part of *D. concavata* Biozone to *D. asymetrica* Biozone).

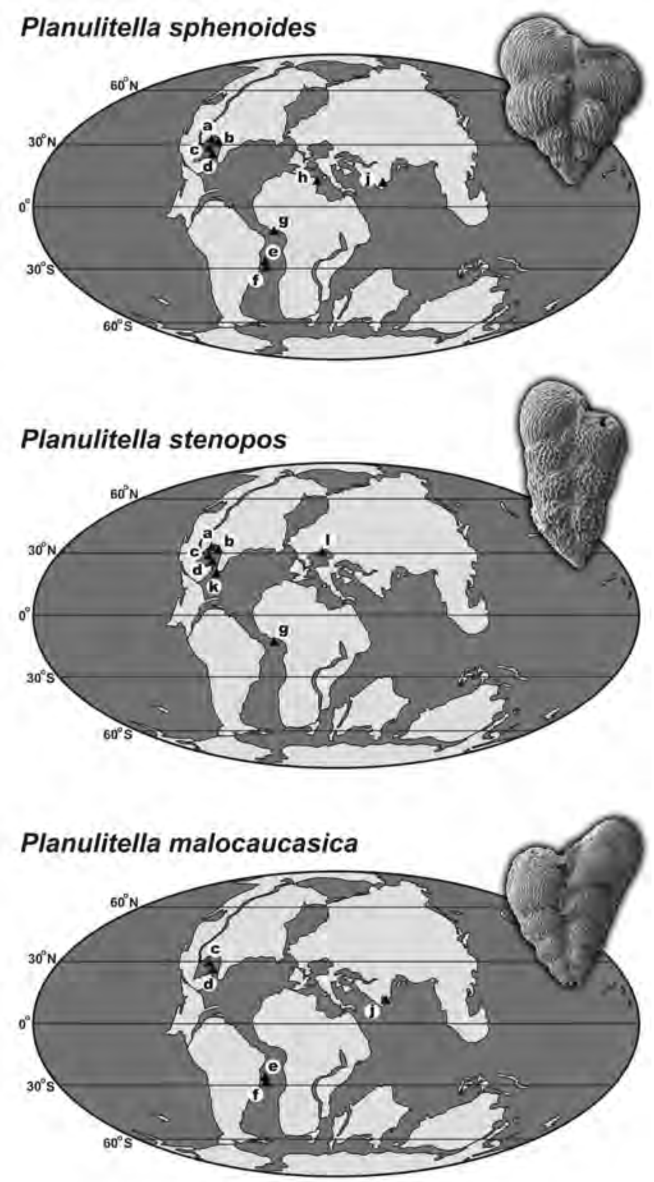
*Geographic distribution*.– USA (Alabama, Texas), Gulf of Mexico, Caribbean region (Jamaica, Yucatan outer shelf), western South Atlantic Ocean (São Paolo Plateau, Rio Grande Rise), Central Asia (Azerbaijan) and Africa (Nigeria, Tunisia) (Fig. 14).

***Planulitella stenopos* (Masters, 1976)** – emended
(Plate 3, Figures 1-4)

1962 *Sigalia deflaensis* (Sigal). – Samuel, p. 194, 13, fig. 3.
1969 *Gublerina deflaensis* (Sigal). – Esker, p. 213, pl. 2, figs. 4-5.
1976 *Heterohelix stenopos* Masters, p. 319, pl. 1, figs. 4-5.
1977 *Heterohelix stenopos* Masters. – Masters, p. 354, pl. 3, fig. 4.
1982 *Heterohelix* sp. 2. – Oláníyí Odébòdé, p. 244, pl. 3, fig. 4.

*Material*.– Circa 150 specimens.

*Emended description*.– Test with subtriangular outline, consisting of 11-15 chambers, which are added alternately with respect to the test growth axis resulting in biserial arrangement and increase in size at various rates; earlier chambers increase at high rate, the last seven or eight at a low rate resulting in nearly parallel sides in lateral view (Pl. 3, Figs. 1, 3). Earlier chambers are globular, most of those in the adult portion subrectangular, except for the last one, which is petaloid. Sutures are distinct, straight and depressed, oblique to the test axis of growth; central suture almost straight in the early portion and with shallow indentations between the last formed seven to eight chambers (Pl. 3, Figs. 1, 3). Test periphery is simple, without periapertural structures (Pl. 3, Figs. 2, 4). Aperture is a medium high arch at the base of the last formed chamber; two symmetrically developed metaflanges border the aperture. Chamber ornamentation consists of leptocostae (3.9-6.3 µm), which are thicker over the earlier portion of the test; well-developed periapertural pustulose area (Pl. 3, Figs. 2, 4). Test wall calcitic, hyaline, perforate (1.9-3.6 µm); pores simple, situated between the leptocostate.


*Planulitella sphenoides*

*Planulitella stenopos*

*Planulitella malocaucasica*

Figure 14. Paleobiogeographical distribution and occurrences of the species included in the new branched lineage *Planulitella*. Letter significance: a – Texas (Masters, 1977), b – Alabama (Masters, 1976), c – Gulf of Mexico (this study), d – Yucatan outer shelf (this study), e – São Paolo Plateau (this study), f – Rio Grande Rise (this study), g – Nigeria (Oláníyí Odébòdé, 1982), h – Tunisia (Nederbragt, 1991), j – Azerbaijan (Geodakchan & Aliyulla, 1959; Ali-Zade *et al.*, 1988), k – Jamaica (Esker, 1969) and l – Slovakia (Samuel, 1962).

*Remarks*.– *Planulitella stenopos* differs from *P. sphenoides* by having a low rate of chamber size increase in the adult portion of the test. It differs from *Planoheterohelix planata* by having (i) variable rate of chamber increase in size resulting in two distinct portions of the test, (ii) chamber ornamented with thicker costae (3.9-6.3 µm rather than

1.8-2.5 µm) and (iii) larger pores (1.9-3.6 µm as compared to 0.6-0.8 µm).

*Stratigraphic range*.– Santonian (*D. asymetrica* Biozone).

*Geographic distribution*.– USA (Alabama, Texas), Gulf of Mexico, Caribbean region (Jamaica, Yucatan outer shelf), Europe (Slovakia), Central Asia (Azerbaijan) and Africa (Nigeria) (Fig. 14).

### ***Planulitella malocaucasic*a (Aliyulla in Geodakchan & Aliyulla, 1959)** – emended

(Plate 3, Figures 5-14)

1959 *Gümbelina malocaucasica* Aliyulla in Geodakchan & Aliyulla, p. 59, pl. 1, fig. 9.

*Material*.– Circa 70 specimens.

*Emended description*.– Test with subtriangular outline, consisting of 11-14 chambers; chambers increase gradually and rapidly in size and are alternately added with respect to the test growth axis resulting in biserial arrangement. Chambers increase in size at a high rate; earlier chambers are globular, those of the adult stage with antero-posterior elongation, resulting in an elongate-petaloid appearance (Pl. 3, Figs. 5, 9, 10, 12, 14). Sutures are distinct, depressed and straight between the earlier chambers and curved between those of the adult stage, with the curvature oriented towards the anterior part (Pl. 3, Figs. 9, 10, 12, 14); central suture is nearly straight, with shallow indentations that are more prominent in the adult portion of the test. Test compressed in edge view, with subrectangular last chamber (Pl. 3, Figs. 6, 8, 11, 13); periphery simple, without peripheral structures. Aperture is a high subogival arch at the base of the last formed chamber (Pl. 3, Figs. 5, 9, 10, 12, 14); two symmetrical metaflanges border the aperture, ocassionally with a small accessory aperture in the proximity of the central suture (Pl. 3, Fig. 14). Chamber surface is ornamented with leptocostae (4.5-6.2 µm), which are often thicker at periphery and/or the earlier portion of the tests; well-developed pustulose periapertural area (Pl. 3, figs. 2, 4, 6-8, 11, 13). Test wall calcitic, hyaline, perforate (1.1-4.0 µm), with simple pores situated between the leptocostae.

*Remarks*.– *Planulitella malocaucasica* differs from *P. sphenoides* only in the morphology of the adult portion of the test, which has chambers with antero-posterior elongation; the earlier stages of the two species are similar, demonstrating the phylogenetic relationship between them. It differs from *P. stenopos* by (i) constant higher rate of chamber increase in size and (ii) curved sutures between the chambers in the adult portion of the test.

*Stratigraphic range*.– Santonian (*D. asymetrica* Biozone).

*Geographic distribution*.– Central Asia (Azerbaijan), Gulf of Mexico, Caribbean region (Yucatan outer shelf) and western South Atlantic Ocean (São Paolo Plateau, Rio Grande Rise) (Fig. 14).

### Directional lineage ***Sigalia* Reiss, 1957** – emended

Type species: *Gümbelina* (*Gümbelina, Ventilabrella*) *deflaensis* Sigal 1952, p. 36, text-fig. 41 (original designation).

1957 *Sigalia* Reiss, p. 243.
partly 1987 *Sigalia* Reiss, 1957. – Loeblich & Tappan, p. 457.
partly 1991 *Sigalia* Reiss, 1957. – Nederbragt, p. 368.

*Emended description*.– Test with biserial chamber arrangement throughout in the primitive species. Evolved species with a flaring multichamber growth adult stage, which initiates with the biaperturate progressive chamber and continues with four to nine sets of up to four chambers each, characterized by irregular chamber increase or reduction in number between successive sets and without a constant pattern throughout the adult stage. Sutures depressed or with calyptoridges in the primitive species and well-developed phaneroridges in the evolved ones. Test compressed in edge view. Periphery is simple in the primitive species and with parallel transverse keels across the periphery in the evolved ones. Aperture is a simple, low to medium high arch in the biserial species and multiple in the tests with multichamber growth adult stage. Chambers ornamented with leptocostae tending to concentrate in the peripheral regions and are often absent in the evolved species; well-developed periapertural pustulose area. Test wall is calcitic, hyaline and perforate.

*Remarks*.– *Sigalia* is emended in the context of evolutionary classification to accommodate a directional lineage characterized by (i) development of calcareous structures over the sutures (i.e., calyptoridges and phaneroridges), (ii) development of an adult stage characterized by multichamber growth and (iii) gradual reduction of leptocostae over the chamber surface. *Sigalia* differs from *Planulitella* by (i) development of adult stage with multichamber growth, (ii) sutures lined with calyptoridges and phaneroridges, (iii) periphery with parallel transverse keels and (iv) reduced and often absent leptocostate ornamentation on the lateral chamber sides. *Lipsonia* Georgescu & Abramovich, 2008a of the upper Maastrichtian sediments differs from *Sigalia*–emended mainly by (i) lacking completely the costate ornamentation and (ii) occurrence of vuggy pores over the chambers in the middle part of the test.

*Species included*.– *Sigalia incipiens* – new species, *S. deflaensis* (Sigal, 1952) and *S. proliferans* – new species.

*Stratigraphic range*.– Santonian (*D. asymetrica* Biozone).

*Geographic distribution*.– Northern Africa (Algeria, Tunisia), Middle East (Iraq, Israel), Central Asia (Azerbaijan), Europe (Germany, Slovakia, Spain), USA (Alabama, Mississippi), Caribbean region (Yucatan outer shelf), Gulf of Mexico and western South Atlantic Ocean (São Paolo Plateau, Rio Grande Rise) (Fig. 15).

### ***Sigalia incipiens*** – new species
(Plate 4, Figures 1-12)

1963 *Sigalia deflaensis* (Sigal). – Salaj & Samuel, p. 105, fig. 1.
1975 *Sigalia deflaensis* (Sigal). – Darmoian, p. 201, pl. 4, figs. 10-12.
1981 *Sigalia deflaensis* (Sigal). – Butt, pl. 17, fig. A.
1987 *Sigalia deflaensis* (Sigal). – Almogi-Labin in Honigstein *et al.*, pl. 3, figs. 1-3.
1993 *Heterohelix sphenoides* Masters. – Nederbragt, pl. 1, figs. 1-2.

*Holotype*.– WKB 010048.

*Dimensions of the holotype*.– Length: L = 0. 406 mm; width: W = 0.277 mm; W/L = 0.682; thickness: T = 0.119 mm; T/L = 0.293; apical angle: A = 45º.

*Paratypes*.– Five specimens, WKB 010049-010053,

*Dimensions*.– L = 0.267-0.458 mm; W = 0.190-0.347 mm; W/L = 0.680-0.787; T = 0.082-0.130 mm; T/L = 0.275-0.307; A = 44-57º (based on average measurements of 11 specimens: holotype, five paratypes and five topotypes).

*Type locality*.– DSDP Site 95, Yucatan outer shelf; geographical coordinates: 24º 09.00′ N and 86º 23.85′ W.

*Type level*.– Sample 10-95-14-1, 102-105 cm (upper Santonian, *D. asymetrica* Biozone).

*Material*.– Circa 100 specimens.

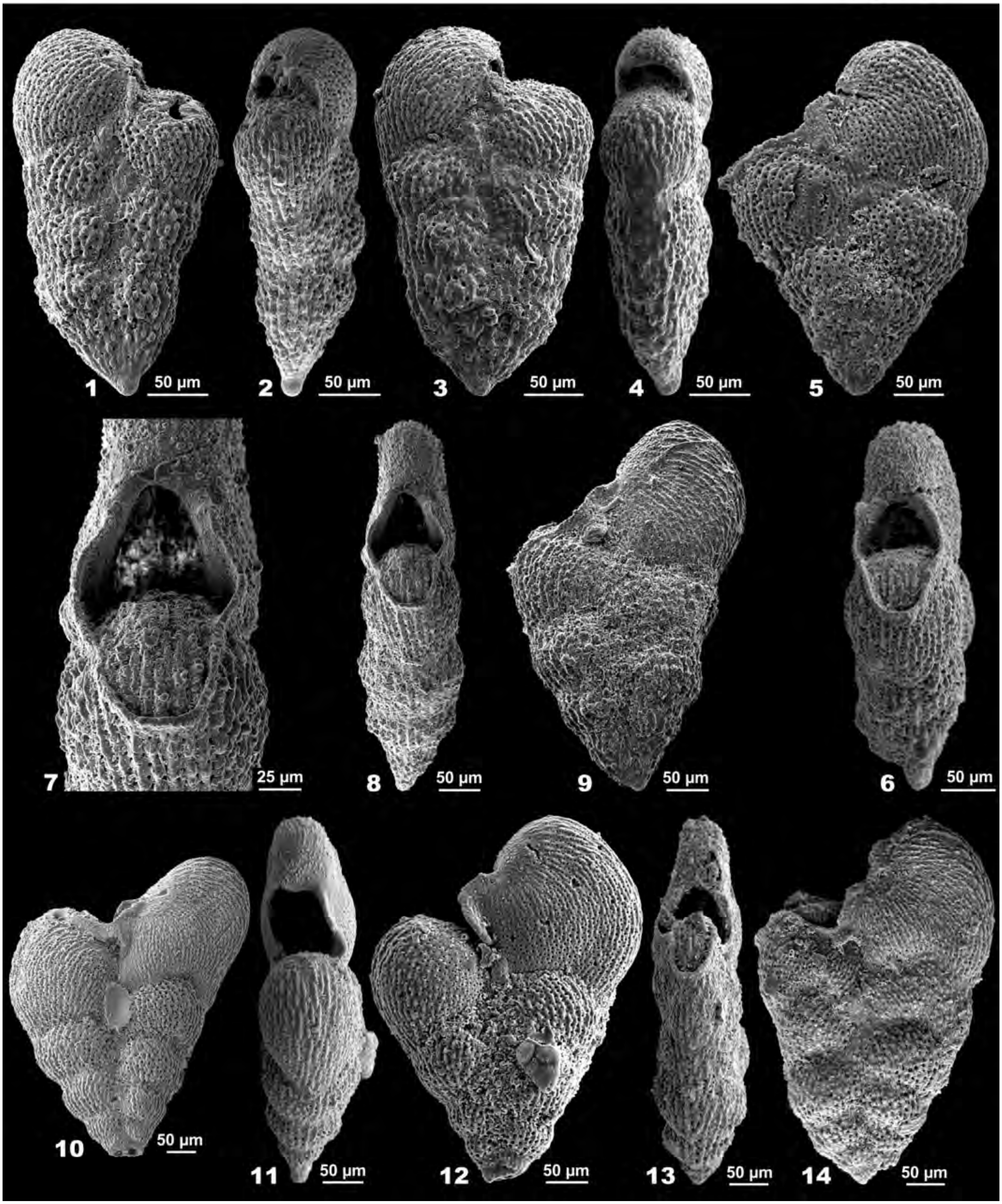
*Etymology*.– Name derived from the Latin verb *incipere* (= to begin), suggesting it is the oldest species of the *Sigalia* directional lineage.

*Diagnosis*.– *Sigalia* with biserial chamber arrangement throughout and calyptoridges.

*Description*.– Test with subtriangular outline, consisting of 13-15 chambers that gradually increase in size. Chambers are alternately added with respect to the test axis of growth resulting in a biserial arrangement; variable rate of chamber increase in size. Earlier chambers globular, those of the adult stage are subrectangular to petaloid. Sutures are distinct and depressed, straight to slightly oblique to the test growth axis; central suture nearly straight to distinctly indented; indentations are more prominent in the specimens with higher rate of chamber size increase (Pl. 4, Figs. 9, 12). Calyptoridges may be developed in the

Plate 3. Specimens of *Planulitella stenopos* (Masters, 1976) and *P. malocaucasica* (Aliyulla, in Geodakchan & Aliyulla, 1959). 1-2, Hypotype of *P. stenopos* from the upper Santonian (*D. asymetrica* Biozone) sediments of Eureka 67-128 well (Gulf of Mexico), Sample top at 1659.03 mbsl. 3-4, Hypotype of *P. stenopos* from the upper Santonian (*D. asymetrica* Biozone) sediments of Eureka 67-128 well (Gulf of Mexico), Sample top at 1659.03 mbsl. 5-6, Hypotype of *P. malocaucasica* from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 99-112 cm. 7-9, Hypotype of *P. malocaucasica* from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 99-112 cm. 10, Hypotype of *P. malocaucasica* from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 99-112 cm. 11-12, Hypotype of *P. malocaucasica* from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 102-105 cm. 13-14, Hypotype of *P. malocaucasica* from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 102-105 cm.

**Plate 3**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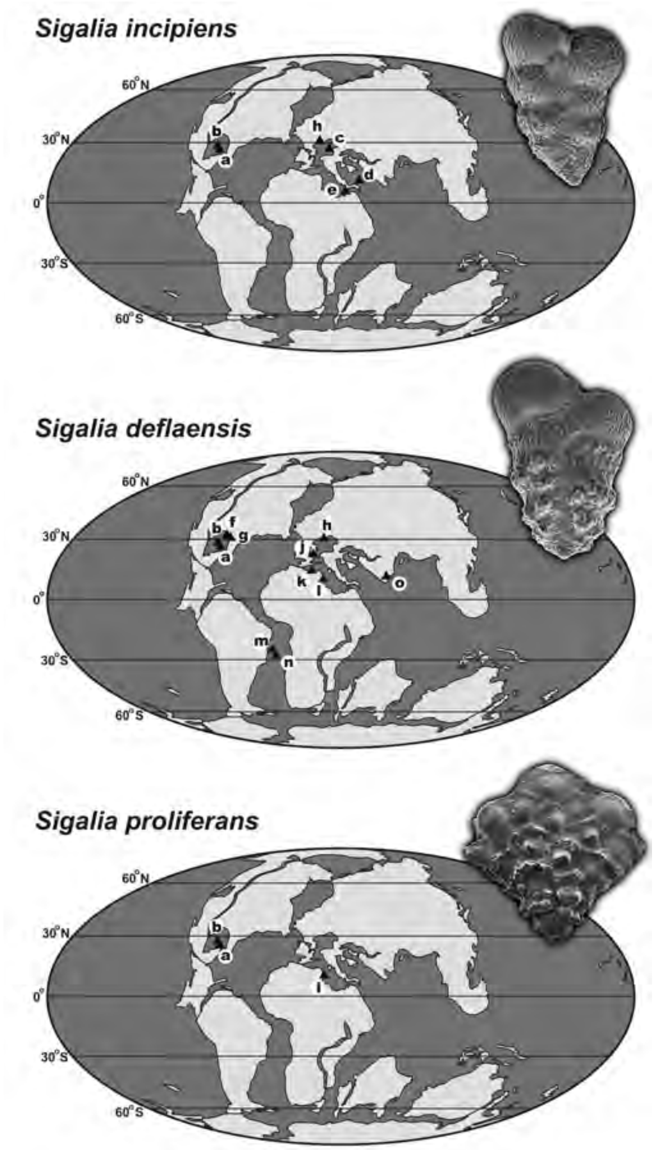


Figure 15. Paleobiogeographical distribution and occurrences of the species included in the directional lineage *Sigalia*. Letter significance: a – Yucatan outer shelf (Georgescu & Almogi-Labin, 2008; this study), b – Gulf of Mexico (Dowsett, 1984; this study), c – Slovakia (Salaj & Samuel, 1963), d – Iraq (Darmoian, 1975), e – Israel (Almogi-Labin in Honigstein et al., 1987), f – Alabama (Dowsett, 1989), g – Missisippi (Dowsett, 1989), h – Germany (Bettenstaedt & Wicher, 1956; Wicher & Bettenstaedt, 1957; Butt, 1981), j – Spain (Lamolda *et al.*, 2007), k – Algeria (Sigal, 1952), l – Tunisia (Nederbragt, 1991), m – São Paolo Plateau (this study), n – Rio Grande Rise (this study) and o – Azerbaijan (Aliyulla, 1977).

central portion of the test (Pl. 4, Figs. 9, 12). Test compressed in edge view; periphery is simple and rounded, without peripheral structures (Pl. 4, Figs. 4, 8, 10, 11). Aperture is a low to medium high arch at the base of the last formed chamber; two symmetrically developed metaflanges border the aperture, ocassionally developing a small accessory aperture in the proximity of the central suture (Pl. 4, Figs. 1, 3). Chambers ornamented with leptocostae (3.4-9.9 µm), which may be more prominent in the peripheral region or over the earlier portion of the test; well-developed periapertural pustulose area (Pl. 4, Figs. 4, 8, 10, 11). Test wall calcitic, hyaline and perforate (1.2-3.8 µm); pores simple, situated in the space between the leptocostae.

*Remarks*.– *Sigalia incipiens* differs from *Planulitella sphenoides*, its ancestor, by having (i) test composed of more chambers (13-15 rather than 10-13), (ii) lower rate of chamber size increase in the adult part and (iii) ocassionally developed calyptoridges in the central portion of the test. It differs from *P. stenopos* by (i) having constant rate of chamber size increase and (ii) having ocassionally developed calyptoridges. The two specimens figured in Honigstein *et al.* (1987) present calyptoridges on the earlier chambers of the test and are probably transitional to *S. deflaensis*.

*Stratigraphic range*.– Santonian (*D. asymetrica* Biozone).

*Geographic distribution*.– Caribbean region (Yucatan outer shelf), Gulf of Mexico, Europe (Slovakia) and the Middle East (Iraq, Israel) (Fig. 15).

### ***Sigalia deflaensis* (Sigal, 1952)** – emended
(Plate 5, Figures 1-12; Plate 6, Figures 1-9)

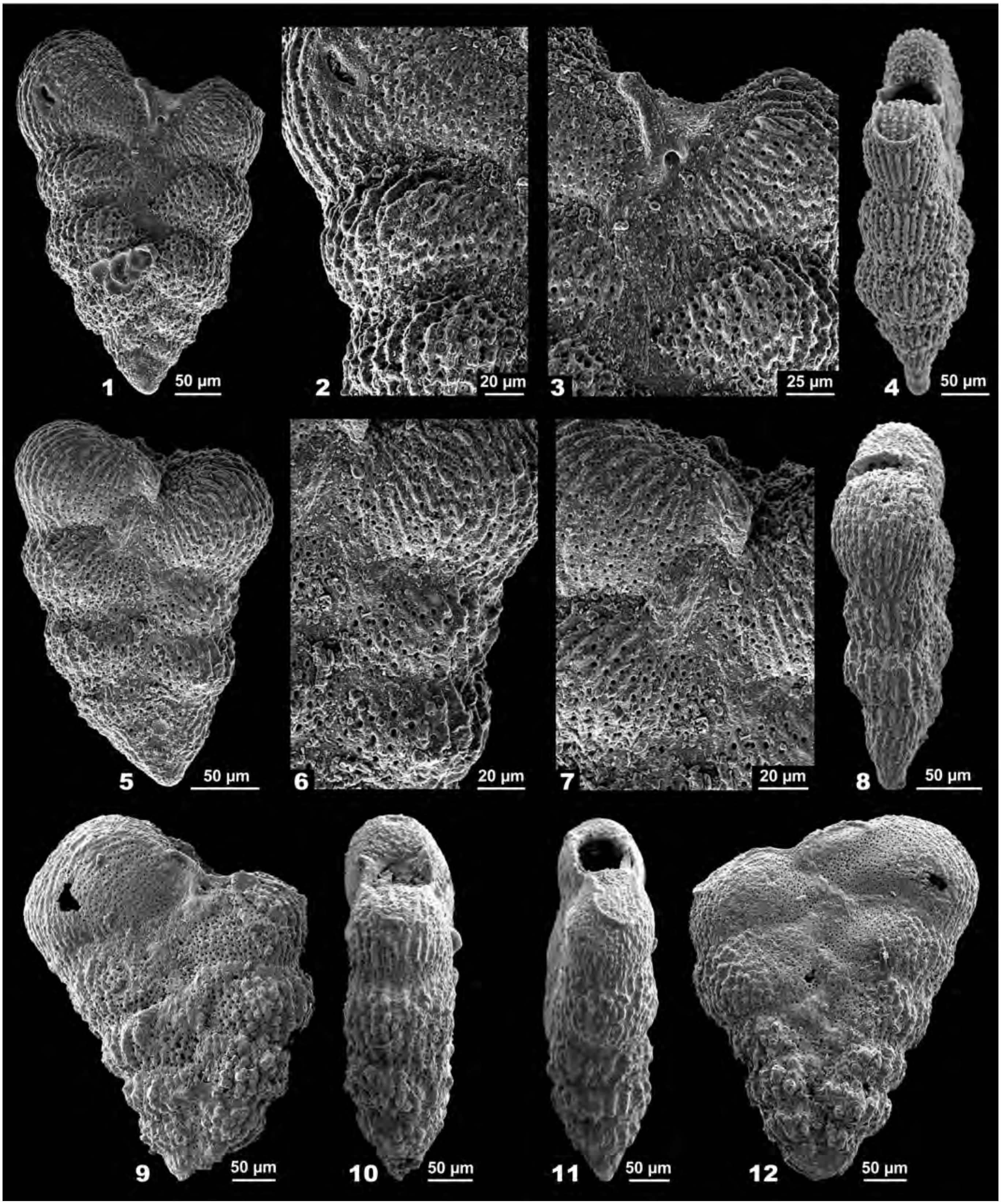
1952 *Gümbelina* (*Gümbelina, Ventilabrella*) *deflaensis* Sigal, p. 36, text-fig. 41.

1956 *Ventilabrella deflaensis* (Sigal). – Bettenstaedt & Wicher, p. 503, pl. 1, fig. 1.

1957 *Ventilabrella deflaensis* (Sigal). – Wicher & Bettenstaedt, fig. 2a.

Plate 4. Specimens of *Sigalia incipiens* – new species. 1-4, Holotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 102-105 cm. 5-8, Topotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-6, 104-118 cm. 9-10, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of Eureka 67-128 well (Gulf of Mexico), Sample top at 1659.94 mbsl. 11-12, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of Eureka 67-128 well (Gulf of Mexico), Sample top at 1659.94 mbsl.

**Plate 4**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(?) 1965 *Gublerina primitiva* Aliyulla, pl. 225, pl. 1, figs. 6-8.
1977 *Gublerina primitiva* Aliyulla. – Aliyulla, pl. 2, fig. 3.
1981 *Sigalia deflaensis* (Sigal). – Butt, pl. 17, fig. A1.
1984 *Sigalia deflaensis* (Sigal). – Weidich, p. 80, pl. 2, figs. 1-4.
1989 *Sigalia deflaensis* (Sigal). – Dowsett, p. 16, pl. 2, fig. 6.
1991 *Sigalia deflaensis deflaensis* (Sigal). – Nederbragt, p. 368, pl. 11, fig. 5.
1991 *Sigalia deflaensis rugocostata* Nederbragt, p. 369, pl. 12, figs. 1-2, 4 (only).
1993 *Sigalia deflaensis* (Sigal). – Nederbragt, pl. 1, figs. 12-14, pl. 2, figs. 1-2.
2007 *Sigalia deflaensis* (Sigal). – Lamolda *et al.*, p. 28, fig. 4: Q1-2, R1-2.
2008 *Sigalia deflaensis* (Sigal). – Georgescu & Almogi-Labin, figs. 4: 7-8, 6: 2-3.

*Material*.– Circa 250 specimens.

*Emended description*.– Tests with subtriangular to subpentagonal outline, exhibiting one or two growth stages, which results in significant morphological variability. Earlier stage consists of 12-15 chambers alternately added with respect to the test axis of growth resulting in a biserial arrangement; over 85% of the tests of this species are entirely biserial. A second growth stage, with multichamber growth, is developed in some individuals, and these represent less than 15% of the total number of specimens; adult stage starts with the biaperturate progressive chamber, followed by up to four sets of chambers, each set being composed of two or rarely three chambers (Pl. 6, Fig. 6). Earlier chambers globular, those of the terminal part of the biserial stage subrectangular; multichamber adult stage with petaloid chambers. Sutures lined with phaneroridges in the central part of the test; phaneroridges straight to slightly curved, absent near the central suture; the sutures between the last formed chambers depressed, straight or curved and oblique to the test growth axis (Pl. 5, Figs. 2, 5, 6, 9, 11, Pl. 6, Figs. 1, 6); central suture straight to slightly indented, often covered by additional layers of calcite. Most of the sutures in the adult test with multichamber growth are depressed (Pl. 6, fig. 6). Test compressed in edge view; periphery rounded, with transverse keels resulting from the fusion of the phaneroridges on the two sides of the test across the periphery (Pl. 5, Figs. 1, 4, 8, 10, 12, Pl. 6, Fig. 7). Aperture is a low to medium high arch at the base of the last formed chamber; two rarely preserved symmetrically developed metaflanges border the aperture. Chambers ornamented with leptocostae (3.2-6.8 μm), which are stronger in the peripheral region; those of the phaneroridges can fuse, resulting in short, thicker and blunt leptocostae; well-developed periapertural pustulose area (Pl. 5, Figs. 1, 4, 8, 10, 12, Pl. 6, Figs. 3, 7). Test wall calcitic, hyaline and perforate (pore diameter 1.0-3.1 μm); pores situated between the leptocostae in the earlier portion of the test or can interrupt them over the chambers in the adult stage.

*Remarks*.– *Sigalia deflaensis* differs from *S. incipiens* by having (i) sutures lined with phaneroridges rather than calyptoridges between most of the chambers of the biserial stage, (ii) biserial stage with variable rate of chamber size increase, (iii) occasionally a multichamber growth adult stage, (iv) finer leptocostae ornamenting the chamber surface on the lateral sides and (v) periphery with transverse costae resulting from fusion of the phaneroridges across the periphery. It differs from all species of the *Planulitella* branched lineage mainly by having (i) phaneroridges in the central part o the test, (ii) occasionally a multichamber growth adult stage and (iii) periphery with transverse keels. Chamber growth variability in *S. deflaensis* was differently interpreted in the past. The original illustrations by Sigal (1952, text-fig. 41) shows that *S. deflaensis* has both adult specimens with biserial throughout and an incipient multichamber growth stage. Moreover, Reiss (1957) noted rare specimens with multichamber growth in Sigal's original material. Although rarely followed in the past (Dowsett, 1989, pl. 2, fig. 6), the occasional occurrence of an adult stage with multichamber growth is fully confirmed in this study. The three specimens of *Gublerina primitiva* (Aliyulla, 1965, pl. 1, fig. 6-8) exhibit no orna-

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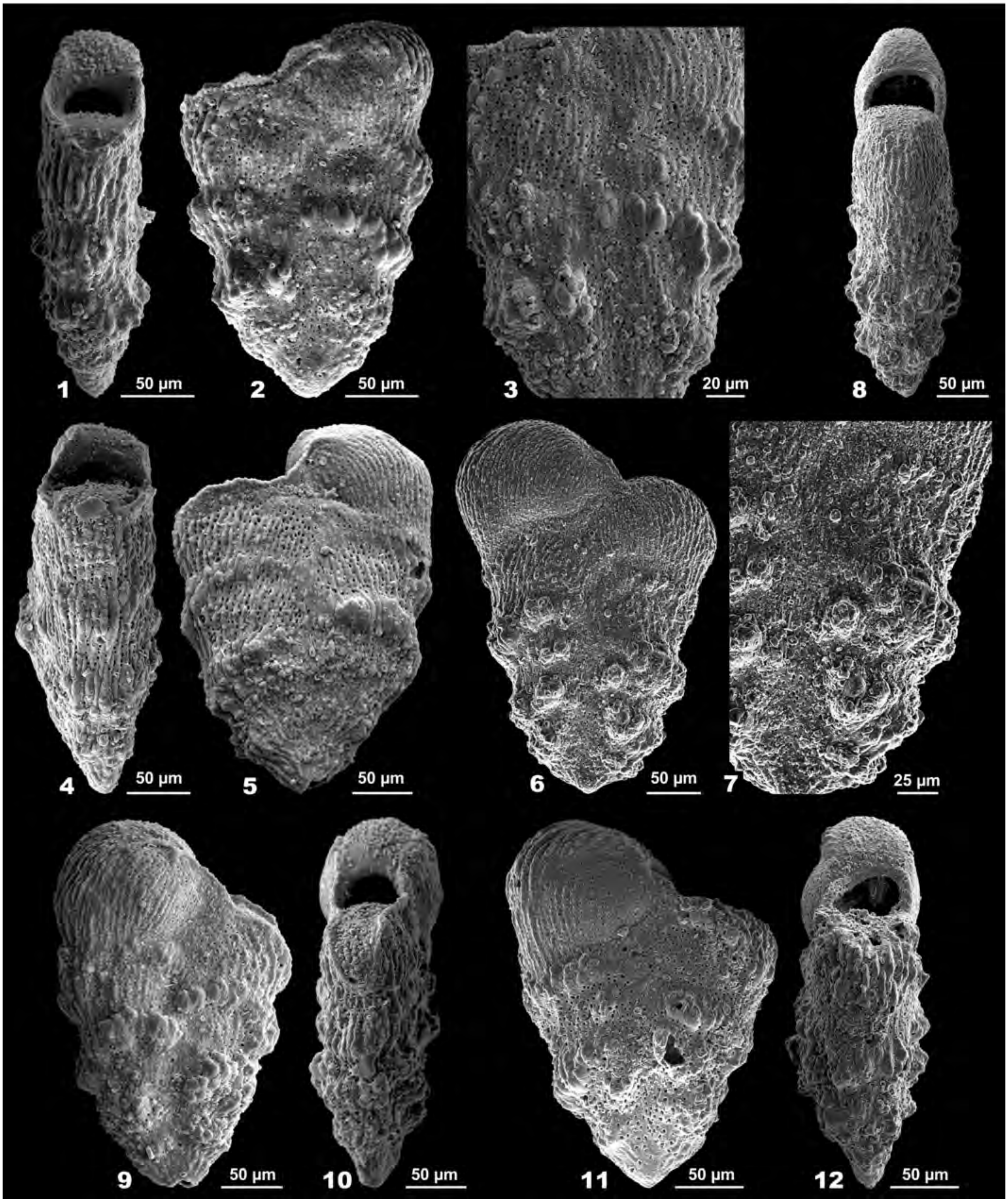
Plate 5. Specimens of *Sigalia deflaensis* (Sigal, 1952). 1-3, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 102-105 cm. 4-5, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-1, 97-100 cm. 6-8, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 99-112 cm. 9-10, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-1, 97-100 cm. 11-12, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 99-112 cm.

**Plate 5**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mentation and it is difficult to assign them precisely to either *S. deflaensis* or *P. carpatica*. The holotype of *Sigalia deflaensis rugocostata* (Nederbragt, 1991, pl. 12, fig. 1) is a specimen with incipient multichamber growth and for this reason this taxon is considered a junior synonym of *S. deflaensis*. Independently Salaj and Samuel (1963, p. 100) and Esker (1969, p. 212) designated as lectotype the first (upper) specimen figured by Sigal (1952) in text-figure 41; this taxonomic clarification is followed herein.

*Stratigraphic range*.– Santonian (upper part of *D. asymetrica* Biozone).

*Geographic distribution*.– Northern Africa (Algeria, Tunisia), Central Asia (Azerbaijan), Europe (Germany, Spain), USA (Alabama, Mississippi), Gulf of Mexico, Caribbean region (Yucatan outer shelf) and western South Atlantic Ocean (São Paolo Plateau, Rio Grande Rise) (Fig. 15).

### ***Sigalia proliferans*** – new species
(Plate 7, Figures 1-10)

1991 *Sigalia deflaensis rugocostata* Nederbragt, pl. 12, fig. 3 (only).
1993 *Sigalia deflaensis* (Sigal). – Nederbragt, pl. 2, figs. 3-6.
2008 *Sigalia rugocostata* Nederbragt. – Georgescu & Almogi-Labin, figs. 4: 3-6, 6: 7-8.

*Holotype*.– WKB 010054.

*Dimensions of the holotype*.– L = 0.442 mm; W = 0.445 mm; W/L = 1.007; T = 0.117 mm; T/L = 0.265; A = 86º.

*Paratypes*.– Five specimens, WKB 010055-010059.

*Dimensions*.– L = 0.401-0.595 mm; W = 0.442-0.531 mm; W/L = 0.892-1.102; T = 0.098-0.125 mm; T/L = 0.165 -0.269; A = 65-105º.

*Type locality*.– DSDP Site 95, Yucatan outer shelf; geographical coordinates: 24º 09.00′ N and 86º 23.85′ W.

*Type level*.– Sample 10-95-14-1, 102-105 cm (upper Santonian, *D. asymetrica* Biozone).

*Material*.– Circa 100 specimens.

*Etymology*.– From the Latin verb *proliferare* (= to increase in number), with reference to the adult stage, which is characterized by an increase in chamber number. *Diagnosis*.– *Sigalia* with weak ornamentation and well-developed adult stage with multichamber growth.

*Description*.– Test with the early subtriangular stage consisting of 9-12 chambers alternately added with respect to the test growth axis resulting in a biserial arrangement; chambers of the early stage increase in size at a moderate rate. The adult flaring stage begins with the biaperturate progressive chamber, which is smaller or equal in size to the last chamber of the early biserial stage; chambers of the multichamber growth adult stage petaloid, with highly variable width/height ratio. Adult stage consists of four to nine sets of two to four chambers each; irregular chamber increase or reduction in number between successive sets, without a constant pattern throughout the adult stage (Pl. 7, Figs. 2, 5, 8). Sutures between the earlier chambers indistinct due to the addition of successive layers of calcite during the ontogeny (Pl. 7, Figs. 2, 5, 8); those in the adult stage lined by curved phaneroridges, which are more prominent in the earlier portion of the test; central suture straight often covered with additional layers of calcite. Test compressed in edge view, with quasi-parallel sides and periphery with transverse keels; transverse keels result from the fusion of the phaneroridges from the opposite sides of the test across the periphery (Pl. 7, Figs. 1, 6, 9). Aperture simple in the earlier biserial stage, an arch at the base of the last formed chamber and multiple in the adult stage (Pl. 7, Figs. 1, 6, 9); chambers of the adult stage can be monoaperturate (relapsed) or biaperturate; apertures are bordered by metaflanges, which are rarely preserved. Chambers ornamented with leptocostae (2.1-6.0 μm), which are more prominent in the periphery, over the earlier chambers and in the phaneroridges; ornamentation is often absent on the lateral sides (Pl. 7, Figs. 2, 5, 8). Periapertural pustulose area well-developed. Test wall calcitic, hyaline and perforate (pore diameter 1.0-5.5 μm); pores simple, situated between the leptocostae in the earlier

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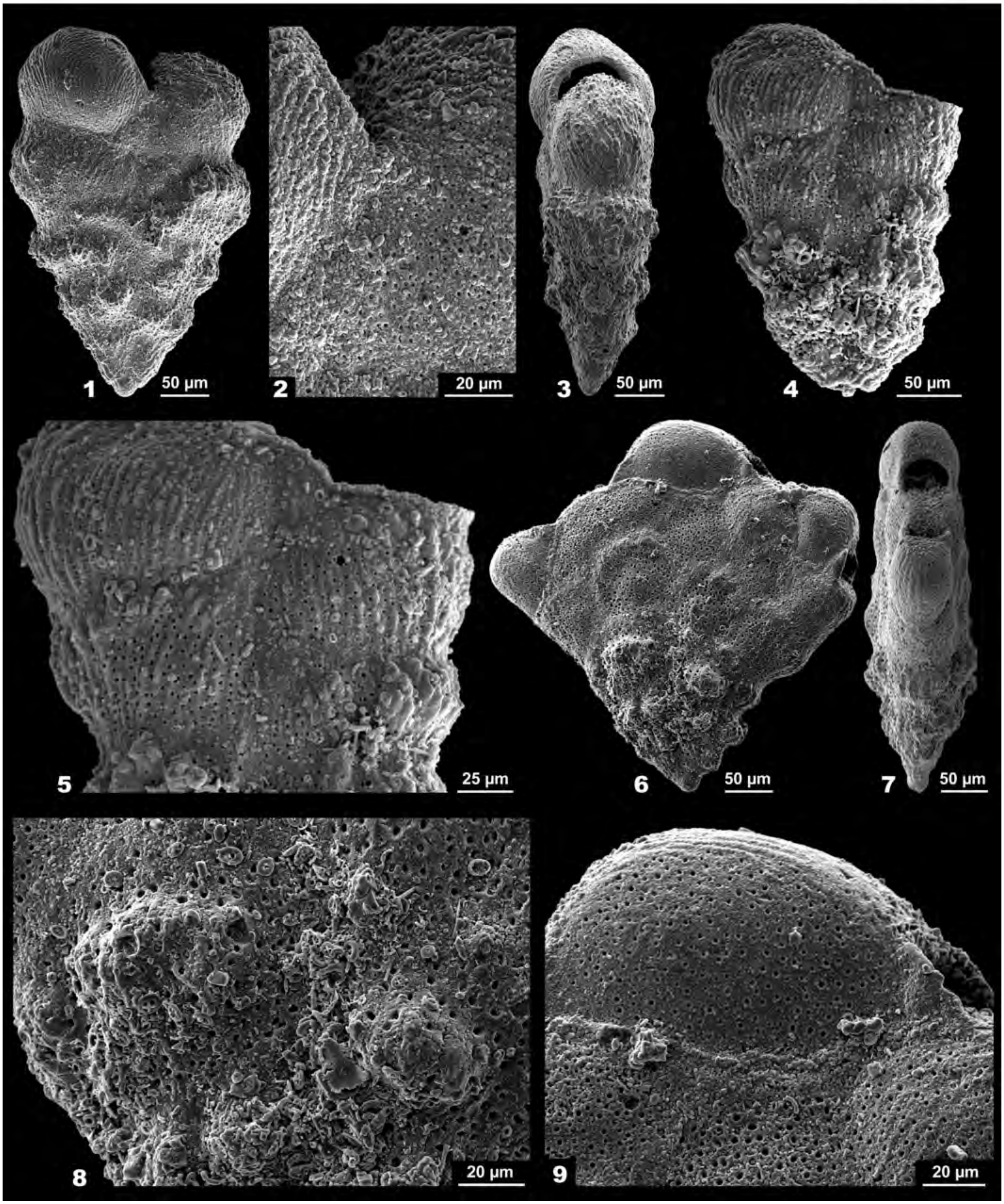
Plate 6. Specimens of *Sigalia deflaensis* (Sigal, 1952). 1-3, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 99-112 cm. 4-5, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 102-105 cm. 6-9, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-13-3, 78-92 cm.

**Plate 6**



portion of the test or interrupting them in the adult stage.

*Remarks*.– *Sigalia proliferans* differs from the earlier species of the directional lineage by the well-developed adult stage with multichamber growth, which consists of up to nine sets of chambers with irregular increase or reduction in number between the successive sets.

*Stratigraphic range*.– Santonian (upper part of *D. asymetrica* Biozone).

*Geographic distribution*.– Caribbean region (Yucatan outer shelf), Gulf of Mexico and northern Africa (Tunisia) (Fig. 15).

### Directional lineage ***Proliferania*** – new

Type species: *Ventilabrella decoratissima* de Klasz 1953, p. 228, pl. 4, fig. 5 (original designation).

*Description*.– Tests with biserial chamber arrangement throughout in the primitive species. Evolved species with adult stage with multichamber growth, which begins with the biaperturate progressive chamber and continues with four to five multichamber sets; chamber number increases by one at an irregular rate in the successive multichamber sets. Sutures are depressed or with calyptoridges in primitive species and strong phaneroridges in evolved ones. Test compressed in edge view. Periphery is simple in the primitive species and with transverse and parallel keels resulting from the fusion of the phaneroridges across the periphery. Aperture is simple, a low to medium high arch in the biserial species and multiple in the multichamber growth adult stage. Early species ornamented with leptocostae tending to concentrate in the peripheral region, the evolved ones exhibit a smooth chamber surface; vestiges of the ancestral costate ornamentation may occur in the phaneroridges. Well-developed periapertural pustulose area. Test wall is calcitic, hyaline and perforate.

*Remarks*.– *Proliferania* and *Sigalia* evolved from the *Planulitella sphenoides* through divergent evolution. The first evolutionary occurrence of the two lineages in the DSDP Site 95 is in the lowermost part of the *D. asymetrica* Biozone (Sample 16-1, 99.5-101 cm). They exhibit relatively similar evolutionary trajectories in the development of (i) calyptoridges and phaneroridges over the sutures, (ii) adult stage with multiserial chamber growth, (iii) periphery with transverse keels and, in addition, ornamentation reduction over the chamber surface, resulting in strong similarities and rather minor morphological differences between them. The development of the adult stage with multichamber growth is abrupt in *Proliferania* (*P. carpatica* is completely biserial and *P. decoratissima*, its direct descendant, exhibits various degrees of chamber proliferation) and gradual in *Sigalia* (*S. deflaensis* exhibits incipient chamber proliferation in less than 15% of specimens, the dominant ones being biserial throughout); the loss of leptocostate ornamentation is early in *Proliferania* (biserial *P. carpatica*, which is also the last member of this directional lineage with biserial chamber arrangement, completely lost leptocostae over the chamber surface) and late in *Sigalia* (*S. deflaensis*, which is the earliest species of *Sigalia* with incipient chamber proliferation, has consistently developed leptocostae over all chambers); although most of the species of *Proliferania* and *Sigalia* have simple, circular to subcircular pores, vuggy pores ocassionally occurs only in the end species of the *Proliferania* directional lineage, namely *P. decoratissima*. Development of the adult stage with multichamber growth resulting in chamber proliferation occurred at different stratigraphical intervals, namely earlier in *Proliferania* and later in *Sigalia*; moreover, the stratigraphical ranges of the species with occasional or well-developed adult stage with multichamber growth in the two directional lineages do not overlap.

*Species included*.– *Proliferania initialis* – new species, *P. carpatica* (Samuel & Salaj, 1963) and *P. decoratissima* (de Klasz, 1953).

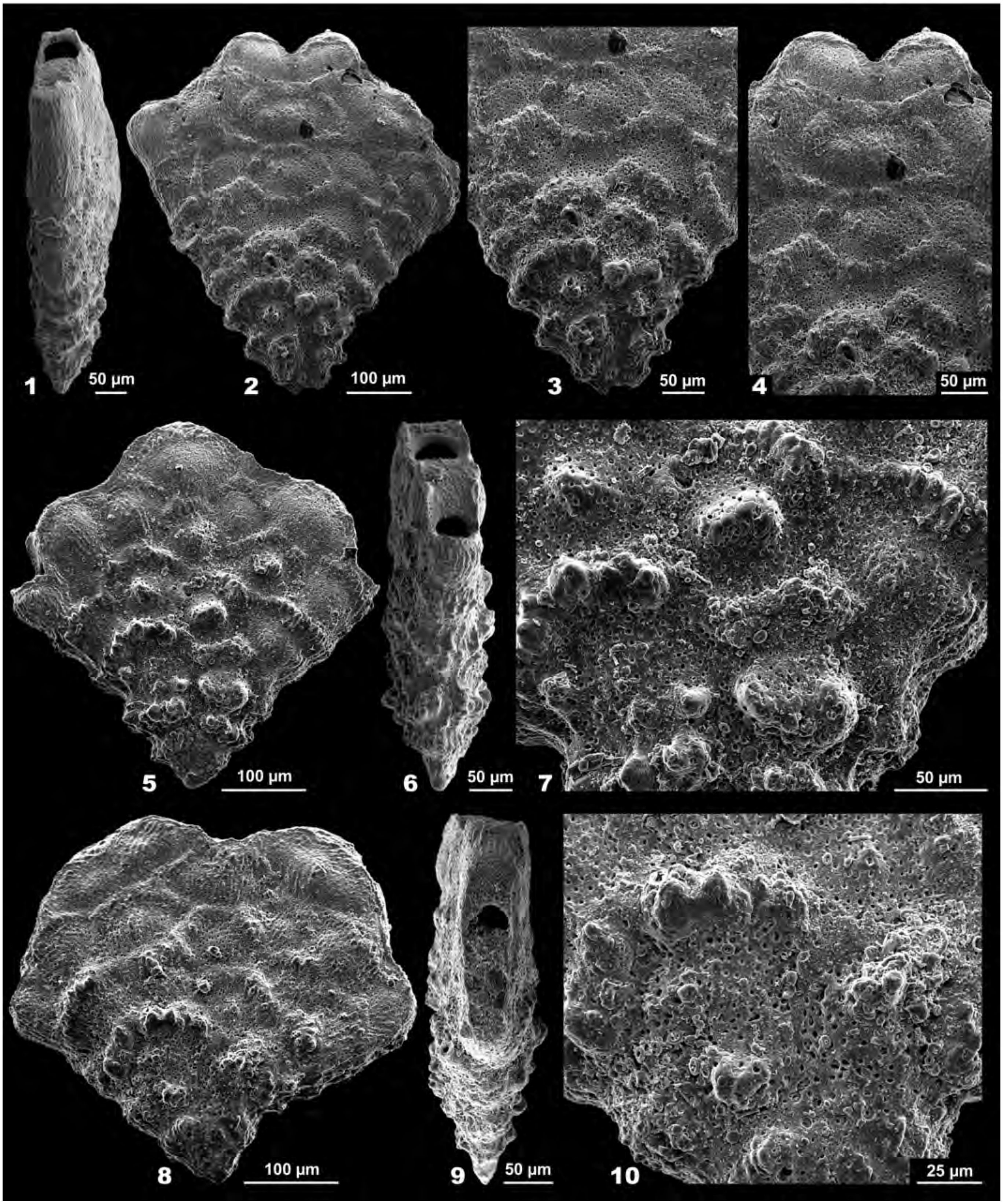
*Etymology*.– Directional lineage name is derived from the Latin verb *proliferare* (= to increase in number), with reference to the adult stage showing multichamber growth.

*Stratigraphic range*.– Santonian (*D. asymetrica* Biozone).

*Geographic distribution*.– Europe (Slovakia, Austria, Spain,

Plate 7. Specimens of *Sigalia proliferans* – new species. 1-4, Topotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-13-3, 78-92 cm. 5-7, Holotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 99-112 cm. 8-10, Paratype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 99-112 cm.

**Plate 7**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France, Germany, Romania), northern Africa (Algeria, Tunisia), Middle East (Iraq, Israel), Gulf of Mexico, Caribbean region (Jamaica, Yucatan outer shelf) and western South Atlantic Ocean (São Paolo Plateau, Rio Grande Rise) (Fig. 16).

### ***Proliferania initialis*** – new species
(Plate 8, Figures 1-12)

1962 *Sigalia deflaensis* (Sigal). – Samuel, p. 194, pl. 13, fig. 2.
1970 *Sigalia* cf. *deflaensis* (Sigal). – Hanzlíková, p. 98, pl. 24, fig. 15.

*Holotype*.– WKB 010060.

*Dimensions of the holotype*.– L = 0.489 mm; W = 0.321 mm; W/L = 0.656; T = 0.135 mm; T/L = 0.276; A = 51º.

*Paratypes*.– Five specimens, WKB 010061-010065.

*Dimensions*.– L = 0.330-0.547 mm; W = 0.208-0.390 mm; W/L = 0.610-0.723; T = 0.123 – 0.144 mm; T/L = 0.271-0.372; A = 37-53º (average based on 15 specimens: holotype, five paratypes and nine topotypes).

*Type locality*.– Yucatan outer shelf; geographical coordinates: 24º 09.00′ N and 86º 23.85′ W.

*Type level*.– DSDP Site 95, Sample 10-95-15-2, 73-87 cm (upper Santonian, *D. asymetrica* Biozone).

*Material*.– Circa 140 specimens.

*Etymology*.– From the Latin verb *initio* (= to initiate), suggesting that it is the earliest species of the *Proliferania* directional lineage.

*Diagnosis*.– *Proliferania* with biserial test throughout and sutures lined by calyptoridges.

*Description*.– Test with subtriangular outline, consisting of 13-17 chambers, which are alternately added with respect to the test growth axis resulting in a biserial arrangement; chambers of the adult stage increase in size at a low to moderate rate. Earlier chambers are globular; those of the adult stage subrectangular or petaloid. Sutures are distinct and oblique to the test axis of growth, often depressed, straight between the earlier chambers and curved towards the anterior part in the adult stage. Calyptoridges can be developed in the early and central parts of the test (Pl. 8, Figs. 8, 9, 11, 12); central suture is slightly indented. Test compressed in edge view; periphery is rounded, without peripheral structures (Pl. 8, Figs. 4, 6, 7). Aperture is a low arch at the base of the last formed chamber; two symmetrical metaflanges border the aperture and in some specimens they can form a small accessory aperture in the proximity of the central suture (Pl. 8, Fig. 9). Chambers ornamented with leptocostae (4.8-10.4 μm), which tend to concentrate in the peripheral regions; ccasionally they can fuse to form an incipiently reticulate network (Pl. 8, Fig. 8-10, 12). Periapertural pustulose area well-developed. Test wall calcitic, hyaline, perforate (pore diameter 1.2-4.1 μm); pores are simple, circular to subcircular in shape; the opening of the incipiently reticulate network can be as wide as 11.1 μm, but their relationship to the preexisting pores is unknown.

*Remarks*.– *Proliferania initialis* differs from *Planulitella sphenoides*, its ancestor, by having (i) a test composed of more chambers (13-17 rather than 10-13), (ii) thicker tests, (iii) low to moderate rather than high chamber increase in size and (iv) having a trend to concentrate the test ornamentation in the peripheral region. It differs from *P. malocaucasica* mainly by lacking the antero-posterior elongation of the chambers in the adult stage. *Proliferania initialis* differs from *Sigalia incipiens* by having (i) thicker tests, (ii) less depressed sutures and (iii) costate ornamentation concentrated in the peripheral region; however, these two species are morphologically close and can be easily confused under the binocular microscope.

*Stratigraphic range*.– Santonian (*D. asymetrica* Biozone).

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Plate 8. Specimens of *Proliferania initialis* – new species. 1-4, Holotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-2, 73-87 cm. 5-6 Topotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-4, 99.5-100.5 cm. 7-8 Topotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-3, 101.5-102.5 cm. 9-10 Topotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 99-112 cm. 11 Topotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-13-3, 78-92 cm. 12 Topotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-16-1, 99.5-101 cm.

# Plate 8


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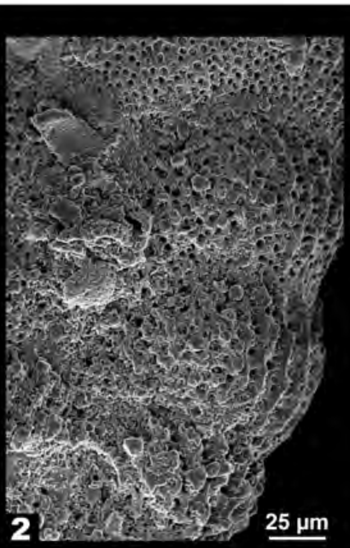
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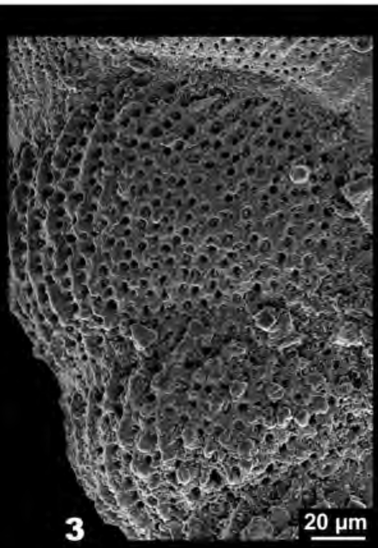
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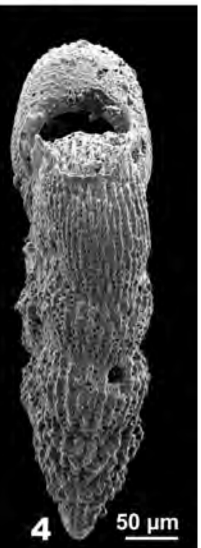
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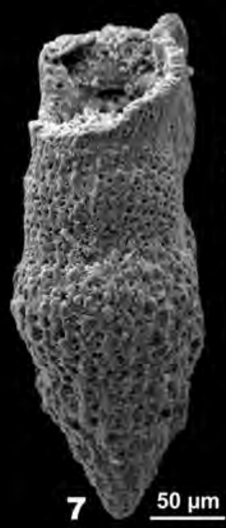
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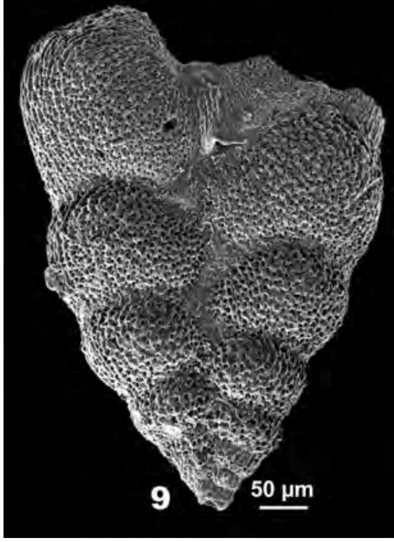
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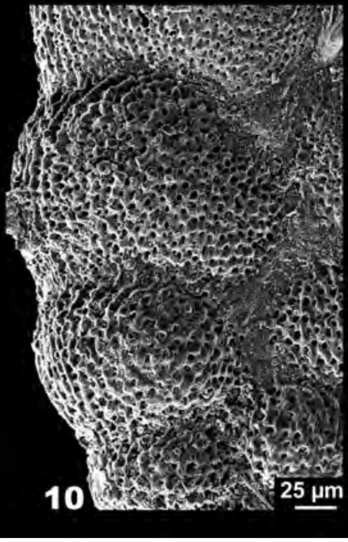
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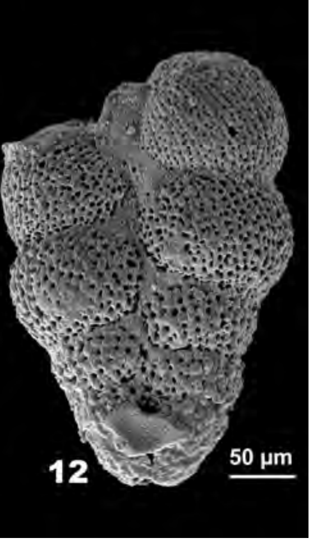
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*Geographic distribution*.– Caribbean region (Yucatan outer shelf), Gulf of Mexico and Europe (Slovakia) (Fig. 16).

### ***Proliferania carpatica* (Salaj & Samuel, 1963)**

(Plate 9, Figures 1-11, Plate 10, Figures 1-11)

1956 *Ventilabrella deflaensis* (Sigal). – Bettenstaedt & Wicher, p. 503, pl. 1, fig. 2 (left figure only).
1956 *Ventilabrella deflaensis* (Sigal). – Küpper, p. 635, pl. 1, fig. 14.
1957 *Ventilabrella deflaensis* (Sigal). – Wicher & Bettenstaedt, fig. 2b.
1963 *Sigalia carpatica* Salaj & Samuel, p. 105, figs. 2-3.
(?) 1965 *Gublerina primitiva* Aliyulla, pl. 225, pl. 1, figs. 6-8.
1966 *Sigalia deflaensis* (Sigal). – Wille-Janoschek, p. 123, pl. 8, fig. 5.
1968 *Sigalia deflaensis* (Sigal). – Scheibnerová, p. 55, pl. 6, fig. 6.
1968 *Gublerina deflaensis* (Sigal). – Barr, pl. 1, fig. 16.
1969 *Sigalia deflaensis* (Sigal). – Brown, p. 42, pl. 3, fig. 8.
1970 *Sigalia deflaensis* (Sigal). – Porthault in Donze *et al*., p. 62, pl. 9, figs. 4-5.
1973 "*Gublerina*" *decoratissima* (de Klasz). – McNeely, pl. 2, fig. 5.
1975 *Sigalia carpatica* (Salaj & Samuel). – Darmoian, p. 200, pl. 3, fig. 20, pl. 4, figs. 1-4.
1977 *Sigalia deflaensis* (Sigal). – Masters, p. 390, pl. 7, figs. 1-2.
1977 *Gublerina primitiva* Aliyulla. – Aliyulla, pl. 2, fig. 3.
1981 *Sigalia carpatica* (Salaj & Samuel). – Butt, pl. 17, fig. B.
1984 *Sigalia deflaensis* (Sigal). – Dowsett, p. 133, pl. 1, figs. 17-18.
1984 *Sigalia decoratissima* (de Klasz). – Weidich, p. 79, pl. 2, fig. 6.
1987 *Sigalia carpatica* (Salaj & Samuel). – Almogi-Labin in Honigstein *et al*., pl. 3, figs. 4-6.
1989 *Sigalia decoratissima* (de Klasz). – Nederbragt, pl. 4, fig. 6.
1991 *Sigalia decoratissima carpatica* Salaj & Samuel. – Nederbragt, p. 369, pl. 11, figs. 2-3.
1993 *Sigalia decoratissima* (de Klasz). – Nederbragt, pl. 2, figs. 7-9.
2007 *Sigalia carpatica* (Salaj & Samuel). – Lamolda *et al*., fig. 4: M, P1-2, S1-2.
2008 *Sigalia carpatica* (Salaj & Samuel). – Georgescu & Almogi-Labin, figs. 3, 6: 1, 6.

*Material*.– Circa 500 specimens.

*Description*.– Test with subtriangular outline, consisting of 14-18 chambers alternately added with respect to the test growth axis resulting in a biserial chamber arrangement; chambers increase gradually in size at various rates, from moderate (Pl. 10, Fig. 1) to high (Pl. 9, Figs. 1, 5, 10, Pl. 10, Figs. 6, 8). Earlier chambers are globular, those of the adult stage subrectangular and with strongly curved anterior and posterior sides in the direction of growth. Sutures are curved, oblique to the test axis of growth and lined with strong phaneroridges (Pl. 9, Figs. 1, 5, 10, Pl. 10, Figs. 1, 6, 8); central suture nearly straight or with shallow indentations. Test compressed in edge view; periphery rounded to subangular and with prominent transverse keels resulting from the fusion of the phaneroridges across the periphery (Pl. 9, Figs. 3, 9, Pl. 10, Figs. 4, 5, 11). Aperture is a very low arch at the base of the last formed chamber and it is bordered by two small, symmetrical metaflanges (Pl. 9, Figs. 3, 4, Pl. 10, Fig. 11). Chamber surface smooth or ornamented with weak, residual leptocostae (Pl. 9, Figs. 2, 6, 7, Pl. 10, Figs. 2, 3, 7, 9 10); vestiges of the ancestral costate ornamentation consisting of thickened costae (14.4-23.9 μm) occur only in the phaneroridges, which, for this reason, have nodular appearance (Pl. 9, figs. 1, 5, 10, Pl. 10, figs. 1, 6, 8). Well-developed periapertural pustulose area (Pl. 9, figs. 3, 4, Pl. 10, fig. 11). Test wall calcitic, hyaline and perforate; pores are simple, circular to subcircular and variable in diameter: those in the central portion of the test are larger (2.4-4.6 μm) when compared to those from the last

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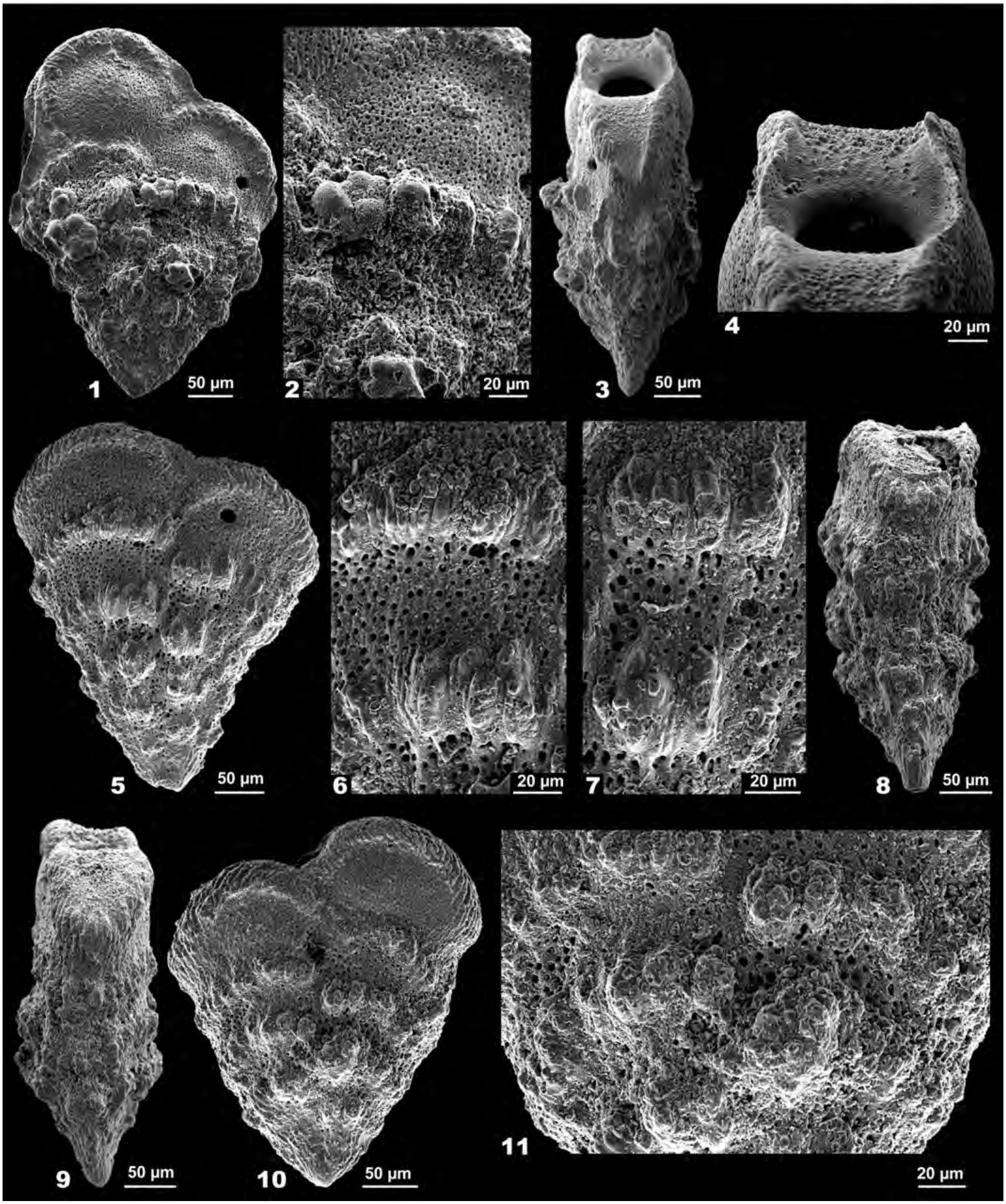
Plate 9. Specimens of *Proliferania carpatica* (Samuel & Salaj, 1963). 1-4, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-2, 73-87 cm. 5-8, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-2, 73-87 cm. 9-11, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-2, 73-87 cm.

**Plate 9**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formed one to four chambers (1.0-2.6 µm) (Pl. 9, Figs. 2, 6, 7, 11, Pl. 10, Figs. 2, 3, 7, 9, 10).

*Remarks*.– *Proliferania carpatica* differs from *P. initialis* by having (i) well-developed phaneroridges, (ii) weaker ornamentation, (iii) periphery with transverse keels and (iv) larger simple pores in the central part of the test. It differs from *Sigalia deflaensis* mainly by (i) having stronger phaneroridges and (ii) lacking the ocassionally developed adult stage with multichamber growth.

*Stratigraphic range*.– Santonian (*D. asymetrica* Biozone).

*Geographic distribution*.– Europe (Slovakia, Austria, Spain, France, Germany), northern Africa (Algeria, Tunisia), Middle East (Iraq, Israel), Gulf of Mexico, Caribbean region (Yucatan outer shelf) and western South Atlantic Ocean (São Paolo Plateau, Rio Grande Rise) (Fig. 16).

### ***Proliferania decoratissima*** **(de Klasz, 1953)** – emended
(Plate 11, Figures 1-12; Plate 12, Figures 1-12)

1953 *Ventilabrella decoratissima* de Klasz, p. 238, pl. 4, fig. 5.
1956 *Ventilabrella decoratissima* de Klasz. – Bettenstaedt & Wicher, p. 503, pl. 1, figs. 2-3.
1957 *Gublerina decoratissima* (de Klasz). – Montanaro Gallitelli, p. 140, pl. 32, fig. 8.
1957 *Ventilabrella decoratissima* de Klasz. – Wicher & Bettenstaedt, fig. 2c.
1963 *Gublerina decoratissima* (de Klasz). – Salaj & Samuel, p. 106, pl. 7, figs. 4-5.
1966 *Sigalia deflaensis* (Sigal). – Wille-Janoschek, p. 123, pl. 8, fig. 6.
1968 *Sigalia deflaensis* (Sigal). – Scheibnerová, p. 55, pl. 6, fig. 5.
1969 *Ventilabrella decoratissima* de Klasz. – Brown, p. 42, pl. 3, fig. 9.
1969 *Sigalia deflaensis* (Sigal). – Brown, p. 42, pl. 2, fig. 1.
1969 *Gublerina decoratissima* (de Klasz). – Esker, p. 212, pl. 1, figs. 7-8.
1970 *Sigalia decoratissima* (de Klasz). – Porthault in Donze *et al.*, p. 63, pl. 9, figs. 6-7.
1972 *Sigalia alpina* (de Klasz). – Martin, pl. 1, fig. 5.
1973 "*Gublerina*" *decoratissima* (de Klasz). – McNeely, pl. 2, fig. 6.

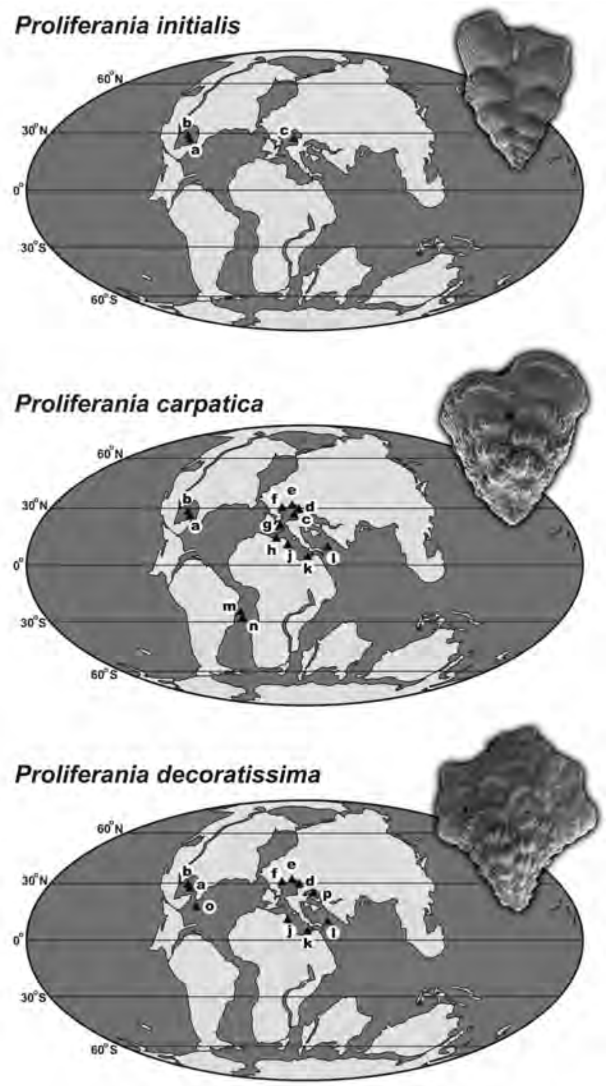
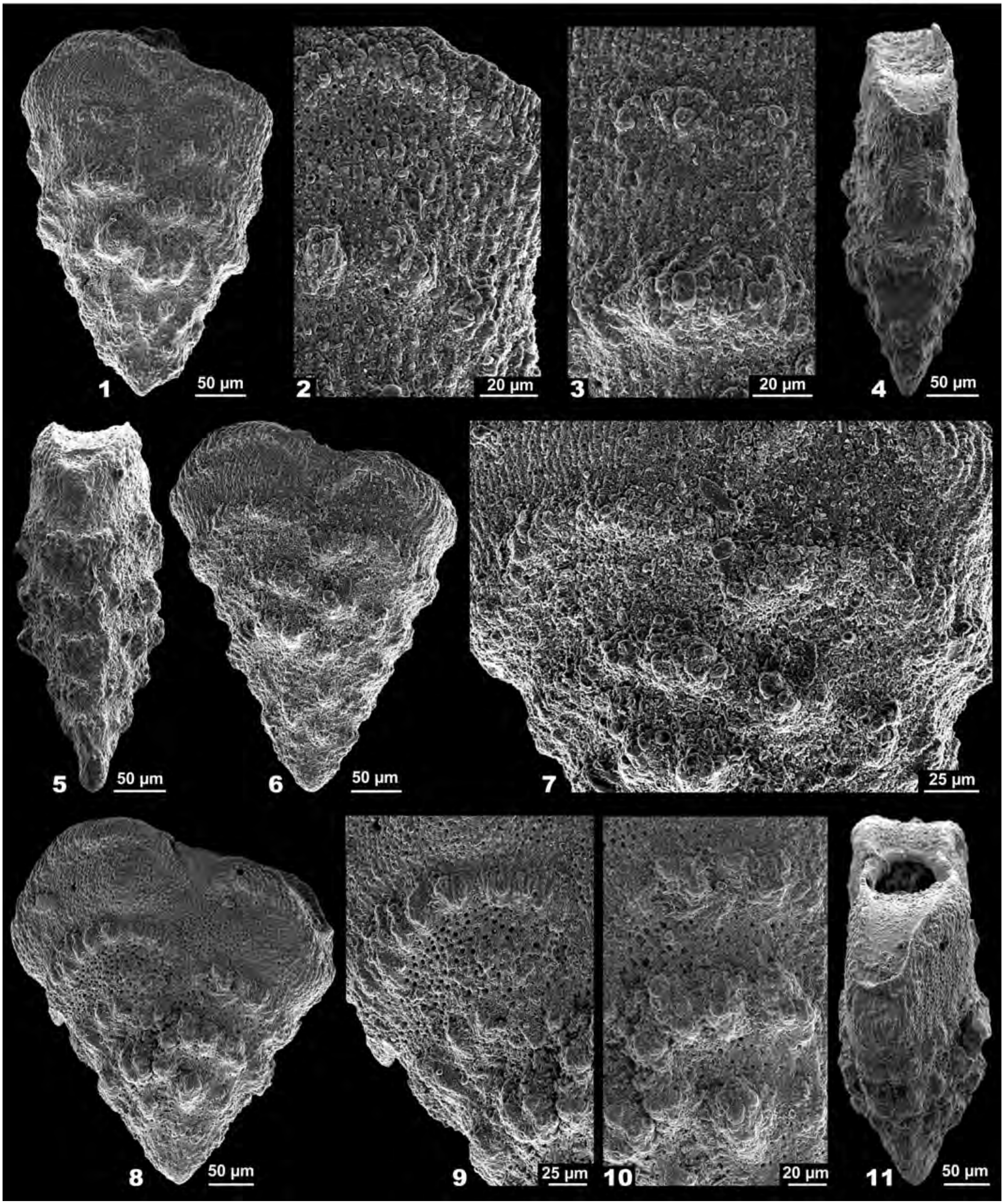


Figure 16. Paleobiogeographical distribution and occurrences of the species included in the directional lineage *Proliferania*. Letter significance: a – Yucatan outer shelf (McNeely, 1973; Georgescu & Almogi-Labin, 2008; this study), b – Gulf of Mexico (Dowsett, 1984; this study), c – Slovakia (Samuel, 1962; Salaj & Samuel, 1963; Scheibnerová, 1968; Hanzlíková, 1970); d – Austria (Wille-Janoschek, 1966); e – Germany (de Klasz, 1953; Bettenstaedt & Wicher, 1956; Küpper, 1956; Wicher & Bettenstaedt, 1957; Butt, 1981; Weidich, 1984); f – France (Porthault in Donze *et al.*, 1970); g – Spain (Lamolda *et al.*, 2007); h – Tunisia (Maamouri & Salaj, 1978; Nederbragt, 1989, 1991, 1993), j – Libya (Barr, 1968), k – Israel (Almogi-Labin in Honigstein et al., 1987), l – Iraq (Darmoian, 1975), m – São Paolo Plateau (this study), n – Rio Grande Rise (this study), o – Jamaica (Esker, 1969) and p – Romania (Neagu, 2006).

Plate 10. Specimens of *Proliferania carpatica* (Samuel & Salaj, 1963). 1-4, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-6, 104-118 cm. 5-7, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-13-3, 78-92 cm. 8-11, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-6, 104-118 cm.

**Plate 10**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1975 *Sigalia decoratissima* (de Klasz). – Darmoian, p. 201, pl. 4, figs. 6-8.
1975 *Sigalia* sp. – Darmoian, pl. 4, fig. 9.
1978 *Ventilabrella decoratissima azzouzi* Maamouri & Salaj, p. 204, pl.1, figs 1-12.
1981 *Sigalia decoratissima* (de Klasz). – Butt, pl. 17, figs. C1-C2.
1984 *Sigalia decoratissima* (de Klasz). – Weidich, p. 79, pl. 2, figs. 7-15.
1987 *Sigalia decoratissima* (de Klasz). – Almogi-Labin in Honigstein *et al.*, pl. 3, fig. 7.
1989 *Sigalia decoratissima* (de Klasz). – Nederbragt, pl. 2, figs. 10-11.
1991 *Sigalia decoratissima decoratissima* (de Klasz). – Nederbragt, p. 368, pl. 11, fig. 4.
1993 *Sigalia decoratissima* (de Klasz). – Nederbragt, pl. 4, fig. 7.
2006 *Sigalia decoratissima* (de Klasz). – Neagu, p. 177, pl. 9, figs. 10-12.
2008 *Sigalia decoratissima* (de Klasz). – Georgescu & Almogi-Labin, fig. 4: 1-2, 6: 4-5.
2008a *Sigalia decoratissima* (de Klasz). – Georgescu & Abramovich, pl. 2, figs. 3-5.

*Material*.– Circa 50 specimens.

*Emended description*.– Test with two distinct growth stages. The early stage, with subtriangular outline, consists of 12-16 chambers added alternately to the test axis of growth resulting in a biserial arrangement; adult stage with multichamber growth. Adult flaring stage initiates with the biaperturate progressive chamber and continues with one to five multichamber sets; chamber numbers increase by one or at an irregular rate in successive multichamber sets. Chambers of the biserial stage are globular, then subrectangular with strongly curved anterior and posterior sides in the direction of growth; chamber of the adult stage petaloid, with variable height/width ratio (Pl. 12, Figs. 1, 6, 7, 9, 11). Sutures are straight in the early stage, oblique to the test growth axis and covered by successively added layers of calcite; those in the test portion with multichamber growth are curved and lined by strong phaneroridges (Pl. 12, Figs. 1-3, 6-8, 11); central suture is straight, rarely with slight indentations. Test compressed in edge view, thicker in the earlier portion and with nearly parallel sides in the adult part; periphery is rounded to subangular, with transverse keels resulting from the fusion of the phaneroridges across the periphery (Pl. 12, Figs. 4, 5, 8, 10, 12). Aperture is a low to medium high arch at the base of the last formed chamber in the biserial portion and multiple in the adult stage (Pl. 12, Figs. 4, 5, 8, 10, 12); symmetrically developed metaflanges border the aperture. Chamber surface smooth; vestiges of the ancestral costate ornamentation can occur in the phaneroridges, where the fused costae result in development of thick (18.8-32.7 µm) and blunt, mostly longitudinally oriented costae, giving a nodular appearance to the earlier portion of the test (Pl. 12, Figs. 1, 6, 7, 9, 11). Test wall is calcitic, hyaline and perforate; pores simple, circular to subcircular in shape and with diameters of 2.3-3.2 µm; vuggy pores (maximum dimension 7.5-8.9 µm) can be developed in the central portion of the test (Pl. 11, Figs. 7, 9).

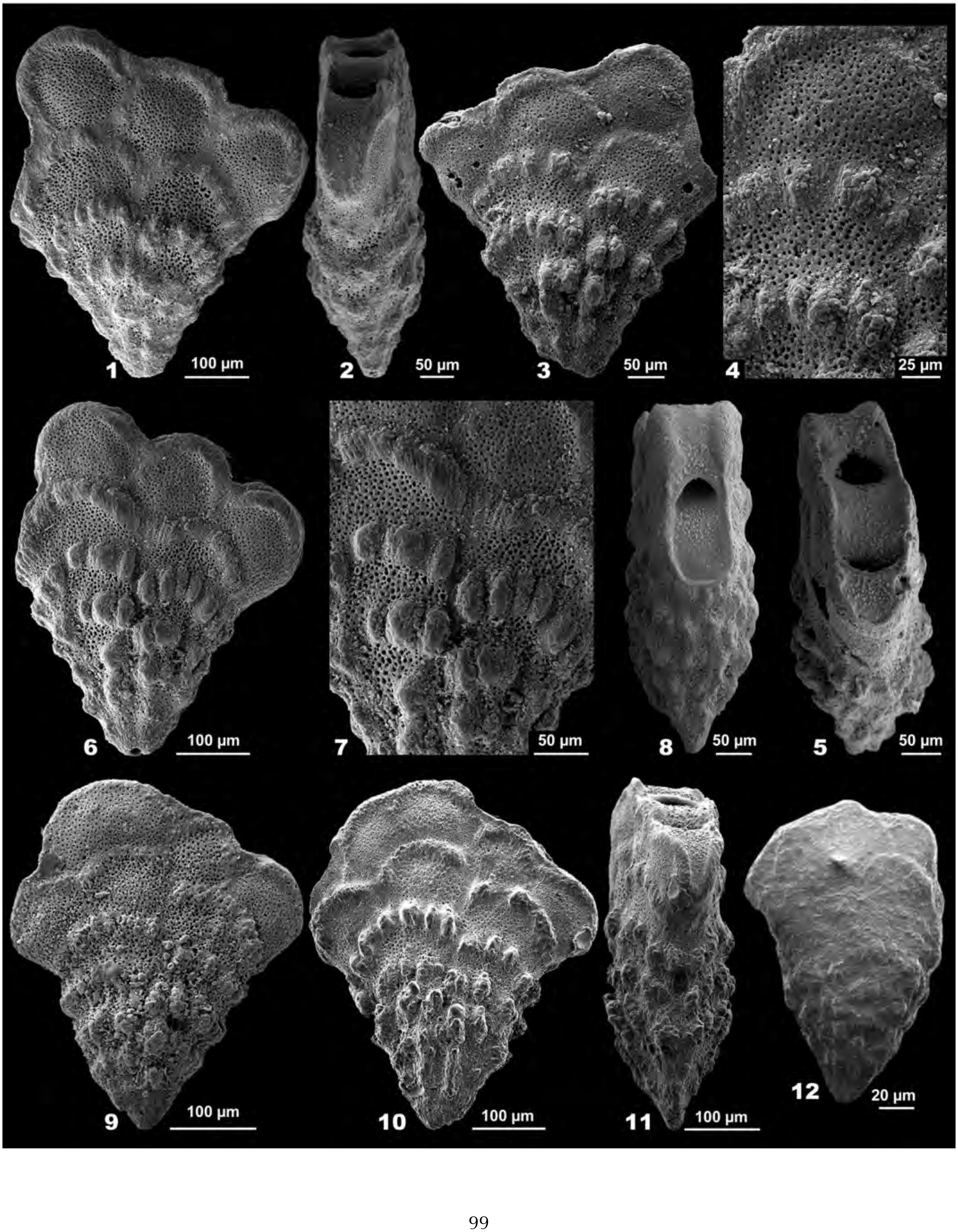
*Remarks*.– *Proliferania decoratissima* differs from all other species of this directional lineage by the well-developed adult stage with multichamber growth. It differs from *L. lipsonae* Georgescu & Abramovich, 2008a by having (i) fewer chamber sets in the adult stage with multiserial chamber growth (maximum five as compared to ten), (ii) less developed vuggy pores in the central portion of the test and (iii) vestigial costae in the phaneroridges. *Ventilabrella decoratissima azzouzi* was described by Maamouri & Salaj (1978) for specimens with progressive chamber, which marks the end of the early biserial stage. Such specimens represent a growth stage of *P. decoratissima* and cannot receive distinct taxonomic status.

*Stratigraphic range*.– Santonian (*D. asymetrica* Biozone).

*Geographic distribution*.– Europe (Austria, Germany, France, Romania), Caribbean region (Jamaica, Yucatan

Plate 11. Specimens of *Proliferania decoratissima* (de Klasz, 1953). 1-2, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-4, 99.5-100.5 cm. 3-5, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-2, 100.5-101.5 cm. 6-8, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-4, 99.5-100.5 cm. 9, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-4, 99.5-100.5 cm. 10-11, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-2, 73-87 cm. 12, Paratype from the Santonian of south of Hörgering, near Eisenärtz, south of Traunstein, Bavaria (Germany) deposited in the NMNH, USNM 498994. Specimen previously figured by Montanaro Gallitelli (1957, pl. 32, fig. 8).

**Plate 11**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outer shelf), Gulf of Mexico, Middle East (Iraq, Israel) and northern Africa (Tunisia) (Fig. 16).

### Branched lineage ***Ventilabrella* Cushman, 1928**

Type species: *Ventilabrella eggeri* Cushman 1928, p. 2, pl. 1, figs. 10, 12 (not 11).

1928 *Ventilabrella* Cushman, p. 2.
partly 1977 *Ventilabrella* Cushman, 1928. – Masters, p. 386.
partly 1987 *Ventilabrella* Cushman, 1928. – Loeblich & Tappan, p. 456.
partly 1991 *Ventilabrella* Cushman, 1928. – Nederbragt, p. 369.

*Description*.– Early stage with chambers alternately added with respect to the growth axis resulting in a biserial arrangement; adult stage with multichamber growth starts with the biaperturate progressive chamber followed by chambers arranged in sets of two to six. Sutures are distinct and depressed. Test is compressed in edge view; periphery rounded and simple, without peripheral structures. Aperture is a simple, low arch at the base of the last chamber in the early biserial stage and multiple in the adult. Chambers ornamented with leptocostae, uniformly distributed or thickened in the early portion of the test and peripheral region; additional layers of calcite often result in formation of pycnocostae over the earlier chambers in the evolved species. Test wall is calcitic, hyaline and perforate; pores can be simple or scalaropores.

*Remarks*.– *Ventilabrella* differs from *Sigalia* and *Proliferania* by having (i) depressed sutures rather than lined with calyptoridges and phaneroridges, (ii) simple periphery rather than with transverse keels and (iii) leptocostate and pycnocostate ornamentation, which is stronger over the earlier portion of the test. *Ventilabrella* is defined in the evolutionary classification as a branched lineage consisting of species with an adult multichamber growth stage.

*Species included*.– *Ventilabrella eggeri* Cushman, 1928, *V. alpina* de Klasz, 1953 and *V. glabrata* Cushman, 1938.

*Stratigraphic range*.– Santonian-early Campanian (from the upper part of *D. asymetrica* Biozone to the lower part of *G. elevata* Biozone).

*Geographic distribution*.– USA (Texas, Kansas, Nebraska, South Dakota, Mississippi, Alabama, New Jersey), Caribbean region (Jamaica, Yucatan outer shelf), Gulf of Mexico, Europe (Germany, Romania), Middle East (Israel), northern Africa (Tunisia) and western South Atlantic Ocean (São Paolo Plateau, Rio Grande Rise) (Fig. 17).

### ***Ventilabrella eggeri* Cushman, 1928** – emended

(Plate 13, Figures 1-11)

1928 *Ventilabrella eggeri* Cushman, p. 2, pl. 1, figs. 10, 12 (non 11).
1981 *Ventilabrella eggeri* Cushman. – Butt, pl. 17, fig. N.
1982 *Ventilabrella glabrata* Cushman. – Oláníyí Odébòdé, p. 244, pl. 3, figs. 6-10.
1983 *Ventilabrella eggeri* Cushman. – Weiss, p. 66, pl. 9, figs. 6-7.
1987 *Ventilabrella eggeri* Cushman. – Almogi-Labin in Honigstein *et al.*, pl. 3, figs. 10-12.
1991 *Ventilabrella eggeri* Cushman. – Nederbragt, p. 369, pl. 12, fig. 7.
1993 *Ventilabrella eggeri* Cushman. – Nederbragt, pl. 1, figs. 6-7, 10-11.
2006 *Ventilabrella eggeri* Cushman. – Georgescu, figs. 5:1-5.2 (only).

*Material*.– Circa 50 specimens.

*Emended description*.– Test with two distinct growth stages. Earlier stage, with subtriangular outline, consisting of 10-12 chambers alternately added with respect to the test growth axis resulting in a biserial arrangement; adult flaring stage initiates with the biaperturate progressive chamber and continues with one or, rarely, two sets of two chambers (Pl. 13, Figs. 1, 3, 6, 8-9); specimens with two such rows of chambers are extremely rare. Earlier chambers are globular; those of the terminal biserial and adult

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Plate 12. Specimens of *Proliferania decoratissima* (de Klasz, 1953). 1-4, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of Eureka 67-128 well (Gulf of Mexico), Sample top at 1662.23 mbsl. 5-6, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of Eureka 67-128 well (Gulf of Mexico), Sample top at 1662.23 mbsl. 7-8, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-2, 100.5-101.5 cm. 9-10, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of Eureka 67-128 well (Gulf of Mexico), Sample top at 1662.23 mbsl. 11-12, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of Eureka 67-128 well (Gulf of Mexico), Sample top at 1662.23 mbsl.

**Plate 12**


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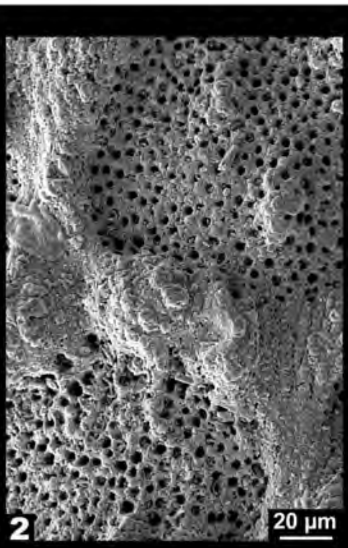
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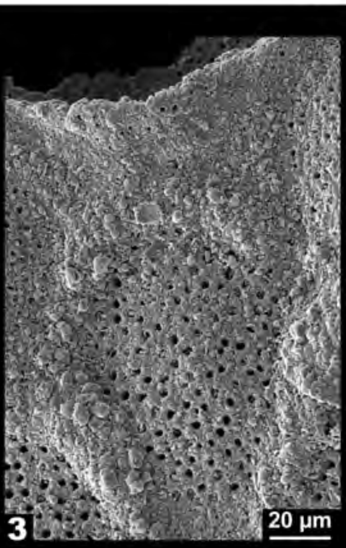
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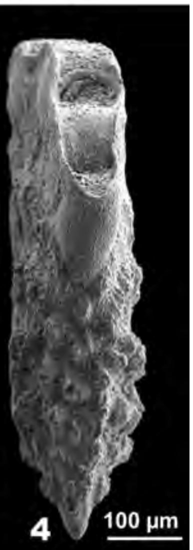
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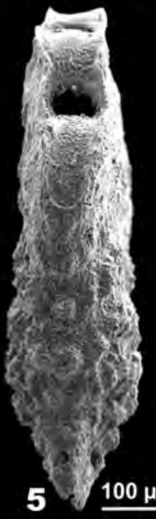
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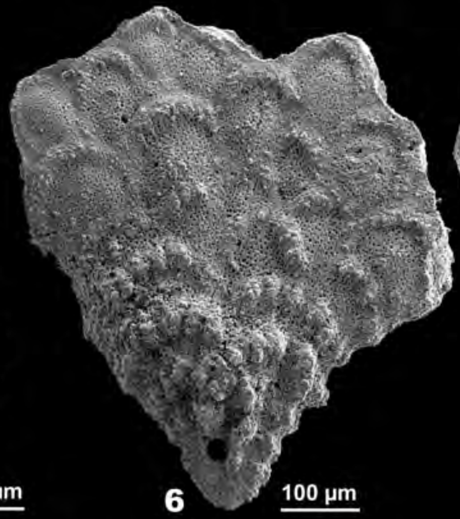
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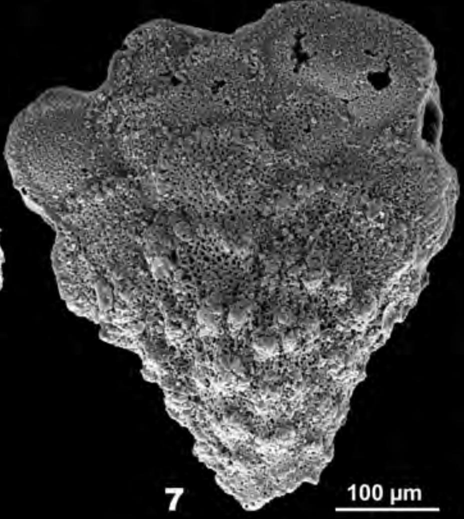
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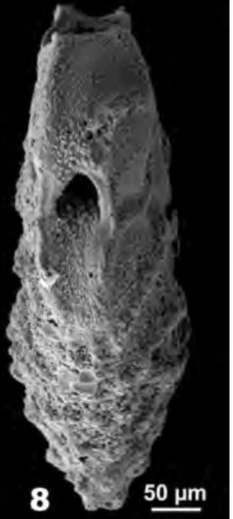
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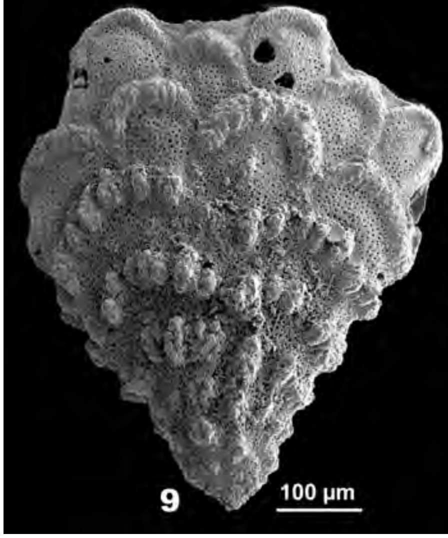
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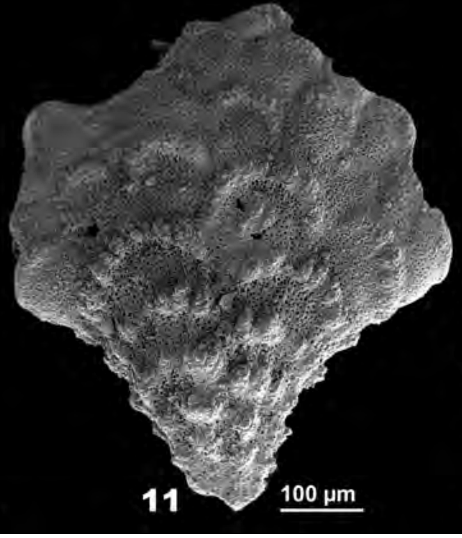
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stages subglobular, overlapping at various rates. Sutures are distinct and depressed; those between the chambers of the biserial stage straight or slightly curved, oblique to the test axis of growth; central suture straight, groove-like. Test compressed in edge view; periphery is rounded, without peripheral structures (Pl. 13, Figs. 2, 4-5, 10). Aperture in the early stage is a low arch at the base of the last formed chamber, those in the adult stage double, one for each of the relapsed chambers (Pl. 13, Figs. 2, 4); the progressive chamber is the only biaperturate chamber of the test. Chamber surface ornamented with thick (6.6-12.9 µm) longitudinal or parallel to the periphery leptocostae; chambers of the adult stage occasionally present leptocostae diverging from the chamber base (Pl. 13, Figs. 1, 3, 9). Ornamentation is often stronger over the earlier portion of the test (Pl. 13, Fig. 6); periapertural pustulose area well-developed. Test wall calcitic, hyaline, perforate (pore diameter 1.1-4.8 µm); pores simple, circular in shape and situated mostly between the costae, rarely interrupting them.

*Remarks*.– *Ventilabrella eggeri* differs from its ancestor, *Planulitella sphenoides*, by having the adult stage with incipient multichamber growth. It differs from *Sigalia deflaensis* with an incipient multichamber growth stage, by (i) having stronger costae and (ii) lacking the phaneroridges developed mostly in the central part of the test. *Ventilabrella eggeri* is emended and restricted to those specimens with incipiently developed multichamber growth stage, as originally described by Cushman (1928) and subsequently followed by Martin (1972) and Almogi-Labin in Honigstein *et al.* (1987). Cushman (1928) did not select a holotype for *V. eggeri* and this fact generated confusion among taxonomists. Montanaro Gallitelli (1957) made an attempt to synonymize genera *Ventilabrella* and *Planoglobulina* based on an error in subsequent synonymies by Cushman (1938, p. 25; 1946, p. 111), admitting that a subsequent taxonomic misinterpretation by the author of a species, rather than the original description is sufficient to challenge the validity of a formally described species; Brown (1969, p. 39-40) contested the interpretation by Montanaro Gallitelli as is done in this paper: *Ventilabrella eggeri* and *Planoglobulina acervulinoides* (Egger, 1902) are two taxa with sharply different test morphologies, stratigraphical ranges and phylogenetic origins. A neotype was selected by Martin (1972) but it appears to be a broken specimen of *V. glabrata*, as suggested by Masters (1977). A new neotype (Pl. 13, Figs. 9-11) is herein selected from the upper Santonian sediments of the Yucatan outer shelf (DSDP Site 95); it shows strong morphological similarities with the first specimen of *V. eggeri* originally figured by Cushman (1928, pl. 1, fig. 10) and was collected from coeval sediments in a relatively close geographical area. The specimens reported from the late Campanian-Maastrichtian (Said & Kenawy, 1956, p. 140, pl. 3, fig. 38; Wille-Janoschek, 1966, p. 125, pl. 8, fig. 7; Hanzlíková, 1970, p. 96, pl. 23, figs. 19, 23; Masters, 1977, p. 392-395; Abdel-Kireem, 1986, p. 228, pl. 3, fig. 1) are not congeneric.

*Stratigraphic range*.– Santonian (*D. asymetrica* Biozone).

*Geographic distribution*.– USA (Texas, New Jersey), Caribbean region (Puerto Rico, Yucatan outer shelf), Gulf of Mexico, Europe (Germany), Middle East (Israel), northern Africa (Tunisia) and western South Atlantic Ocean (São Paolo Plateau, Rio Grande Rise) (Fig. 17).

### ***Ventilabrella alpina* de Klasz, 1953** – emended
(Plate 14, Figures 1-9; Plate 15, Figures 1-9)

1953 *Ventilabrella alpina* de Klasz, p. 228, pl. 4, fig. 6.
1953 *Ventilabrella bipartita* de Klasz, p. 228, pl. 4, fig. 7.
1956 *Ventilabrella alpina* de Klasz. – Bettenstaedt & Wicher, p. 503, pl. 1, fig. 4.
1956 *Ventilabrella eggeri* Cushman. – Küpper, p. 636, pl. 1, fig. 13.
1972 *Ventilabrella browni* Martin, p. 85, pl. 1, figs. 3-4.
1977 *Ventilabrella browni* Martin. – Petters, pl. 1, fig. 3.
1977 *Ventilabrella browni* Martin. – Premoli Silva & Boersma, pl. 2, fig. 4.
1991 *Ventilabrella eggeri* Cushman. – Nederbragt, pl. 12, fig. 5.

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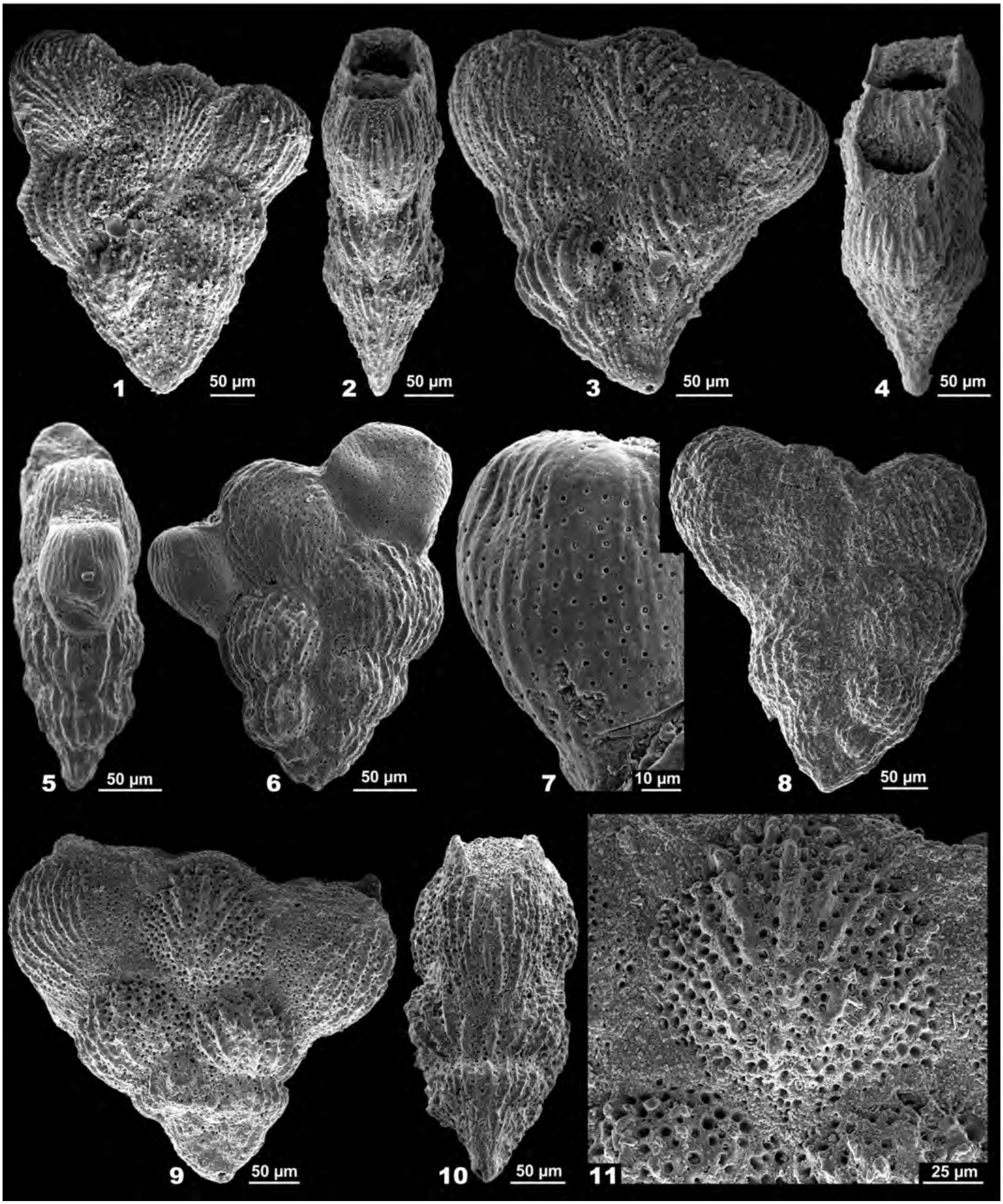
Plate 13. Specimens of *Ventilabrella eggeri* Cushman, 1928. 1-2, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 100-102 cm. 3-4, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-15-4, 99.5-100.5 cm. 5-7, Hypotype from the upper Santonian (*G. arca* Biozone) sediments of ODP Leg 174AX at Bass River Site (New Jersey coastal plain), Sample 505.35-505.38 mbsf. 8, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 356 (São Paolo Plateau), Sample 39-356-36-4, 110-124 cm. 9-11, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-13-3, 78-92 cm.

**Plate 13**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1992 *Ventilabrella browni* Martin. – Olsson & Usmani, fig. 6:4.
2008 *Ventilabrella browni* Martin. – Georgescu & Almogi-Labin, fig. 7:1-2.

*Material*.– Circa 300 specimens.

*Description*.– Test with two distinct growth stages; an earlier stage with subtriangular outline consists of 10-12 chambers alternately added with respect to the test growth axis resulting in a biserial chamber arrangement. Flaring adult stage, with well-developed multichamber growth, starts with the biaperturate progressive chamber and continues with up to five chamber sets, in which the number of chambers gradually increases by one (i.e., first two, then three, then four, etc). Earlier chambers are globular, those of the terminal biserial stage and adult stage petaloid, overlapping at various rates. Sutures are distinct and depressed, straight to curved; central suture groove-like, straight or with shallow indentations. Test compressed in edge view, thicker in the early stage and thinner and with nearly parallel sides in the adult portion (Pl. 14, Figs. 2, 7, Pl. 15, Figs. 3, 5, 7); periphery is rounded and simple, without peripheral structures. Aperture is a simple low arch at the base of the last formed chamber in the early biserial stage and multiple in the adult stage; chambers of the adult stage biaperturate or relapsed. Chamber surface ornamented with leptocostae, which are stronger over the early portion (11.8-19.3 μm) and thinner over the last added chambers (4.4-8.1 μm) (Pl. 14, Figs. 1, 8, Pl. 15, Figs. 1-2, 4, 6, 8-9); incipient reticulation may be ocassionally developed over the chambers of the adult stage. Periapertural pustulose area well-developed. Test wall calcitic, hyaline and perforate (pore diameter 1.8-4.3 μm); pores simple or scalaropores, with circular to, rarely, elliptical shape, situated in the spaces between the costae or interrupting them.

*Remarks*.– *Ventilabrella alpina* differs from *V. eggeri* by having (i) a well-developed adult stage with multichamber growth and (ii) stronger ornamentation on the earlier portion of the test. It differs from *S. proliferans* and *P. decoratissima* mainly by lacking phaneroridges over the sutures. *Ventilabrella bipartita* (de Klasz, 1953) was described to accommodate the tests with strong ornamentation over the earlier test and deeply incised central suture in the biserial portion; such tests are rare in the assemblages studied and, when they occur, appear end members of in the *V. alpina* variability range. *Ventilabrella browni* Martin, 1972 is morphologically identical to *V. alpina* and for this reason considered the latter's junior synonym.

*Stratigraphic range*.– Santonian-early Campanian (from the upper part of *D. asymetrica* Biozone to the lower part of *G. elevata* Biozone).

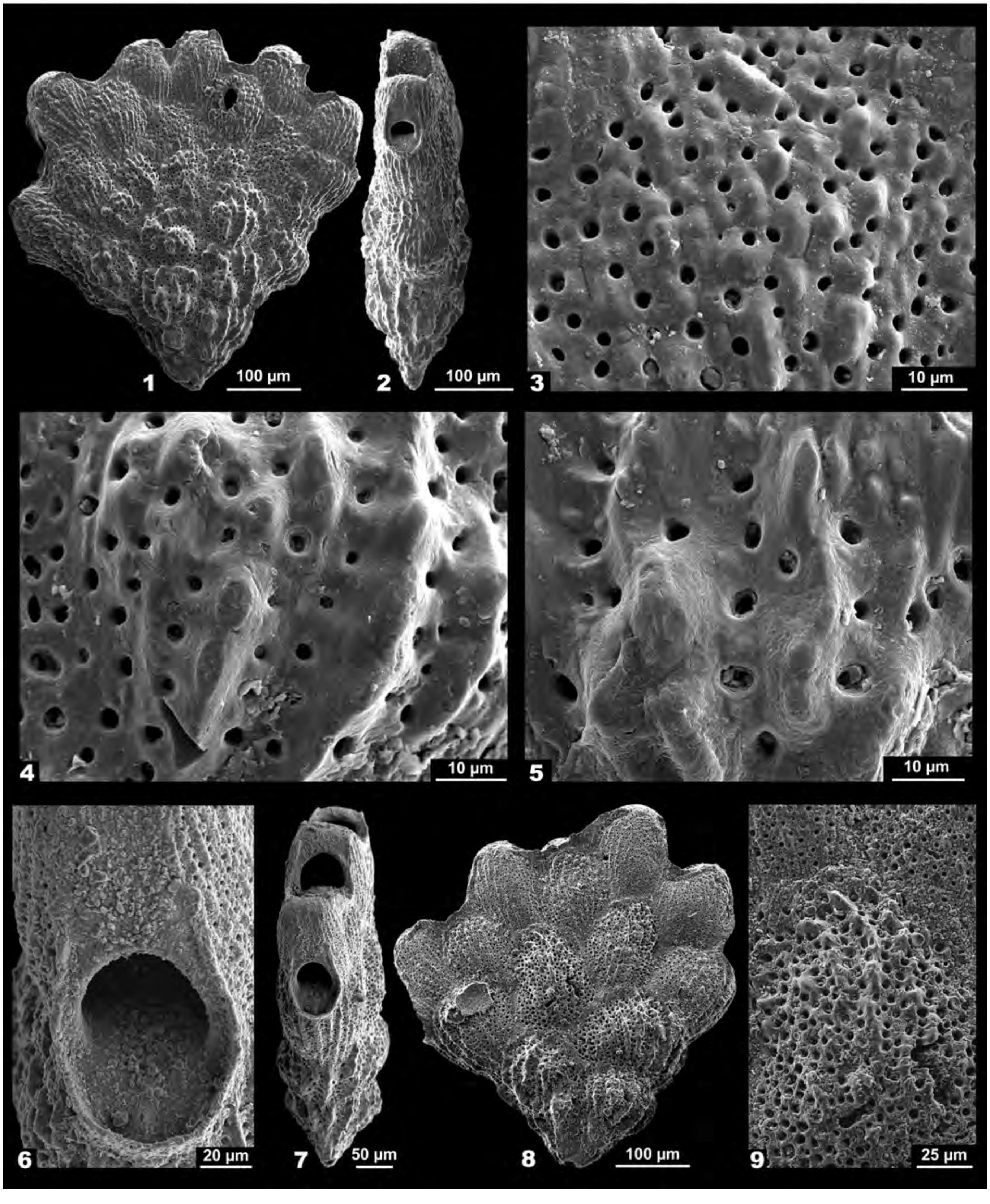
*Geographic distribution*.– Europe (Germany), USA (Texas, Arkansas, New Jersey), Gulf of Mexico, Caribbean region (Puerto Rico, Yucatan outer shelf) and western South Atlantic Ocean (São Paolo Plateau, Rio Grande Rise) (Fig. 17).

### ***Ventilabrella glabrata* Cushman, 1938**
(Plate 16, Figures 1-10)

1928 *Ventilabrella eggeri* Cushman, pl. 1, fig. 11 (only).
1937 *Ventilabrella eggeri* Cushman. – Loetterle, p. 35, pl. 5, fig. 5.
(?) 1938 *Planoglobulina taylorana* Cushman, p. 23, pl. 4, figs. 9-10.
1938 *Ventilabrella eggeri* var. *glabrata* Cushman, p. 26, pl. 4, figs. 15-17.
1938 *Ventilabrella eggeri* Cushman. – Cushman, p. 25, pl. 4, figs. 13-14.
(?) 1946 *Planoglobulina taylorana* Cushman. – Cushman, p. 110, pl. 47, figs. 10-11.
1946 *Ventilabrella eggeri* Cushman. – Cushman, p. 111, pl. 47, figs. 17-19.
1946 *Ventilabrella eggeri* var. *glabrata* Cushman. – Cushman, p. 111, pl. 47, figs. 20-22.
1957 *Planoglobulina glabrata* (Cushman). – Montanaro Gallitelli, pl. 32, figs. 10-12.
1967 *Planoglobulina glabrata* (Cushman). – Pessagno, p. 272, pl. 88, figs. 12, 13, 17.
1969 *Planoglobulina glabrata* (Cushman). – Esker, pl. 2, fig. 10.

Plate 14. Specimens of *Ventilabrella alpina* (de Klasz, 1953). 1-5, Hypotype from the upper Santonian (*G. arca* Biozone) sediments of ODP Leg 174AX at Bass River Site (New Jersey coastal plain), Sample 505.35-505.38 mbsf. 6-9, Hypotype from the upper Santonian (*G. arca* Biozone) sediments of ODP Leg 174AX at Bass River Site (New Jersey coastal plain), Sample 505.05-505.08 mbsf.

**Plate 14**



1972 *Ventilabrella glabrata* Cushman. – Martin, p. 86, pl. 1, figs. 8-9.
1975 *Ventilabrella glabrata* Cushman. – Darmoian, p. 202, pl. 4, figs. 14-16.
1975 *Ventilabrella ornatissima* Cushman and Church. – Darmoian, p. 202, pl. 4, figs. 17-20.
1977 *Ventilabrella eggeri* Cushman. – Masters, p. 392, pl. 7, figs. 3-4.
1977 *Ventilabrella glabrata* Cushman. – Masters, 395, pl. 8, figs. 1-2.
1977 *Ventilabrella glabrata* Cushman. – Petters, pl. 2, figs. 1-2.
1981 *Ventilabrella eggeri* Cushman. – Butt, pl. 17, fig. N.
1981 *Ventilabrella eggeri* Cushman. – Frerichs & Dring, pl. 1, figs. 17-18.
1983 *Ventilabrella eggeri* Cushman. – Weiss, p. 66, pl. 9, fig. 8.
1984 *Ventilabrella* cf. *glabrata* Cushman. – Weidich, p. 81, pl. 1, figs. 20-21.
1987 *Ventilabrella eggeri* Cushman. – Almogi-Labin in Honigstein *et al.*, pl. 3, figs. 8-9.
1989 *Ventilabrella eggeri* Cushman. – Dowsett, p. 16, pl. 3, fig. 7.
1991 *Ventilabrella eggeri* Cushman. – Nederbragt, p. 369, pl. 12, fig. 6.
1993 *Ventilabrella eggeri* Cushman. – Nederbragt, pl. 1, figs. 8-9.
1996 *Ventilabrella eggeri* Cushman. – Mancini *et al.*, fig. 4:10.
2006 *Ventilabrella eggeri* Cushman. – Georgescu, figs. 5.3-5.5 (only).
2006 *Ventilabrella ornatissima* Cushman and Church. – Neagu, p. 177, pl. 5, figs. 24-26.

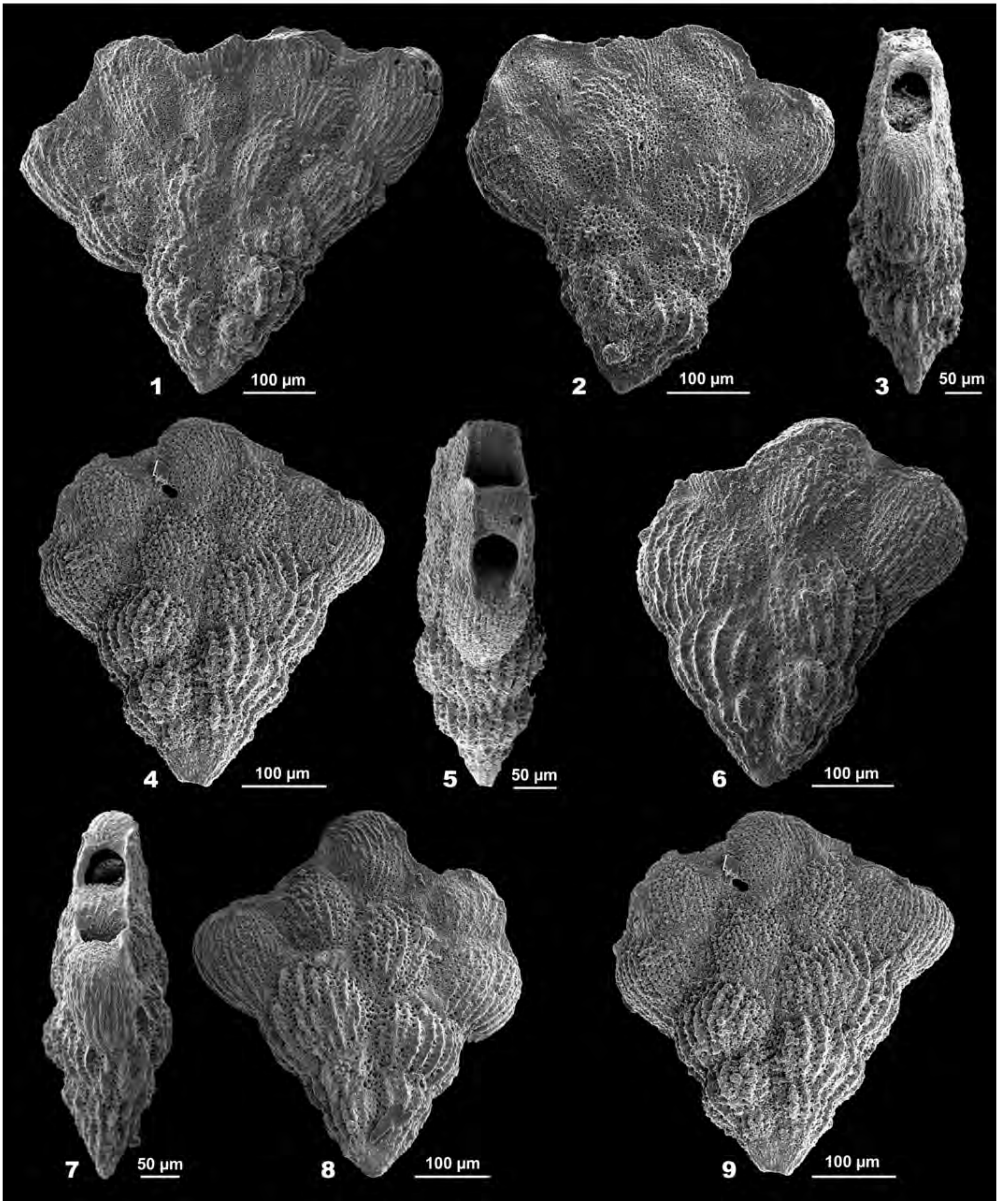
*Material*.– Circa 500 specimens.

*Emended description*.– Test with two distinct growth stages; early biserial stage with subtriangular outline, consists of 10-12 chambers alternately added with respect to the test growth axis resulting in biserial chamber arrangement; flaring adult stage with multiserial chamber growth (Pl. 16, Figs. 2-4, 8). Earlier chambers are globular to subglobular, those of the adult stage subglobular, overlapping at various rates. Adult stage begins with the biaperturate progressive chamber, followed by up to six multichamber sets; each of the earlier one to three sets composed of two chambers, one relapsed and one biaperturate, the subsequent ones with increasing numbers of chambers (i.e., three, then four, then five). Sutures are distinct and depressed, straight to curved; central suture groove-like, straight to slightly indented. Test compressed in edge view, with nearly parallel sides in the adult portion; periphery is rounded and simple, without peripheral structures (Pl. 16, Figs. 1, 7, 9). Aperture is simple in the early biserial stage, a low arch at the base of the last formed chamber and multiple in the adult stage, one or two for each chamber; periapertural structures consist of symmetrically developed metaflanges. Chamber ornamented with longitudinal or parallel to the periphery leptocostae; leptocostae thickness is relatively constant over the test surface (3.5-5.7 μm). Thickened ornamentation consisting of pycnocostae may be ocassionally developed over the early portion of the test. Periapertural pustulose area well-developed. Test wall calcareous, hyaline and perforate (pore diameter 1.5-3.7 μm); pores simple or scalaropores, circular to subcircular in shape, mostly situated in the spaces between the costae or, rarely, interrupting the leptocostae or pycnocostae. Test wall with variable calcification; the thickest wall is in the distal part of the biserial stage, progressive chamber and the earlier chamber sets of the adult stage.

*Remarks*.– *Ventilabrella glabrata* differs from its ancestor, *V. eggeri*, mainly by having a well-developed multichamber growth stage, which consists of one to five chamber sets, rather one to two; moreover, the number of chambers gradually increases by one in the case of the former species, when compared to the latter where all the sets of chambers in the adult stage consist of two relapsed chambers. It differs from *V. alpina* by having (i) a multichamber growth stage with less regular chamber increase in number between the successively added sets and (ii) weaker ornamentation on the earlier portion of the test. It differs from

Plate 15. Specimens of *Ventilabrella alpina* (de Klasz, 1953). 1, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 100-102 cm. 2-3, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 100-102 cm. 4-5, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 100-102 cm. 6, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 100-102 cm. 7-8, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 100-102 cm. 9, Hypotype from the upper Santonian (*D. asymetrica* Biozone) sediments of DSDP Site 95 (Yucatan outer shelf), Sample 10-95-14-1, 100-102 cm.

**Plate 15**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*Sigalia proliferans* by having (i) depressed sutures throughout rather than lined with phaneroridges, (ii) a simple test periphery rather than one with transverse keels, (iii) all chambers ornamented with costae rather than showing an obvious reduction in the ornamentation towards the distal parts of the test and (iv) ocassionally developed scalaropores. It differs from *Proliferania decoratissima* by having (i) depressed sutures throughout rather than lined with calyptoridges or phaneroridges, (ii) a simple test periphery rather than one with transverse keels, (iii) pores simple or scalaropores rather than vuggy pores in the central part of the test and (iv) chamber surface ornamented with costae rather than smooth. *Planoglobulina taylorana* (Cushman, 1938, p. 23; 1946, p. 110) is probably a deformed and broken specimen of *V. glabrata*. Although *P. taylorana* has page priority over *V. glabrata* (p. 23 over p. 26), its senior species status is not validated here because of the lack of morphological distinctive features when compared to *V. glabrata* and poor preservation of the type material, the latter being a source of potential misunderstandings. The reports of *V. glabrata* or *Planoglobulina glabrata* (Said & Kenawy, 1956, p. 140, pl. 3, fig. 46; Eternod Olvera, 1959, p. 77, pl. 2, fig. 9; Skinner, 1962, p. 42, pl. 5, fig. 15; Barr, 1968, pl. 1, figs. 6, 9; Hanzlíková, 1969, p. 42, pl. 8, fig. 3; Hanzlíková, 1970, p. 97, pl. 24, figs. 2, 7; Masters, 1977, p. 395; Abdel-Kireem, 1986, p. 228, pl. 3, figs. 2-3) are not congeneric.

*Stratigraphic range*.– Santonian-early Campanian (from the upper part of *D. asymetrica* Biozone to the lower part of *Globotruncanita elevata* Biozone).

*Geographic distribution*.– USA (Texas, Kansas, Nebraska, South Dakota, Mississippi, Alabama, New Jersey), Gulf of Mexico, Caribbean region (Jamaica, Yucatan outer shelf), Europe (Germany, Romania), northern Africa (Tunisia) and Middle East (Iraq, Israel) (Fig. 17).

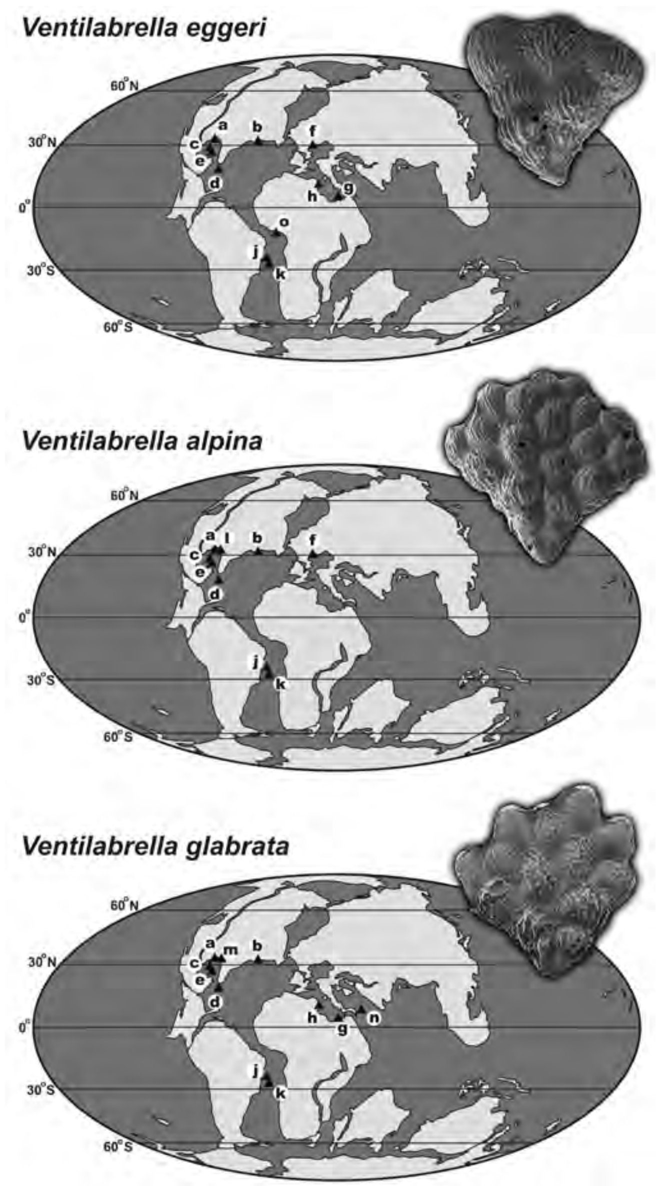
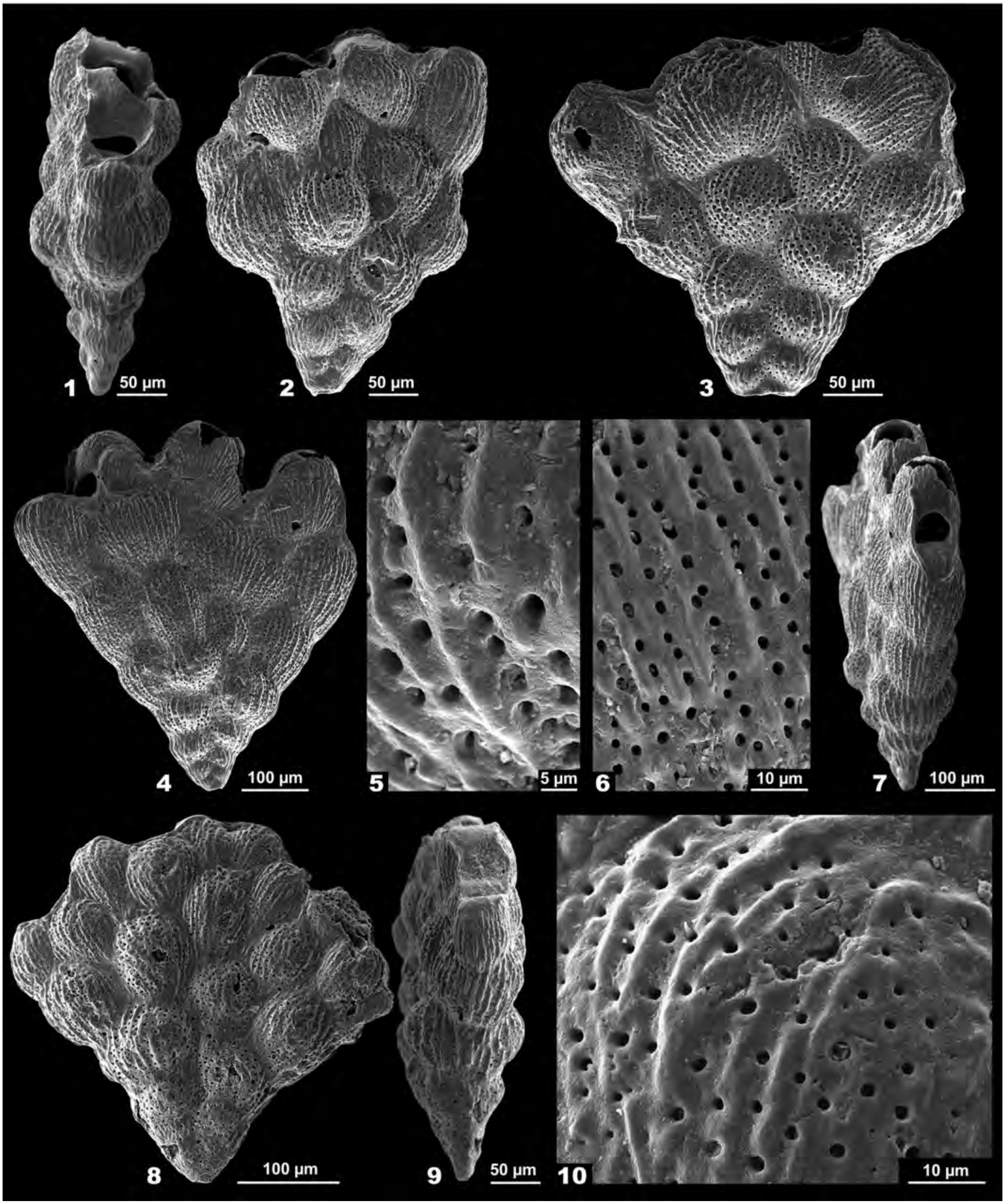


Figure 17. Paleobiogeographical distribution and occurrences of the species included in the directional lineage *Ventilabrella*. Letter significance: a – Texas (Cushman, 1928, 1938, 1946; Pessagno, 1967; Martin, 1972; Masters, 1977), b – New Jersey coastal plain (Petters, 1977; Olsson & Usmani, 1992; Georgescu, 2006; Georgescu & Almogi-Labin, 2008, this study), c – Gulf of Mexico (this study), d – Jamaica (Esker, 1969), e – Yucatan outer shelf (McNeely, 1973; Georgescu & Almogi-Labin, 2008; this study), f – Germany (de Klasz, 1953; Bettenstaedt & Wicher, 1956; Küpper, 1956; Butt, 1981; Weidich, 1984), g – Israel (Almogi-Labin in Honigstein *et al.*, 1987), h – Tunisia (Nederbragt, 1991), j – São Paolo Plateau (Premoli Silva & Boersma, 1977; this study), k – Rio Grande Rise (Premoli Silva & Boersma, 1977; this study), l – Arkansas (Martin, 1972), m – combined Kansas, Nebraska, South Dakota, Mississippi, Alabama occurrences (Frerichs & Dring, 1981; Dowsett, 1989; Mancini *et al.*, 1996), n – Romania (Neagu, 2006) and o – Nigeria (Oláníyí Odébòdé, 1982).

Plate 16. Specimens of *Ventilabrella glabrata* Cushman, 1938. 1-2, Hypotype from the upper Santonian (*G. arca* Biozone) sediments of ODP Leg 174AX at Bass River Site (New Jersey coastal plain), Sample 505.05-505.08 mbsf. 3, Hypotype from the upper Santonian (*G. arca* Biozone) sediments of ODP Leg 174AX at Bass River Site (New Jersey coastal plain), Sample 505.35-505.38 mbsf. 4-7, Hypotype from the upper Santonian (*G. arca* Biozone) sediments of ODP Leg 174AX at Bass River Site (New Jersey coastal plain), Sample 505.35-505.38 mbsf. 8-10, Hypotype from the upper Santonian (*G. arca* Biozone) sediments of ODP Leg 174AX at Bass River Site (New Jersey coastal plain), Sample 505.05-505.08 mbsf.

**Plate 16**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## 6. DISCUSSION AND CONCLUSIONS

Taxonomic reevaluation of the late Coniacian-early Campanian planktic foraminifera that developed adult multichamber growth stages shows that the process happened in four lineages, three directional and one branched. Species are grouped into two distinct supraspecific categories which are given significance in evolutionary classification: directional lineages and branched lineages. A directional lineage (DL) is defined as a lineage showing continuous development of two or more features in a monophyletic-linear succession of species. At least one feature has a divergent pattern in a branched lineage (BL), resulting in a monophyletic-branched succession of species. Directional and branched lineages are taxonomic units with significance in evolutionary classification.

*Texasia* is formalized as a new directional lineage that led to the development of multichamber growth in the adult stage and commenced its evolution in the late Coniacian. It includes two species, *T. papula* and *T. austinana* of the late Coniacian-early Campanian and latest Coniacian-Santonian respectively, the former with completely biserial test, the latter with flaring multichamber adult stage. Multichamber growth adult stage begins with the progressive chamber and consists of up to three sets of two chambers and occurs only in the latter (Fig. 18). The globular chambers, periapertural structures consisting of narrow metaflanges and chamber ornamented with leptocostae

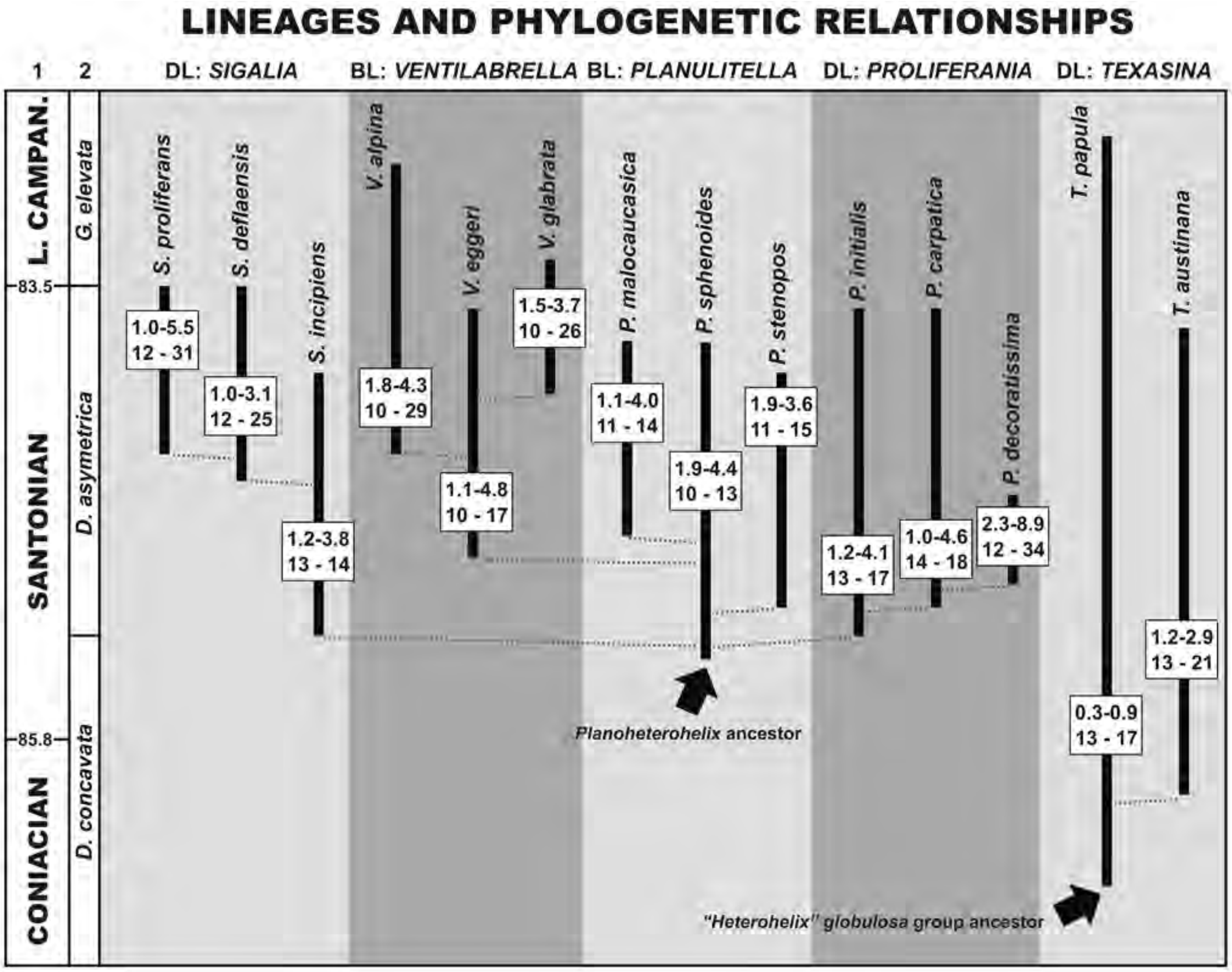


Figure 18. Stratigraphic distribution, inferred phylogenetic relationships and lineage architecture in the late Coniacian-early Campanian planktic foraminifera that developed a flaring adult stage with multichamber growth. 1 – Ages after Gradstein *et al.* (2004). 2 – Planktic foraminiferal standard zonation after Robaszynski & Caron (1995). DL – directional lineage, BL – branched lineage. The white squares include two paramount parameters in recognizing the evolutionary continuum: pore diameter in µm (top) and chamber number (bottom).

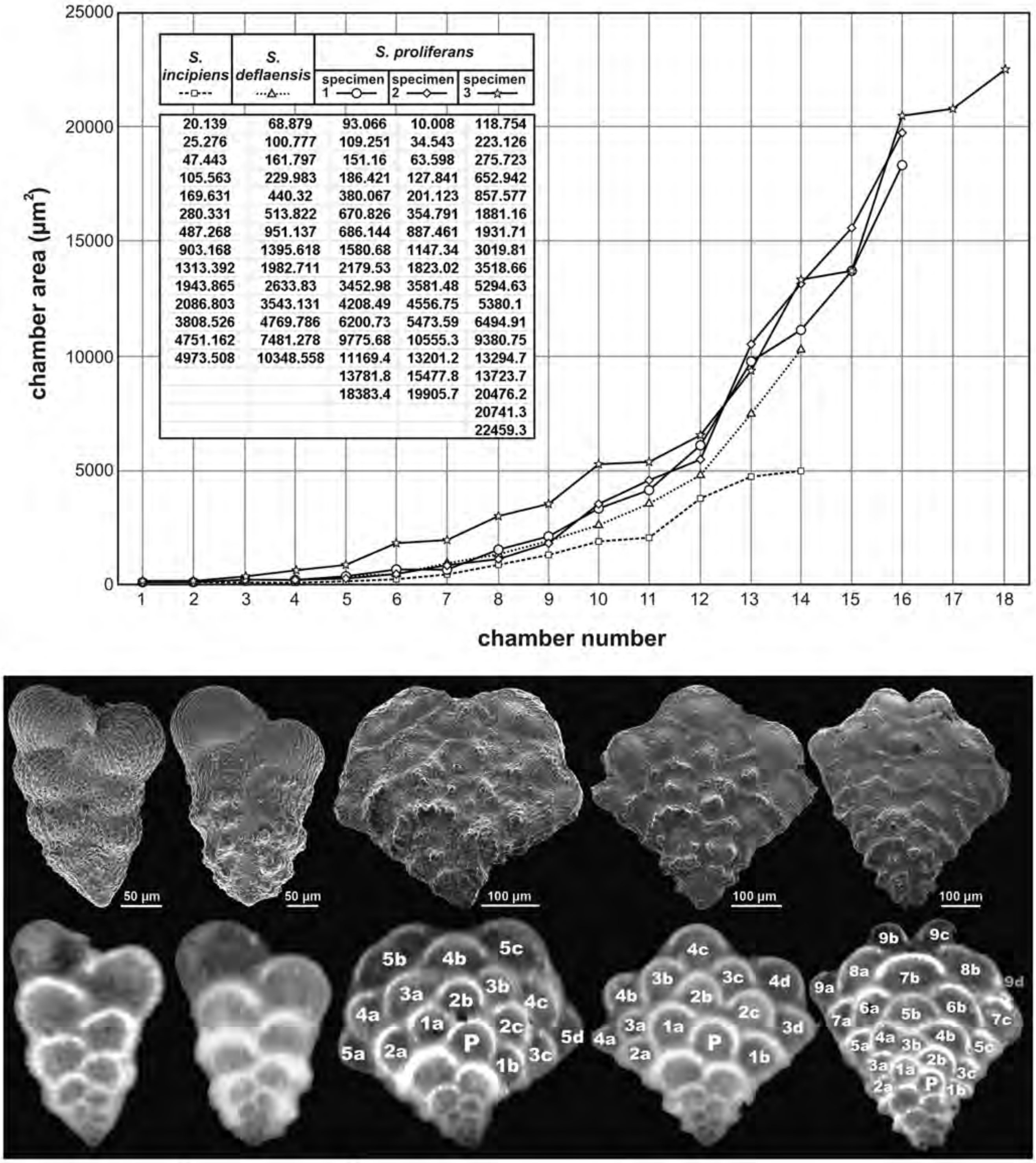
indicate that *T. papula* evolved from "*H.*" *globulosa*. Pores increase in size, being smaller in *T. papula* (0.3-0.9 µm) and larger (1.2-2.9 µm) in its descendant, *T. austinana*.

*Planulitella* is a new branched lineage, which consists of three species: *P. sphenoides*, *P. stenopos* and *P. malocaucasica* (Fig. 18). The former is the stem species. *Planulitella* evolved in the early Santonian (uppermost part of the *Dicarinella concavata* Biozone) from *Planoheterohelix* as indicated by similarities in its general test appearance, periapertural structures and chamber ornamentation. Representatives of this lineage have tests with a biserial chamber arrangement (Fig. 18) and can be recognized among the Cretaceous heterohelicids by the distinctly flattened test appearance. This branched lineage radiated two directional lineages (i.e., *Sigalia* and *Proliferania*) and one branched lineage (i.e., *Ventilabrella*) in the lower part of *D. asymetrica* Biozone). *Planulitella* became extinct in the upper part of the *D. asymetrica* Biozone, just before the Santonian/Campanian boundary.

*Sigalia* is one of the two directional lineages evolved from *Planulitella* in the lower part of the *D. asymetrica* Biozone (Fig. 18). It is emended as an evolutionary classification unit, resulting in the recognition of a directional lineage that consists of three species: *S. incipiens*, *S. deflaensis* and *S. proliferans*, two of which are new, namely *S. incipiens* and *S. proliferans*. Most significant morphological changes in this lineage regard development of the sutural ridges and adult flaring stage with multichamber growth. The earlier species of the directional lineage, *S. incipiens*, has depressed sutures or with calyptoridges; phaneroridges are developed only in *S. deflaensis* and *S. proliferans*. The development of a flaring adult stage with multiserial chamber growth is gradual; *S. incipiens* is completely biserial, *S. deflaensis* only ocassionally has incipient chamber proliferation in the adult stage (<15% of the total number of specimens) and *S. proliferans* is the only species that exhibits well-developed chamber proliferation. Ontogenetic trajectories reconstructed with the aid of the x-ray micrographs, show gradually increasing chamber area along the lineage, with the highest rates in the adult stage, apparently related to the adult stage with multichamber growth (Fig. 19). *Sigalia* became extinct at the Santonian/Campanian boundary.

The other directional lineage that began its evolution in the lower part of the *D. asymetrica* Biozone is formalized herein as *Proliferania*. It includes three species: *P. initialis*, *P. carpatica* and *P. decoratissima* (Fig. 18). Morphological changes in the evolution of this directional lineage show remarkable resemblances with those known from the directional lineage *Sigalia*. The earliest species, *P. initialis*, is biserial throughout and has depressed sutures or with calyptoridges. Its descendant, *P. carpatica*, is also biserial throughout but has well-developed phaneroridges. Multichamber growth is developed only in *P. decoratissima*, which is the end member of this directional lineage. Ontogenetic trajectories of the *Proliferania* species show that there is a significant decrease in chamber size between *P. initialis* and *P. carpatica*, followed by a marked increase with the development of the multichamber growth adult stage in *P. decoratissima* (Fig. 20). Noteworthy, the chamber shape in the adult stage of *P. decoratissima* strongly resembles that of the earlier chambers in *Orbitoides* d'Orbigny, 1848 (in Lyell, 1848), which further supports the phylogenetic relationships between planktic foraminifera as ancestors and large-sized orbitoidid benthics as descendants (Küpper, 1954; Van Hinte, 1965; Georgescu & Almogi-Labin, 2008). This study indicates that the adaptation to the benthic way of life was gradual and probably *P. carpatica* and/or *P. decoratissima* could have had at least a benthic stage during their life cycles.

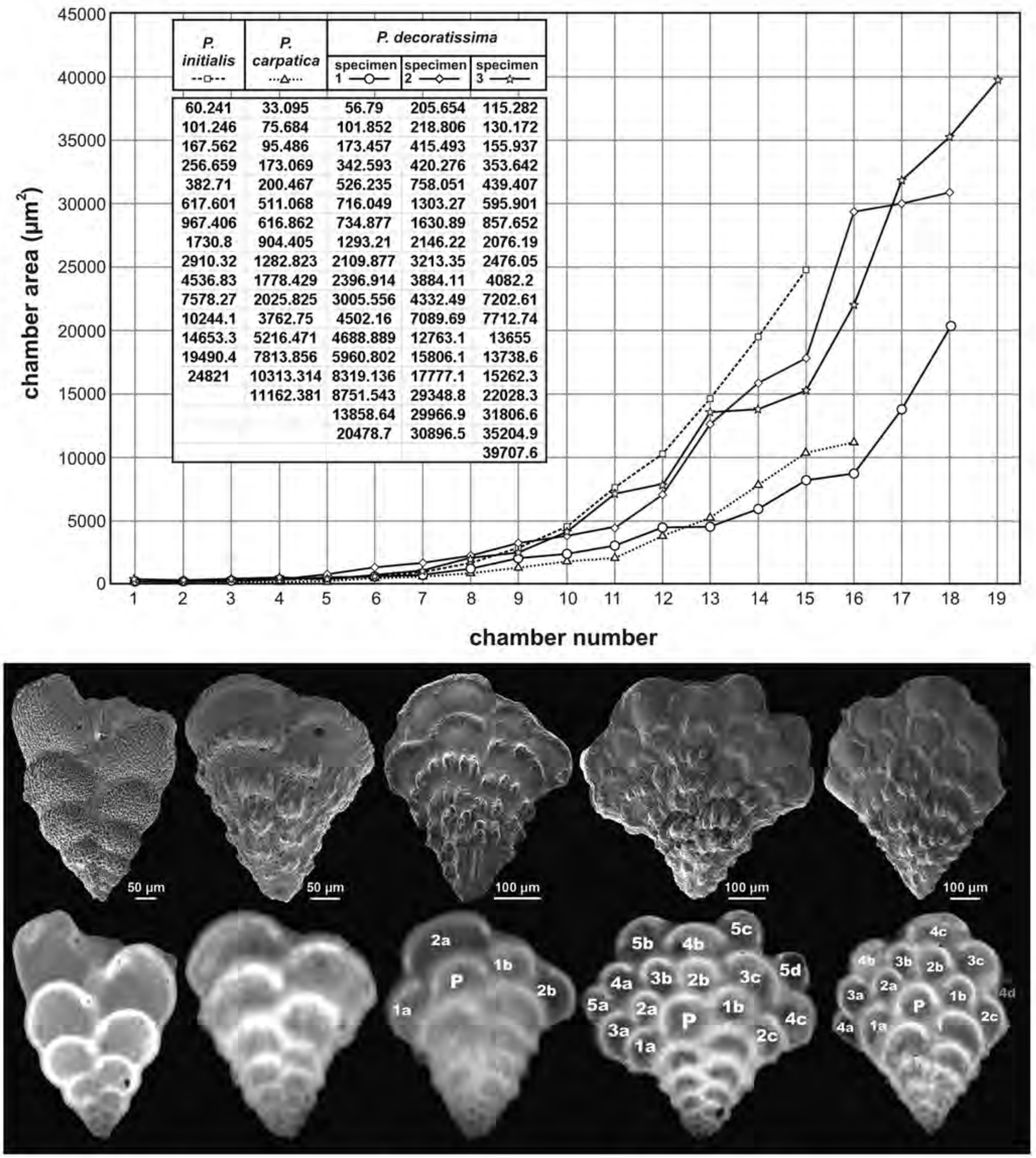
*Ventilabrella* is emended in this evolutionary classification as a branched lineage. It evolved from *P. sphenoides* in the late Santonian (*D. asymetrica* Biozone) as indicated by the similarities between this species and the early stages of all the species of *Ventilabrella*. The branched lineage consists of three species, *V. eggeri*, *V. alpina* and *V. glabrata* in which the former is the basal species (Fig. 18), which have depressed sutures throughout. *Ventilabrella eggeri* presents incipient multichamber growth stage consisting of the progressive chamber followed by two sets with two chambers each. Chamber proliferation is further developed in the two descendant species both in number and chamber area (Fig. 21). *Ventilabrella alpina* is the only species of the late Coniacian-early Campanian with chamber growth characterized by progressive and constant increase of chamber number in each successive set. *Ventilabrella* survived the heterohelicid extinction event at the Santonian/Campanian boundary and its range is extended in the early Campanian.



| *S. incipiens* --□-- | *S. deflaensis* ···△··· | *S. proliferans* specimen 1 —○— | specimen 2 —◇— | specimen 3 —☆— |
|---|---|---|---|---|
| 20.139 | 68.879 | 93.066 | 10.008 | 118.754 |
| 25.276 | 100.777 | 109.251 | 34.543 | 223.126 |
| 47.443 | 161.797 | 151.16 | 63.598 | 275.723 |
| 105.563 | 229.983 | 186.421 | 127.841 | 652.942 |
| 169.631 | 440.32 | 380.067 | 201.123 | 857.577 |
| 280.331 | 513.822 | 670.826 | 354.791 | 1881.16 |
| 487.268 | 951.137 | 686.144 | 887.461 | 1931.71 |
| 903.168 | 1395.618 | 1580.68 | 1147.34 | 3019.81 |
| 1313.392 | 1982.711 | 2179.53 | 1823.02 | 3518.66 |
| 1943.865 | 2633.83 | 3452.98 | 3581.48 | 5294.63 |
| 2086.803 | 3543.131 | 4208.49 | 4556.75 | 5380.1 |
| 3808.526 | 4769.786 | 6200.73 | 5473.59 | 6494.91 |
| 4751.162 | 7481.278 | 9775.68 | 10555.3 | 9380.75 |
| 4973.508 | 10348.558 | 11169.4 | 13201.2 | 13294.7 |
|  |  | 13781.8 | 15477.8 | 13723.7 |
|  |  | 18383.4 | 19905.7 | 20476.2 |
|  |  |  |  | 20741.3 |
|  |  |  |  | 22459.3 |

| *S. incipiens* | *S. deflaensis* | *S. proliferans* specimen 1 | *S. proliferans* specimen 2 | *S. proliferans* specimen 3 |
|---|---|---|---|---|
| Sample: DSDP<br>10-95-15-6, 104-118 cm | Sample: DSDP<br>10-95-14-1, 99-112 cm | Sample: DSDP<br>10-95-14-1, 99-112 cm | Sample: DSDP<br>10-95-14-1, 99-112 cm | Sample: DSDP<br>10-95-13-3, 78-92 cm |

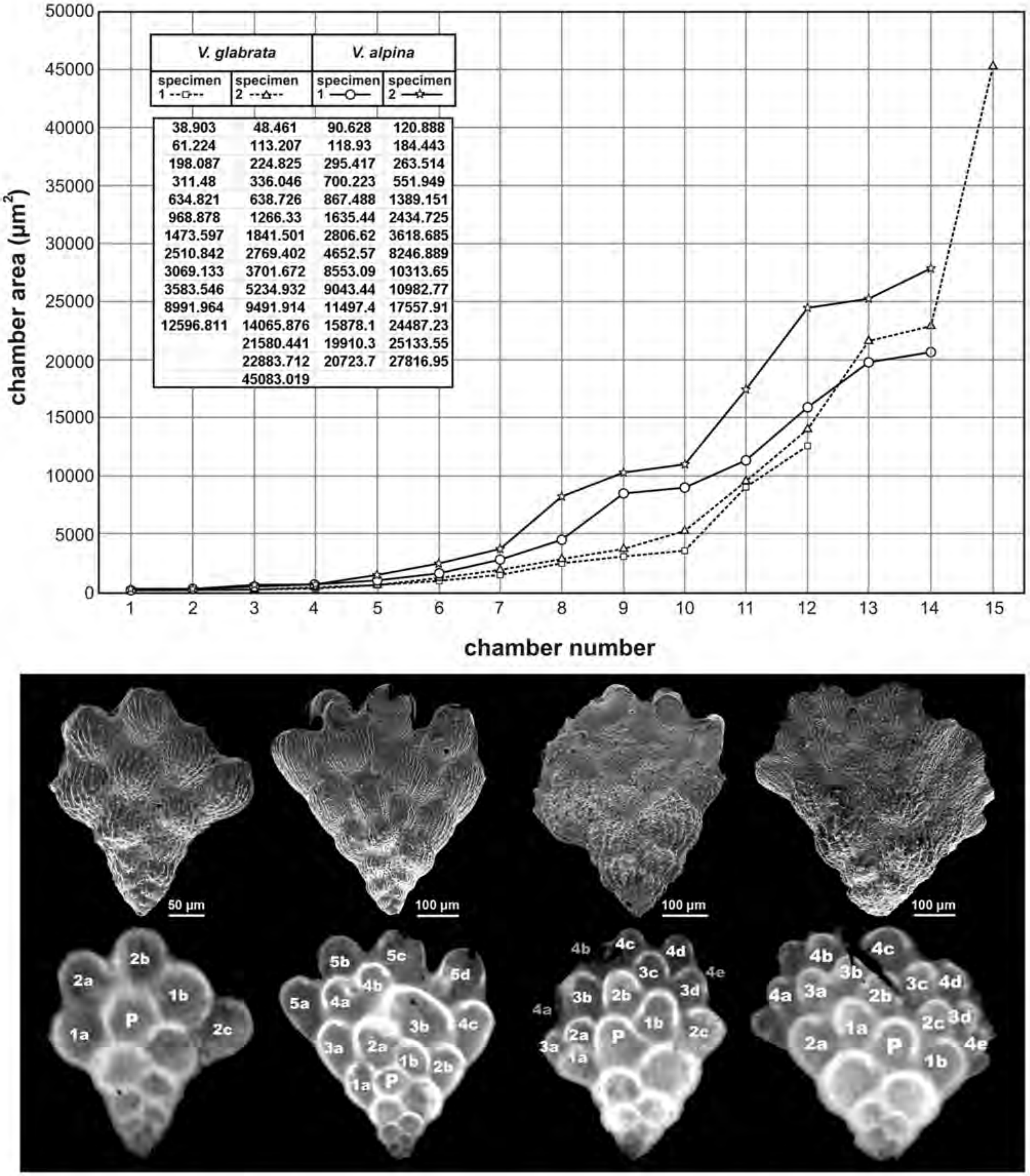
Figure 19. Ontogenetic trajectories for five specimens of the *Sigalia* directional lineage. Note the gradual increase in test size with the development of multichamber growth in *S. deflaensis* and *S. proliferans*.



| *P. initialis* --□-- | *P. carpatica* ···△··· | *P. decoratissima* specimen 1 —○— | | |
|---|---|---|---|---|
| | | specimen 1 —○— | specimen 2 —◇— | specimen 3 —☆— |
| 60.241 | 33.095 | 56.79 | 205.654 | 115.282 |
| 101.246 | 75.684 | 101.852 | 218.806 | 130.172 |
| 167.562 | 95.486 | 173.457 | 415.493 | 155.937 |
| 256.659 | 173.069 | 342.593 | 420.276 | 353.642 |
| 382.71 | 200.467 | 526.235 | 758.051 | 439.407 |
| 617.601 | 511.068 | 716.049 | 1303.27 | 595.901 |
| 967.406 | 616.862 | 734.877 | 1630.89 | 857.652 |
| 1730.8 | 904.405 | 1293.21 | 2146.22 | 2076.19 |
| 2910.32 | 1282.823 | 2109.877 | 3213.35 | 2476.05 |
| 4536.83 | 1778.429 | 2396.914 | 3884.11 | 4082.2 |
| 7578.27 | 2025.825 | 3005.556 | 4332.49 | 7202.61 |
| 10244.1 | 3762.75 | 4502.16 | 7089.69 | 7712.74 |
| 14653.3 | 5216.471 | 4688.889 | 12763.1 | 13655 |
| 19490.4 | 7813.856 | 5960.802 | 15806.1 | 13738.6 |
| 24821 | 10313.314 | 8319.136 | 17777.1 | 15262.3 |
| | 11162.381 | 8751.543 | 29348.8 | 22028.3 |
| | | 13858.64 | 29966.9 | 31806.6 |
| | | 20478.7 | 30896.5 | 35204.9 |
| | | | | 39707.6 |

| *P. initialis* | *P. carpatica* | *P. decoratissima* | | |
|---|---|---|---|---|
| | | specimen 1 | specimen 3 | specimen 2 |
| Sample: DSDP<br>10-95-14-1, 99-112 cm | Sample: DSDP<br>10-95-15-2, 73-87 cm | Sample: DSDP<br>10-95-15-2, 73-87 cm | Sample: Eureka 67-128 well,<br>depth1662.23 mbsl | Sample: Eureka 67-128 well,<br>depth1662.23 mbsl |

Figure 20. Ontogenetic trajectories for five specimens of the *Proliferania* directional lineage. Note the significant decrease in the rate of chamber increase of size between *P. initialis* and *P. carpatica*, probably documenting a significant change in the growth strategy.



| *V. glabrata* | | *V. alpina* | |
|---|---|---|---|
| specimen 1 --□-- | specimen 2 --△-- | specimen 1 —○— | specimen 2 —☆— |
| 38.903 | 48.461 | 90.628 | 120.888 |
| 61.224 | 113.207 | 118.93 | 184.443 |
| 198.087 | 224.825 | 295.417 | 263.514 |
| 311.48 | 336.046 | 700.223 | 551.949 |
| 634.821 | 638.726 | 867.488 | 1389.151 |
| 968.878 | 1266.33 | 1635.44 | 2434.725 |
| 1473.597 | 1841.501 | 2806.62 | 3618.685 |
| 2510.842 | 2769.402 | 4652.57 | 8246.889 |
| 3069.133 | 3701.672 | 8553.09 | 10313.65 |
| 3583.546 | 5234.932 | 9043.44 | 10982.77 |
| 8991.964 | 9491.914 | 11497.4 | 17557.91 |
| 12596.811 | 14065.876 | 15878.1 | 24487.23 |
| | 21580.441 | 19910.3 | 25133.55 |
| | 22883.712 | 20723.7 | 27816.95 |
| | 45083.019 | | |

| *V. glabrata* | | *V. alpina* | |
|---|---|---|---|
| specimen 1 | specimen 2 | specimen 1 | specimen 2 |
| Sample: ODP Leg 174AX, 505.35-505.38 mbsf | Sample: ODP Leg 174AX, 505.35-505.38 mbsf | Sample: DSDP 10-95-13-3, 78-92 cm | Sample: DSDP 10-95-13-3, 78-92 cm |

Figure 21. Ontogenetic trajectories for four specimens of the *Ventilabrella* branched lineage. Note the similarities in the earlier ontogenetic stages and significant increase in test size with the increase in number of chamber sets in the adult stage.

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# Palaeogeographical distribution of *Pseudomphalocyclus blumenthali* Meriç (Foraminiferida) in the Maastrichtian of the eastern central Tethys with a short taxonomical review of some orbitoidid Foraminifera

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## Resumen

Los foraminíferos orbitoideos incluyen bien conocidos e importantes fósiles guía de edad Campaniense superior-Maastrichtiense de los géneros *Orbitoides*, *Omphalocyclus* y *Lepidorbitoides*. En el presente artículo se analizan nuevos datos sobre el género *Pseudomphalocyclus* Meriç, 1980. *P. blumenthali,* que es su especie tipo, fue originalmente descrita en el Maastrichtiense de Turquía. Nuevos estudios indican su presencia en el noreste de Somalia. Este estudio se centra en la distribución paleogeográfica y el significado paleoambiental de *P. blumenthali*, los orbitoideos asociados y otros foraminíferos bentónicos como *Loftusia*. Los nuevos registros somalíes junto con la fauna asociada, documentan la distribución de *P. blumenthali* en medios marinos poco profundos de ambas orillas de la zona central del Tethys, y su estatus como posible fósil guía para el Maastrichtiense tardío de la región. Las asociaciones faunísticas maastrichtienses de Turquía y Somalia son bastante similares. Probablemente, esto también pueda aplicarse a los de las plataformas de Arabia que están situadas entre Turquía y Somalia, es decir, el noreste de Siria, norte de Irak, Irán, Arabia Saudita, Qatar, Omán y Yemen que tienen características similares en términos de contenido faunístico de foraminíferos loftusoides y orbitoideos.

**Palabras clave:** *Pseudomphalocyclus*, taxonomía, Maastrichtiense, paleogeografía, paleoambiente, Tethys.

## Abstract

Orbitoid Foraminifera include important upper Campanian-Maastrichtian index forms such as the well known genera *Orbitoides, Omphalocyclus* and *Lepidorbitoides*. In the present paper we review new data related to genus *Pseudomphalocyclus* Meriç, 1980. The type species, *P. blumenthali* was originally described from the Maastrichtian of Turkey. Now this species can be shown to be present not only in several Turkish localities but also in northeastern Somalia. This study focuses on the palaeogeographical distribution and palaeoenvironmental significance of *Pseudomphalocyclus blumenthali* and associated orbitoids and other larger benthic Foraminifera, like *Loftusia*. New findings of *P. blumenthali* in Somalia together with its associated fauna document distribution of this species in the shallow marine environments on both sides of the central Tethyan Ocean and its status as a possible index fossil for the Late Maastrichtian of the region. Maastrichtian faunal associations in Turkey and Somalia appear rather similar. This most probably also applies to the Arabian platforms situated between Turkey and Somalia, namely northeast Syria, northern Iraq, Iran, Saudi Arabia, Qatar, Oman and Yemen which have similar features in terms of loftusiid and orbitoid foraminiferal faunal contents.

**Key words**: *Pseudomphalocyclus*, taxonomy, Maastrichtian, palaeogeography, palaeoenvironment, Tethys.

## 1. INTRODUCTION

*Pseudomphalocyclus blumenthali* has been described for the first time from Kalkanya area of Turkey located between Ulukışla and Pozantı (eastern Taurides) by Meriç (1980). Subsequently, it was recorded from various localities of Maastrichtian shallow marine carbonates of Turkey exclusively. These are: Haymana and Polatli (Ankara) (Sirel *et al.*, 1986), Kahta (Adıyaman) (Meriç, 1987),Tecer Mountains and Koyulhisar (Sivas) and Ulukışla (Niğde) (İnan, 1988 a-c; 1992), Hekimhan (Malatya) (Görmüş, 1990, 1994; Bozkaya, 1991), Koyulhisar (Sivas) (İnan *et al.*, 1992; Yalçın & İnan, 1992; İnan, 1996), Gerger (Adıyaman) (Özcan, 1993) (for all locations in Turkey see Fig. 1).

More recently, it has also been found in the Maastrichtian shallow-marine limestones of the Auradu Formation of various localities of northeastern Somalia in the easternmost Ahl Medo and the Ahl Meskat mountain areas by Luger & Dominik (2007, 2009). As the Turkish locations and northeastern Somalia are located either on the northern or southern margin of the Maastrichtian central Tethyan Ocean (see Fig. 2), embracing the broad Late Cretaceous Arabian carbonate platform (with also well known Maastrichtian shallow marine foraminiferal faunas) in between, it appears worthwhile to discuss the palaeogeography of the genus (and associated foraminiferal faunas) and for a better understanding of the latest Cretaceous orbitoid foraminiferal genera - at first to give a brief historical and taxonomical overview of the related genera (e.g. *Orbitoides, Lepidorbitoides* and *Omphalocyclus*).

## 2. MORPHOLOGY AND HISTORICAL BACKGROUND OF SELECTED LATE CRETACEOUS ORBITOIDS

A typical omphalocyclinid test is relatively smaller than the biconvex test of *Orbitoides* (with more or less clearly developed lateral chamberlets) and has a biconcave disc-shaped test. Principally, it is composed of equatorial chamberlets without lateral chamberlets (Fig. 3). The first recognised genus *Omphalocyclus* is well documented

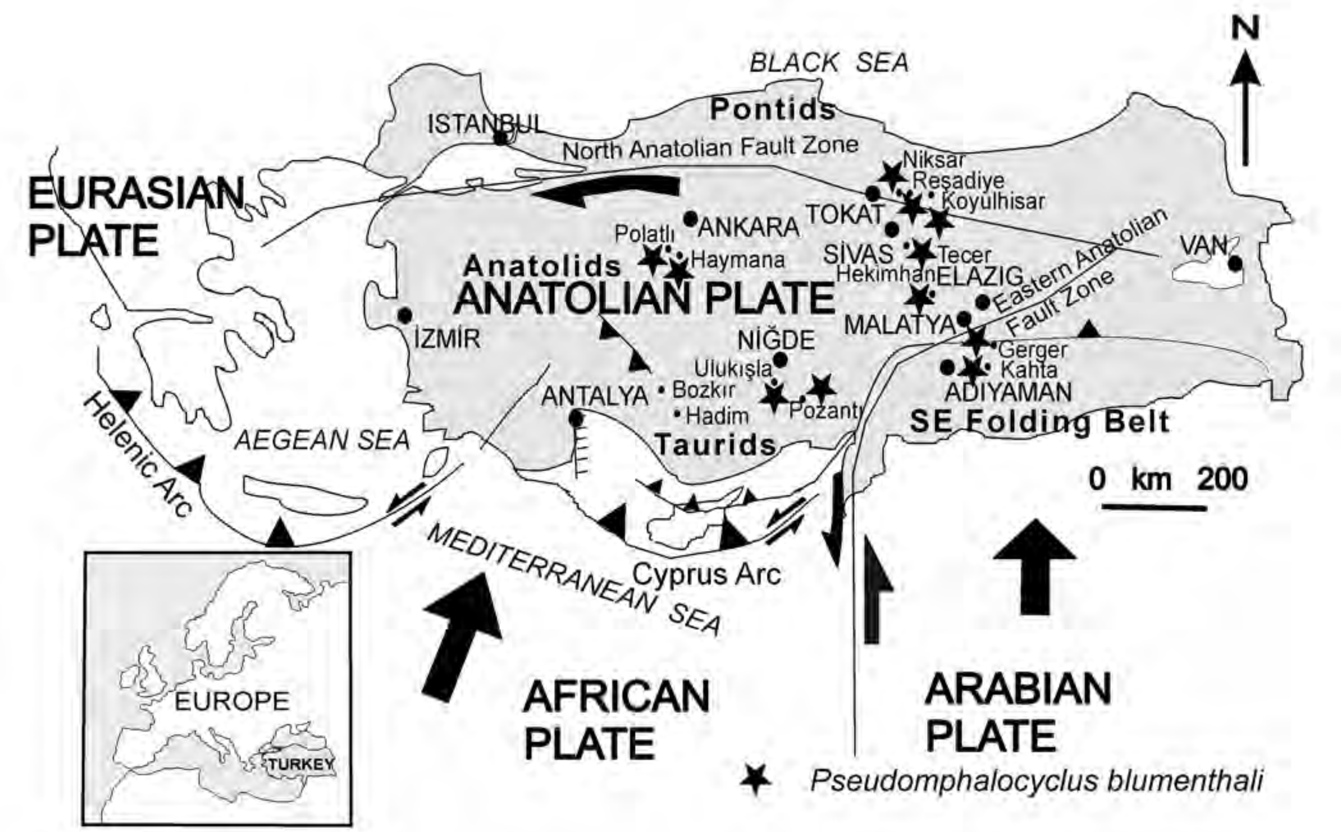

Figure 1. Distribution of *P. blumenthali* in Turkey (modified from Şengör & Yılmaz, 1981; Sintubin *et al.*, 2003; Görmüş & Nielsen, 2006).

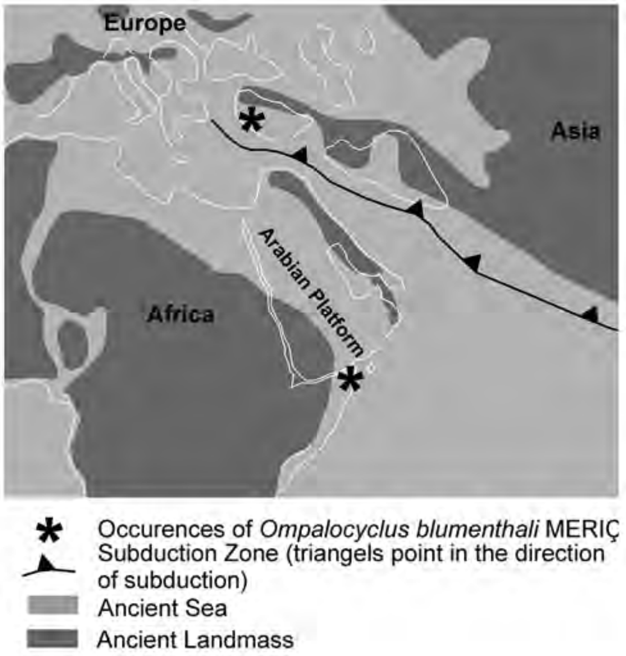

Figure 2. Distribution of *P. blumenthali* in the Tethyan Ocean during the Maastrichtian. Redrawn after http://www.scotese.com/K/t.htm. Not explained within the figure: Thin white lines indicate modern landmasses.

from the Late Cretaceous (Maastrichtian) Tethyan Ocean. It was first named O*rbitulites macropora* by Lamarck (1816). Bronn (1853) introduced the generic name *Omphalocyclus* for this species. It is characterised by a centrally depressed disc-shaped test with one, two or three rows of equatorial chamber layers without lateral chamberlets. More recently, quantitative studies of the genus *Omphalocyclus* from Turkey revealed the presence of two new species identified as *O. anatoliensis* and *O. cideensis* (Özcan, 2007). However, the age of the genus is controversial. Therefore faunal associations of the genus with other benthic Foraminifera such as *Loftusia* spp., *Siderolites calcitrapoides* and planktonic Foraminifera should be studied in detail. Later on the genus *Pseudomphalocyclus* from the Maastrichtian of Turkey was recognised by Meriç (1980) based on an omphalocyclinid species showing lateral chamberlets (Fig. 3); thus easily to be differentiated from *Omphalocyclus*.

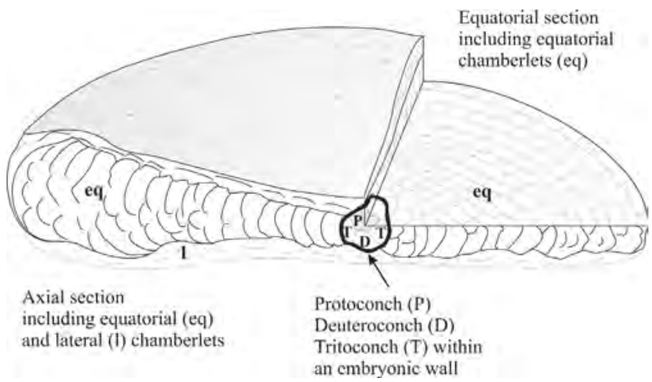

Figure 3. Schematic three dimensional view of *P. blumenthali* to show its external and internal features.

A third genus, *Praeomphalocyclus*, was erected by Meriç & Çoruh (1991) for the species *concavatus*, which had originally been attributed to *Orbitoides* by Rahaghi (1976) and first been described form the Campanian of Iran. This genus is characterised by a heterohelicid initial stage of the microspheric forms and presents only one equatorial layer. Up to now, last genus of similar Foraminifera is *Postomphalocyclus* İnan (1992). It has been recorded from the Maastrichtian of Turkey - which is similar to *Pseudomphalocyclus* (Fig. 4). A transitional form between *Praeomphalocyclus* and *Omphalocyclus* was reported from NW Siirt, Çelikli Well, SE Anatolia (Meriç & Çoruh, 1991) but it was not named as a genus of the omphalocyclinids yet due to insufficient material (see Fig. 4).

Presently all these genera are grouped within the Orbitoididae, together with the biconvex group of *Orbitoides* (and closely related forms with more or less well developed lateral chambers); *Pseudomphalocyclus* and *Postomphalocyclus* are even comprised within the Orbitoidinae due the development of lateral chambers. All of these are separated from the Lepidorbitoidae by their trilocular or quadrilocular embryonic stages within a periembryonic wall instead of bilocular embryonic macrospheric initial stages in the Lepidorbitiodidae, which may in some cases show similar vertical cross-sections (see Fig. 4 for a compilation).

## 3. PALAEOGEOGRAPHICAL DISTRIBUTION OF *PSEUDOMPHALOCYCLUS BLUMENTHALI* MERİÇ

In the lights of the plate tectonic reconstruction and discussions for the Late Cretaceous (Şengör & Yılmaz, 1981; Luger *et al.*, 1994; Luger, 2003), the distribution of *P. blumenthali* on the Gondwana and Laurasia platforms can be

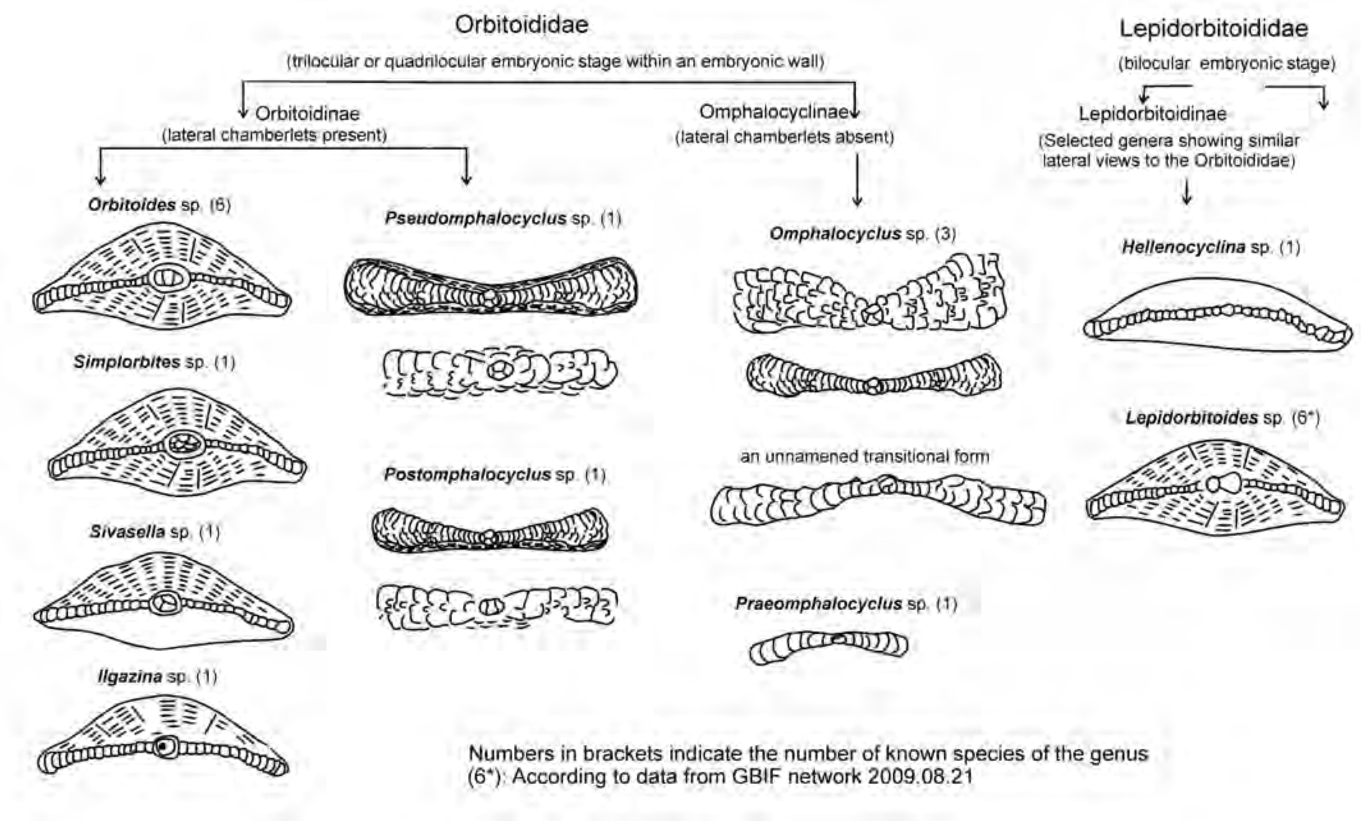

Figure 4. Comparison of closely related Late Cretaceous orbitoid foraminiferal genera discussed in the present paper.

summarized as follows (see Figs. 1, 4a). Examples of thin sections of *P. blumenthali* from Turkey are shown in figure 5; those of northeastern Somalia in figure 6.

Pontid Platform: This platform covers NW and Northern Turkey (Fig. 1). Occurrences of *P. blumenthali* on this platform are in the Reşadiye, Niksar (Tokat) and Koyulhisar (Sivas) areas (Fig. 1). Table 1 shows the larger foraminiferal associations in the platform.

Anatolid Platform: The Anatolid platform was located between the Pontid and Taurid platforms (Fig. 1). *P. blumenthali* was found in the Haymana and Polatli (Ankara) areas (Fig. 1). Shallow water clastic carbonates contain the larger Foraminifera (Sirel *et al.*, 1986, Table 1).

Taurid Platform: This region extends from south of Greece to the city of Van throughout Antalya region in SW Turkey, Hadim-Bozkır, Malatya and Elazığ in the northern part of the Tethyan Ocean (Fig. 1). *P. blumenthali* was recorded from the following localities of the platform: Kalkankaya (Ulukişla-Niğde), Pozanti (Adana), Hekimhan (NW Malatya) and Tecer (Sivas).

Arabian Platform (Turkish part): In the Kahta and Gerger (Adıyaman) areas on the NW platform in SE Anatolia, Turkey - (Fig. 1). Table 1 shows larger benthics with *P. blumenthali* in the platform.

Northeast African Platform: The new findings of *P. blumenthali* Meriç (Luger, this paper, Fig. 6) are recorded from the Maastrichtian of northeastern Somalia, which formed the southeastern margin of the central Tethys during the Cretaceous (Luger & Dominik, 2007, 2009) (Table 1). These were recovered in the northeastern Ahl Medo - and the western Ahl Meskat Mountains (in the sections at Tisje, Biyo Kulule and Galgalo [see: sections Tis, BKu, Gal in location map in: http://AdG2007.gfz-potsdam.de/fileadmin/GFZ/site_graphik/adg/pdf/adg__20070707_08_ Luger.pdf: Fig. 2; examples of the Biyo Kulule and the Tisje sections are also given therein as Figs. 12, 13] or Luger & Dominik, 2009: Fig. 1; Fig. 5: here in samples Tis 9, 10, 18, 19, 21).

The Maastrichtian sediments of northeastern Somalia – forming the lowermost Auradu Formation in these areas -

are generally made up of carbonates with only minor siliciclastic contents. These marls and limestones are mostly rich in fossils, typically shallow marine macrofossils (e.g. rudists [see: Pons *et al.*, 1992] and corals etc.; no ammonites) and contain rich and diverse microfossil assemblages (Foraminifera, Ostracoda). The foraminiferal faunas directly associated with *P. blumenthali* are shown in Table 1.

<table>
<tr><th>Pontid [1]</th><th>Anatolid [2]</th><th>Taurid [3]</th><th>Arabian [4]</th><th>Northeast African[5]</th></tr>
<tr><td>*Orbitoides gruenbachensis* Papp<br>*Dizerina anatolica* Meriç<br>*Ilgazina unilateralis* Erdoğan<br>*Nummofallotia kastamonica* Özgen-Erdem<br>*Sirelina orduensis* Meriç & İnan</td><td colspan="2">*Cuneolina ketini* İnan<br>*Loftusia ketini* Meriç<br>*Loftusia turcica* Meriç & Avşar<br>*Pseudedomia hekimhanensis* Görmüş</td><td>*Broeckinella arabica* Henson<br>*Clypeorbis mamillata* (Schlumberger)<br>*Goupillaudina schirazensis* Rahaghi<br>*Loftusia arabica El Asa'ad*<br>*Loftusia kahtaensis* Meriç<br>*Loftusia matsumarui* Meriç & Görmüş</td><td>*Fallotia jacquoti* Douvillé<br>*Gyroconulina columellifera* Schröder & Darmorian<br>*Loftusia coxi* Henson sensu Meriç and Görmüş<br>*Pseudedomia hamaouii* Rahaghi</td></tr>
<tr><td colspan="3"></td><td colspan="2">*Pseudorbitolina* cf. *marthae* Douvillé</td></tr>
<tr><td colspan="3">*Cideina soezerii* (Sirel)<br>*Hellenocyclina beotica* Reichel<br>*Laffitteina marsicana* Farinacci<br>*Postomphalocyclus merici* İnan<br>*Selimina spinalis* İnan<br>*Smoutina cruysi* Drooger</td><td colspan="2"></td></tr>
<tr><td colspan="4">*Lepidorbitoides minor* (Schlumberger)<br>*Lepidorbitoides socialis* (Leymerie)<br>*Loftusia anatolica* Meriç<br>*Simplorbites papyraceus* Boubeé<br>*Siderolites denticulatus* Douvillé<br>*Sirtina orbitoidiformis* Brönnimann<br>*Siderolites calcitrapoides* Lamarck</td><td></td></tr>
<tr><td colspan="5">*Omphalocyclus macroporus* (Lamarck)<br>*Orbitoides apiculatus* Schlumberger<br>*Orbitoides medius* (d'Archiac)<br>***Pseudomphalocyclus blumenthali*** Meriç</td></tr>
<tr><td></td><td></td><td colspan="2">*Loftusia baykali* Meriç<br>*Loftusia oktayi* Meriç<br>*Sulcoperculina globulosa* de Cizancourt<br>*Sulcoperculina obesa* de Cizancourt<br>*Sulcoperculina vermunti* (Thiadens)</td><td></td></tr>
<tr><td></td><td></td><td colspan="3">*Antalyna korayi* Farinacci & Köylüoğlu<br>*Loftusia elongata* Cox<br>*Loftusia harrisoni* Cox<br>*Loftusia minor* Cox<br>*Loftusia morgani* Douvillé</td></tr>
</table>

Table 1. Comparison of larger benthic foraminifera of the platforms. Differently shaded parts show genera distribution on the platforms ([1]İnan *et al.*, 1992; Yalçın & İnan, 1992; [2]Sirel *et al.*, 1986; [3]Meriç, 1980; İnan, 1988 a-c; 1992; Görmüş, 1990, 1994; Bozkaya, 1991; [4]Meriç, 1987; Özcan, 1993; [5]Silvestri, 1948; Ducci & Pirini-Radrizzani, 1969; Cherchi *et al.*, 1993; Luger & Dominik, 2007, 2009).

## 4. DISCUSSION

The northern Tethyan Ocean included Pontid, Anatolid, Taurides and the northern Arabian platforms, while Somalia was located at southern part of the Ocean (see: Fig. 2). *P. blumenthali* is observed on both sides of the Ocean according to the obtained data. The Maastrichtian foraminiferal associations in Turkey and northern Somalia appear similar. Between them, the Arabian platform including northeast Syria, north Iraq, Iran, Saudi Arabia, Qatar and Oman have similar features in the views of microfaunal associations such as loftusiid and orbitoidal foraminiferal faunal contents (Meriç & Görmüş, 2001).

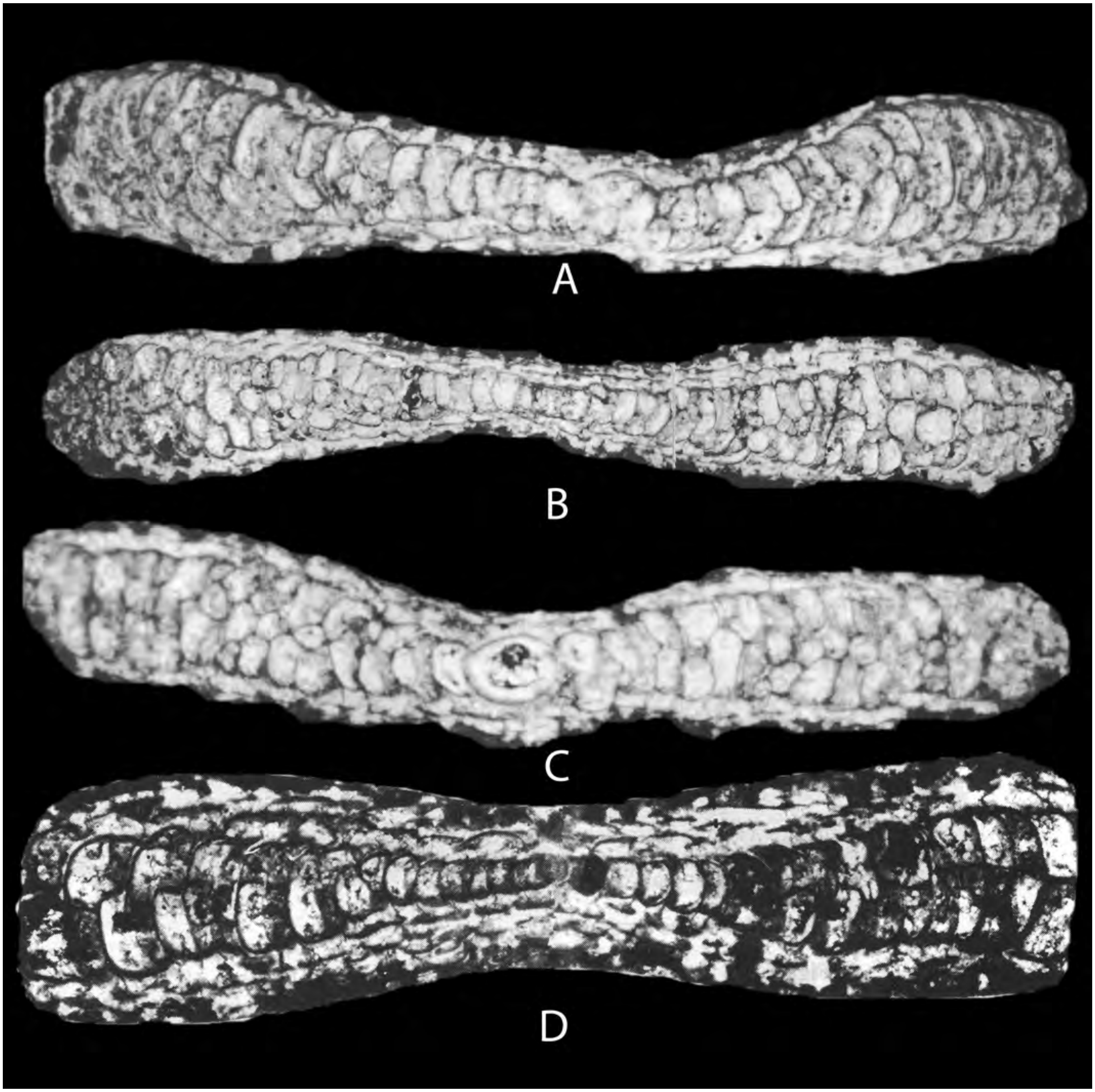

Figure 5. *P. blumenthali* from Turkey, A: Axial section, x 31, Horoz village (Pozanti-Adana), B: Transverse section, x 31, Horoz village (Pozanti-Adana), C: Axial section, x 54, Kalkankaya (Ulukişla, Niğde) (from Meriç, 1980), D: Transverse section, x 50, Tecer (Sivas) (from İnan, 1988b).

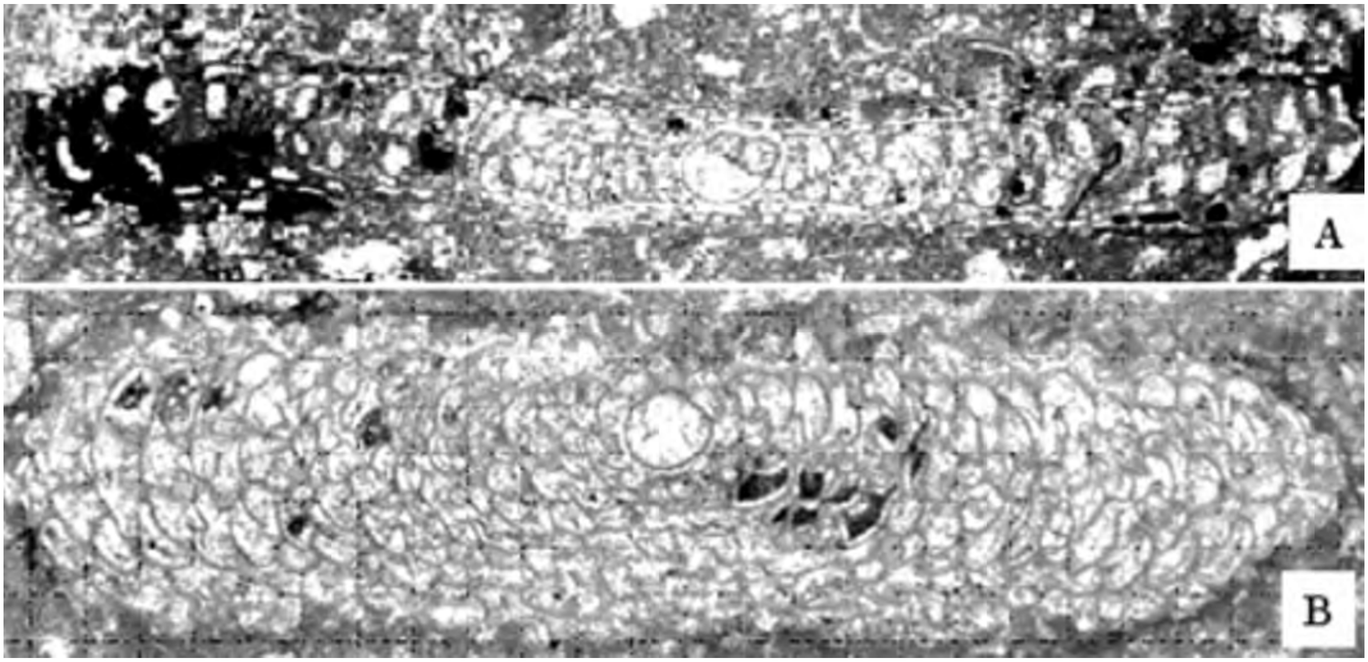

Figure 6. *P. blumenthali* from northeastern Somalia, A. axial section, x 60, Tisje section, B. oblique section, x 36.5, Galgalo section. (For locations see Luger *et al*., 1994 or Luger & Dominik, 2007, 2009).

Apart from the mentioned areas, the Sharwayn Formation in Yemen (66 meters in thickness) contains from bottom to top marl, clay, marly limestone, marl and marly limestones of Late Cretaceous age. Its fauna was reported as *Loftusia persica* Brady, *L. morgani* Douvillé, *Lepidorbitoides minor* (Schlumberger), *L. socialis* (Leymerie) and *Omphalocyclus macroporus* (Lamarck) (Beydoun, 1964; Beydoun & Greenwood, 1968; Beydoun *et al*., 1998). Goldbeck & Langer (2009) have presented biogeographic provinces in selected upper Cretaceous larger foraminifera.

It is expected that further findings of *P. blumenthali* Meriç may also be possible in the other localities of the Arabian platforms. A schematized model for the Maastrichtian foraminiferal paleoenvironment is given in Fig. 7. Assemblages with *Pseudomphalocyclus*, *Orbitoides*, *Siderolites* and *Omphalocyclus* can be found in close proximity to shallow water rudist reefs and are hardly ever associated with the open marine globotruncanid facies.

## 5. OUTLOOK

The genera *Praeomphalocyclus,* the transitional form, *Omphalocyclus, Pseudomphalocyclus* and *Postomphalocyclus* should be supported with new observations. Therefore, quantitative studies of the external and internal test parameters of the genera with palaeoenvironmental and stratigraphical data may provide valuable findings. Furthermore it is to be expected that future studies in the neighbouring or intermediate areas to those discussed in this paper will provide additional observations on the palaeogeographical distribution of the named foraminiferal genera.

## 6. CONCLUSIONS

All faunal associations, including the new occurrences of *P. blumenthali* are found in carbonate sediments; and both - sedimentary facies and fauna - are strongly indicative of very shallow water palaeoenvironments. The species *P. blumenthali* is definitely to be regarded as an index fossil of the Maastrichtian; moreover it may have been restricted to the Late Maastrichtian as in Turkey the faunal associations - which occur together with *P. blumenthali* - indicate a later to Late Maastrichtian age (Meriç, 1980; Çoruh *et al*., 1997; Özer *et al*., 2009). In northern Somalia this can not be proved with certainty, since there the Campanian/ Maastrichtian boundary deposits are made up of unfossiliferous siliciclastic sediments.

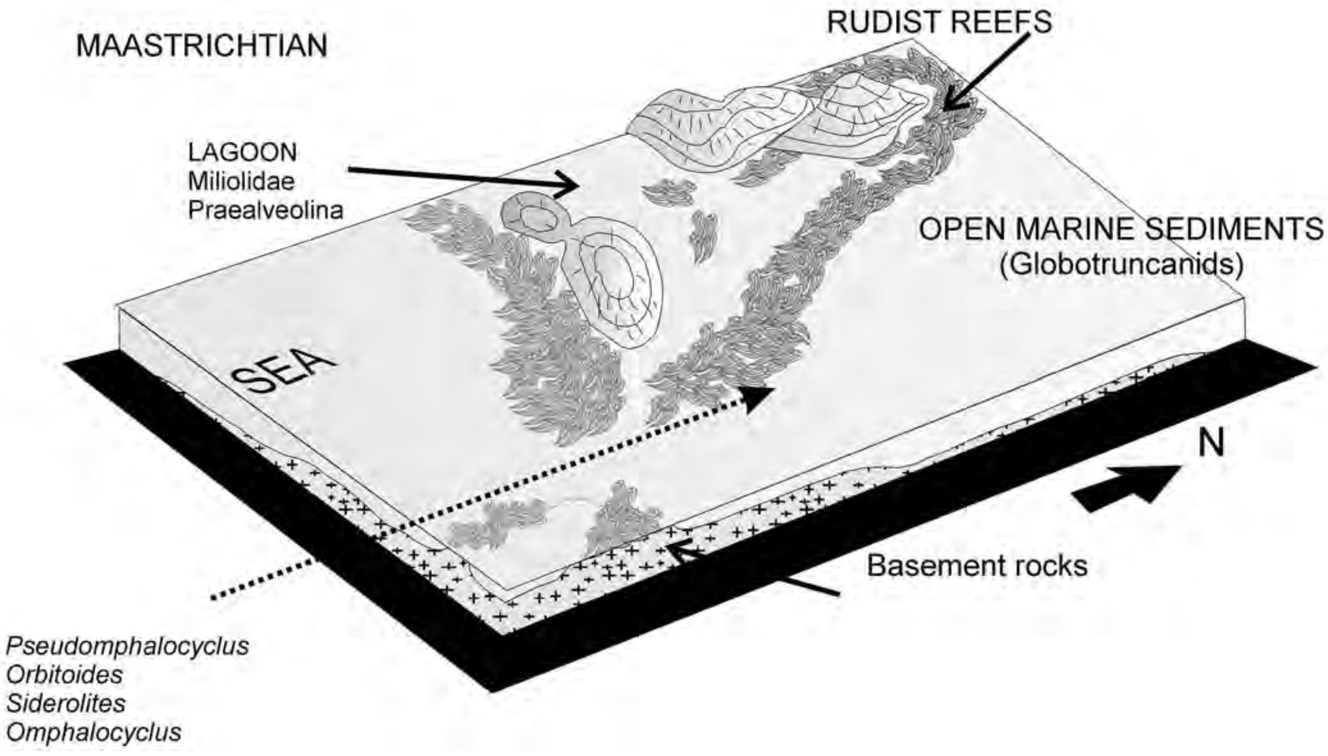

Figure 7. Paleoenvironmental approach to the late Cretaceous larger benthonic Foraminifera from eastern Anatolia (modified from Görmüş & Nielsen, 2006).

## 7. ACKNOWLEDGEMENTS

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Müller, A. H. 1979. Fossilization (Taphonomy). In: *Treatise on Invertebrate Paleontology* (Eds. R. A. Robison and C. Teichert). The University of Kansas Press & The Geological Society of America, Boulder, 2-78.

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