

The phylogenetic and palaeographic evolution of the miogypsinid larger benthic foraminifera

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Abstract

One of the notable features of the Oligocene oceans was the appearance in Tethys of American lineages of larger benthic foraminifera, including the miogypsinids. They were reef-forming, and became very widespread and diverse, and so they play an important role in defining the Late Paleogene and Early Neogene biostratigraphy of the carbonates of the Mediterranean and the Indo-Pacific Tethyan sub-provinces. Until now, however, it has not been possible to develop an effective global view of the evolution of the miogypsinids, as the descriptions of specimens from Africa were rudimentary, and the stratigraphic ranges of genera of Tethyan forms appear to be highly dependent on palaeogeography. Here we present descriptions of new samples from offshore South Africa, and from outcrops in Corsica, Cyprus, Syria and Sumatra, which enable a systematic and biostratigraphic comparison of the miogypsinids from the Tethyan sub-provinces of the Mediterranean-West Africa and the Indo-Pacific, and for the first time from South Africa, which we show forms a distinct bio-province. The 116 specimens illustrated include 7 new species from the Far East, *Neorotalia tethyana*, *Miogypsinella bornea*, *Miogypsina subiensis*, *M. niasiensis*, *M. regularia*, *M. samuelia*, *Miolepidocyclina banneri*, 1 new species from Cyprus, *Miogypsinella cyprea* and 4 new species from South Africa, *Miogypsina mcmillania*, *M. africana*, *M. ianmacmilliana*, *M. southernia*. We infer that sea level, tectonic and climatic changes determined and constrained in turn the palaeogeographic distribution, evolution and eventual extinctions of the

miogypsinid. The global sea level regressions in the Early Oligocene facilitated trans-Atlantic migration of *Neorotalia* and miogypsinids from the Americas. This eastward migration followed two, distinct, unidirectional dispersals. One dispersal route was to the south towards South Africa, where distinct miogypsinids phylogenetic lineage similar to their American ancestors were found in the Burdigalian. They became extinct together with their American ancestors, at the end of the Burdigalian; a time that coincided with a major global transgressions, circulation changes on closure of Panama and the major, globally significant eruption of the Columbia River Flood basalts. The other route was to the north, through the Tethyan Mediterranean corridor. Our observations indicate that during the Chattian and Aquitanian significant miogypsinid forms evolved in the Mediterranean from the morphologically distinct Tethyan *Neorotalia* and migrated, within a few million years of their first appearance, eastward into the Indo-Pacific, where the tropical conditions and varied habitats enabled further local, less widespread forms to develop and diversify. The tectonically driven closure of the seaway between the Mediterranean and the Indo-Pacific in the Burdigalian, coupled with the other global events at this stage, triggered a crisis for the Mediterranean miogypsinids, which after a brief transgression and short-lived influx of Indo-Pacific fauna, led by their eventual extinction in the Langhian. Miogypsinids survived in the Indo-Pacific into the Serravallian, but progressive global cooling finally resulted in their total extinction from their last refuge at the end of this stage.

1. INTRODUCTION

Miogypsinidae were larger benthic foraminifera (LBF), and as such were marine protozoa. Stratigraphically, fossilised miogypsinids range from Rupelian (Planktonic Zone P18, see for example BouDagher-Fadel and Banner (1999) and Gradstein *et al.* (2004) for definition) to

the Serravallian (N13), and are found in the Americas, South Africa, and both the Mediterranean-West African and Indo-Pacific Tethyan sub-provinces. They were reef-forming and are thought to have hosted photosynthesising symbionts. They may often have been attached to sea-grass or other shallow-water substrates. Morphologically, the largest forms grew up to 10mm in diameter. They have a flattened to convex test with a fan of equatorial chamberlets (see Fig. 1). The latitudinal global distribution of the miogypsinids was mainly controlled by temperature (they were limited to tropical and sub-tropical waters), and their distribution and morphological adaptations were also dependent on the light requirements of their endosymbionts and substrates (Murray, 2006; BouDagher-Fadel, 2008). Their palaeogeographic and palaeoenvironmental distribution, when coupled with the porosity of the reef-related lithologies that they formed, means that today fossil miogypsinids are found in many potentially valuable oil reservoirs. Their study and the definition of their stratigraphic range is therefore of considerable commercial importance. As such, they have been the subject of many regional micropalaeontological investigations (see BouDagher-Fadel (2008) for a recent review), however until now, it has not been possible to develop an effective global view of their evolution, as the descriptions of specimens from Africa were rudimentary, and the stratigraphic ranges of Tethyan genera are controversial and appear to be highly dependent on palaeogeography. In this paper, we present descriptions of new samples from offshore South Africa, and from outcrops in Corsica, Cyprus, Syria and Sumatra, which enable the first systematic and biostratigraphic comparison of the miogypsinids from the Tethyan sub-provinces of the Mediterranean-West Africa and the Indo-Pacific. Additionally we establish for the first time that South Africa formed at this time a distinct LBF micropalaeontological province.

>>> Fig. 1.

The analysis of the different forms of miogypsinids requires an understanding of their morphology, which is dominated by the development of internal chambers within their tests. Fig. 2 shows the relationship between the principle miogypsinid forms, which include *Miogypsinella*, *Miogypsinoides*, *Miogypsinodella* and *Miogypsinina*. In the most advanced form, *Miogypsinina*, the chamberlets are developed as obliquely stacked columns (Figs 1 and 2). In axial view, they seem to be arranged in three-layers, with a thin median layer and two lateral walls, which are sub-divided into little chamberlets in the more advanced forms. The embryont (or first chamber) occurs near the apex or about midway between the centre of the test and the periphery. The sequential development of new characteristics in the miogypsinids (Fig. 2), such as the gradual development of the lateral chamberlets, may have been driven by environmental stress or the opportunity to occupy new niches. It has been suggested that the division of the solid lateral walls of *Miogypsinoides* into the small, thin-walled, transparent chamberlets of *Miogypsinina*, enabled, in favourable warm light-filled shelf environments, nests of photosynthetic symbionts (e.g. diatoms) to be hosted (see BouDagher-Fadel, 2008). Each of the small chamberlets would have acted not only as a small convex lens to focus sunlight, but they could also act as a “greenhouse” for the containment and development of symbionts. By analogy with other living LBF, it is inferred that the enclosed symbionts enabled the host miogypsinids to acquire nutrients without the use of food-gathering pseudopodia (Röttger, 1971).

In *Miogypsinella* the flange of the median chamberlets is relatively small (not much broader than the coil of the nepiont); in *Miogypsinoides* the flange was broader and became laterally heavily thickened. These thickened lateral walls would have reduced the amount of sunlight which could reach the median layer, and so offered the evolutionary opportunity of

chamberlet subdivision, as in *Miogypsinodella*, with the divisions becoming many layers of convex chamberlets in *Miogypsina*. The requirement for, and use of direct sunlight, by *Miogypsina* is shown by its occurrence only in shallow water marine limestones, associated with fossil algae. The irregular shape of many species of *Miogypsina* (e.g. *M. bifida*, Plate 3, fig. 8) suggests that their morphology was determined by the shape of the substrate up on which they grew, such as the stems or leaves of sea-grass (the substrate being biodegradable is not preserved in thin sections). Only in strong ambient sunlight, which would benefit both this form and its vegetable substrate, could true *Miogypsina* flourish (BouDagher-Fadel *et al.*, 2000).

>>>> Fig. 2

In order to study the phylogenetic evolution of the miogypsinids, Drooger (1952), in his thesis on American Miogypsinidae, introduced the population concept for classification purposes, that is to say average morphometric measurements from numerous specimens are used to define taxa. Drooger went on to perform many biometric studies on the nepiont of miogypsinids when seen in equatorial section. Indices “X” and “V” are used as the primary characteristics for subdivision, where X is the total number of spirally coiled nepionic chambers in *Miogypsinoides* and early *Miogypsina*, while the biometric factor V, which is equal to $200\alpha/\beta$ (see Fig. 3 for definition), reflects the degree of symmetry between the two spirals in more advanced forms of *Miogypsina*.

>>>> Fig. 3

The index “ γ ” is the angle of deviation of the line of symmetry of the embryont from the apical line, which is the line of symmetry of the adult test (see Fig. 3). For long-spiralled juveniles this value is considered as a negative number, but positive when there is less than one juvenile whorl and there is a second nepionic spiral.

The biometric method, therefore, appears in principle to be a useful tool in the study of the evolution of a single lineage of *Miogypsina* and of miogypsinids in general. In this study however, the specimens described are from randomly cut thin sections of core material and so biometric measurements were not always possible. Nevertheless, where possible, we applied the biometric method of Drooger (1952) and whenever possible, the biometric indices X and V are quoted. The biometric factor V is low in older species, and high in the nearly symmetrical embryont of the younger species (Drooger, 1993). The evolutionary lineage involves the reduction of the nepionic spiral and the increase in size of the protoconch (Drooger, 1993; BouDagher-Fadel, 2008). Species of *Miogypsina* are defined initially on the decreasing number of nepionic chambers, and later, when the genus had developed two epi-auxiliary chambers, on the degree of asymmetry of the nepiont and the orientation of the embryont relative to the apex of the fan of orbitoidal chambers.

In the American and Tethyan provinces we can differentiate between two forms of *Miogypsina* that represent different stages in their complex reproductive cycle. The so-called microspheric forms of *Miogypsina* retain the uniserial coils of their *Miogypsinella/Miogypsinoides* ancestors (Fig. 3A, B), while the so-called megalospheric forms possess a deuteroconch larger than either the protoconch (or first auxiliary chamber), and the latter form biserial whorls surrounding the proloculus (Fig. 3C, D). In the most advanced species of *Miogypsina*, the biserial embryont evolved to achieve bilateral

symmetry, (e.g. *M. mediterranea* and *M. indonesiensis*) and regular obliquely stacked columns. By contrast, in South Africa, the miogypsinids were always of the microspheric generation, retaining the uniserial coil, but developing a multiserial growth that results in irregular obliquely stacked columns.

Many parallel lineages of miogypsinids are recognised in the Mediterranean, Indo-Pacific and American bioprovinces (Van der Vlerk, 1966; Raju, 1974; Raju and Meijer, 1977; De Bock, 1976; Chapronière, 1983, 1984; Cahuzac, 1984; Ferrero, 1987; Wildenborg, 1991; Ferrero *et al.*, 1994; Drooger, 1952, 1953, 1963, 1984, 1993; Drooger and Raju, 1973; Cahuzac and Poignant, 1991; Mishra, 1996; BouDagher-Fadel and Lord, 2000; BouDagher-Fadel and Price, 2010a; Ferrandini *et al.*, 2011), and various miogypsinid species have been used to zone and date the Tethyan Neogene. They also have been used in biostratigraphic correlation, particularly in the Neogene of the Indo-Pacific (e.g., Chapronière, 1983, 1984).

In the past, the study of the relationship between the American, African and Tethyan lineages has been hampered by the geographic scatter of the miogypsinid assemblages described in the literature and by the scarcity of the material described from West and South Africa. Information on forms from West Africa relies on just three articles (Brun and Wong, 1974; Küpper, 1960; Raju and Meijer, 1977), and only recently have the phylogenetic lineages of the American miogypsinids been clarified as a result of data becoming available from material obtained from the hydrocarbon exploration of LBF-bearing carbonate facies from some Atlantic basins offshore from Central and South America (Mello e Sousa *et al.*, 2003; BouDagher-Fadel and Price, 2010a, BouDagher-Fadel *et al.*, 2010).

In this paper, we present descriptions of new samples (studied in thin section and in SEM) from offshore South Africa and from outcrops from the Mediterranean (Cyprus, Corsica, Syria) and the Indo-Pacific (Sumatra). The 116 specimens illustrated include 12 new species, of which 7 new species are from Nias, east of Sumatra, *Neorotalia tethyana*, *Miogypsinella bornea*, *Miogypsina subiensis*, *M. niasiensis*, *M. regularia*, *M. samuelia*, *Miolepidocyclina banneri*, (see BouDagher-Fadel *et al.* (2000), and Samuel (1994) for type localities), 1 new species is from Cyprus, *Miogypsinella cyprea* (see Lord *et al.* (2009) for type localities), and 4 new species *Miogypsina mcmillania*, *M. africana*, *M. ianmacmilliana*, *M. southernia* are from South Africa (see Dingle (1973), and Rogers and Bremner (1991) for offshore, Childs Bank localities).

By comparing the stratigraphic ranges of the African and Tethyan miogypsinids described here (Fig. 4), and in the literature, with recently described American forms, we have been able to reconstruct the phylogenetic and palaeogeographic evolution of the African and Tethyan miogypsinids (see Figs 6 to 9) from their origins in the American province (Rupelian, P18) to their Early Miocene extinction (Burdigalian, earliest N8) in South Africa; their earliest Middle Miocene (Langhian, top of N8) extinction in the Mediterranean, and their final global extinction in the latest Middle Miocene (Serravallian, earliest N13) in the Indo-Pacific.

>>> Fig. 4

2. SYSTEMATIC TAXONOMY, BIOSTRATIGRAPHY AND PHYLOGENETIC RELATIONSHIPS OF THE MIOGYPSINIDS

The systematic taxonomy of the Foraminifera is still undergoing active revision. The recognition of the Foraminifera as a class has emerged from biological research over the past two decades, including molecular systematics that are revealing the very early divergence of the Granuloreticulosa from other protocistan lineages (Hallock, pers. communication). Below, we follow Lee's (1990) elevation of the Order Foraminiferida to Class Foraminifera, and the concomitant elevating of the previously recognized suborders to ordinal level. Throughout the paper, the suffix “-oidea” is used in the systematics to denote superfamilies, rather than the older suffix “-acea”, following the recommendation of the International Commission on Zoological Nomenclature (see the International Code of Zoological Nomenclature 1999, p. 32, Article 29.2). The specimens figured in this paper are mainly of core material and are currently deposited at the collections of the Department of Earth Sciences, University College London.

In Appendix A, we provide the systematic description of the major genera and species (including those newly described in this paper) needed to differentiate and define the phylogenetic and biogeographic evolution of the miogypsinids, and which are figured in Plates 1 to 6. The biostratigraphic ranges of these forms are given in Fig. 4.

Traditionally, in the Oligocene the LBF are considered to define two major, distinct palaeogeographic realms, namely the American and the Tethyan provinces. On the basis of the identification of the new forms described in Appendix A, however, we are able to establish for the first time that there were in fact three distinct palaeogeographic miogypsinid provinces, the American, the Tethyan, and the newly defined South African realm. The respective biostratigraphic and phylogenetic evolution of the miogypsinids from these latter

two provinces are outlined below (the evolution of the American forms having been discussed in BouDagher-Fadel and Price (2010a)).

2.1. *The Tethyan Province*

From Figs 6, 7 and 8, it can be seen that the miogypsinids in the Tethyan province can be divided into two related but distinct sub-provinces, namely those of the Mediterranean (including West Africa) and of the Indo-Pacific. The forms found in Tethys are similar to those described in the Americas, but we will show that they are in fact distinct, and that miogypsinids in these two provinces developed independently of each other, but exhibited a parallel evolutionary trend.

As inferred by BouDagher-Fadel and Price (2010a), the American province saw the first development of the miogypsinids from a trochoid ancestor *Neorotalia* (with an enveloping canal system and pillars on both sides of the test) into advanced forms of *Miogypsina* and *Miolepidocyclina*, within a short period from Early to Middle Oligocene (P18 to P20). The earliest Mediterranean form (*Neorotalia tethyana*) dates from the Rupelian (P19). It has no apparent Tethyan ancestor, but from the morphological similarity it is reasonable to suggest that it was derived from an American ancestor. Once in Tethys *Neorotalia* evolved into a Tethyan miogypsinid lineages, independently from, yet in a parallel way to their American ancestors, by the means of gradual nepionic acceleration (shortening of the initial coil; see Fig. 2). Crucially, however they lack the typical features of American miogypsinids, such as strong fissures around the periphery of the test (see Fig. 5), indicating that they are a distinct, yet parallel, lineage

>>>Fig. 5

2.1.1. The Mediterranean Sub-Province

In the Mediterranean during the latest Rupelian, *Neorotalia* (e.g. *Neorotalia tethyana*, Plate 4, fig. 1) developed small chamberlets on the periphery of the last trochoid stage (see Fig. 6) as it gave rise to the Tethyan *Paleomiogypsina* (e.g. *P. boninensis*, Plate 4, fig. 2; P21, which is equivalent to the latest Td and Te1 letter stages used in the biostratigraphic description of the Indo-Pacific province (see Bou-Dagher-Fadel (2008) for more details)). The Tethyan *Paleomiogypsina* (which is distinct from the American form) in turn gave rise to the Tethyan *Miogypsinella* (e.g. *Mlla cyprea* new sp., Plate 4, figs. 3-8), which like the American form possesses a single spire of auxiliary chambers arising from the proloculus and a broad fan of equatorial chamberlets, but lacks the strong fissures around the periphery of the test characteristic of the American form. The P21 (equivalent to the latest Rupelian-Early Chattian) marks the earliest evolutionary appearance of the Tethyan *Miogypsinella*. The latter gave rise almost immediately to a fringeless Tethyan *Miogypsinoides* (e.g. *Mdes complanatus*, Plate 4, figs 9-10), with lateral thickening and a planispiral embryont, in the Chattian (see Fig. 6). The Mediterranean *Miogypsinoides* evolutionary sequence of assemblage-species (*Mdes complanatus-formosensis-bantamensis-dehaarti*) spans the Late Oligocene to Early Miocene (late P21 to early N8) and involves the reduction of the nepionic spiral, and the increase in size of the protoconch (Drooger, 1993; BouDagher-Fadel, 2008). Drooger (1993) set numerical limits to the X values to define the species, thus: *complanatus*-17-*formosensis*-13-*bantamensis*-10-*dehaarti*. In *Miogypsinoides dehaarti* the proloculus is followed by a single whorl of auxiliary chambers (Van der Vlerk, 1966). *Miogypsinoides* disappeared completely at the top of the Burdigalian in the Mediterranean (early N8).

>>>Fig. 6

The Tethyan *Miogypsina* evolved in the latest Oligocene (upper part of the Chattian, late P22) in the Mediterranean (see Fig. 7). The general trend of evolution in this group is towards shorter nepionic spirals and larger embryos in successively younger species with an X index range of *basraensis* - 12.5 - *gunteri* - 9 - *tani*. At X values between 7 and 6, and γ values close to zero, V values become significant and the morphometric limits of the species are as follow: *globulina* - 45 - *intermedia* - 70 - *cushmani* - 90 - *mediterranea*. Another descendant from the Tethyan *Miogypsina*, the genus *Miolepidocyclina*, has been distinguished on the more central location in the median plane of the nepiont. Most Miogypsinidae disappeared at the end of the Burdigalian (early N8) in the Mediterranean, with very few forms persisting into the Middle Miocene (see Figs 6 and 7) where they finally died out within the Early Langhian (N8).

>>>Fig. 7

2.1.2. The Indo-Pacific Sub-Province

In the Indo-Pacific, *Neorotalia* (e.g. *N. tethyana*, Pl. 1, Fig. 2-4), appeared in the Middle Rupelian (P19), while the Tethyan *Paleomiogypsina* made its first appearance at the base of the Chattian (c.f. the base of P21 in the latest Rupelian in the Mediterranean) which locally defines the base of Te letter stage (e.g. *P. boninensis*, Plate 1, Fig. 5). The morphological similarity between the major Mediterranean and Indo-Pacific forms suggests that they are in fact the same, but that they originated in the Mediterranean and migrated to into the Indo-Pacific a million years or so after they first appeared in the Western Tethys.

Miogypsinella (identical to that in the Mediterranean) also became prominent from the base of the Chattian and ranged into the Early Aquitanian (Te 2 to Middle Te5 letter stages) (e.g. *Mlla bornea*, Plate 1, Figs 9-15; *Mlla borodinensis*, Plate 1, Fig. 8; *Mlla ubaghsi*, Plate 1, Figs 6-7). The Chattian (P22/Te2) also saw the emergence of the first *Miogypsinoides* (see Fig. 6) and the establishment of the lineage *Mdes complanatus-formosensis-bantamensis-dehaarti* in parallel with that of the Mediterranean forms, but with morphologically similar species again appearing later in the Indo-Pacific than in the Mediterranean. But unlike the Mediterranean forms, the Indo-Pacific *Miogypsinoides* species persisted into the Early Langhian (Middle Tf1) in the Indo-Pacific (*Mdes indica*, see Fig. 6).

In the Indo-Pacific, the oldest form of *Miogypsina* (e.g. *M. borneensis*, Plate 1, Figs 24-25) is found with *Miogypsinoides bantamensis* at the start of the Miocene (Fig. 8). In the Miocene, unlike the original Mediterranean stock, the forms that migrated into the Indo-Pacific sub-province exhibited local speciation and gave rise to a wider specific diversity, probably as a result of the larger variety of geographic niches in the many Indo-Pacific islands and the enhanced tropical temperatures. Many of these local species are short ranged, and for example the distinction between Oligocene and Early Miocene parts of the Te stage is drawn on the occurrence of *Miogypsinella borodinensis* (Plate 1, fig. 8) in the former and true *Miogypsina* (e. *M. tani* (Plate 2, fig. 5) in the latter. The X parameter, when applied to *Miogypsina*, gives rise to the subdivision as follows: *borneensis* - 12 - *gunteri* - 9 - *tani* - 8 - *subiensis*, while V values become significant and the morphometric limits of the main Indo-Pacific species are as follow: *globulina* - 45 - *regularia* - 50 - *intermedia* - 70 - *samuelia* - 80 - *cushmani* - 90 - *antillea* 100 - *bifida*. The morphometric data indicate sequences phylogenetically analogous to those in the Mediterranean, but with shorter ranges and

additional gradations provided by the new, sub-provincial species that makes them biostratigraphically more useful.

>>> Fig. 8

As in the American province, there are in the Tethyan sub-provinces later developments within the group of Miogypsinidae with lateral chamberlets (*Miogypsina* s.l.), towards forms in which the embryo tends to shift towards the centre of the test. These forms were previously considered to be distinctly different in each of the bioprovinces: the subgenera *Helicosteginoides* and *Miogypsinita* in Central America, *Miolepidocyclina* in Central America and the Western Tethys, and *Lepidosemicyclina* in the Indo-Pacific. However, in the present study, forms similar to *Miolepidocyclina* were found in the Burdigalian of the Indo-Pacific province (e.g. *Miolepidocyclina* sp.1 from the Late Burdigalian of Borneo, Plate 3, Fig. 24), thus illustrating other examples of parallel evolution between the American and Tethyan provinces. Unlike the Mediterranean miogypsinids, all those of the Indo-Pacific survived into the Middle Miocene, Late Serravallian (Tf3) (Fig. 8).

2.2. *The South African Province*

The South African forms are not directly linked to the Tethyan miogypsinids, but are closer in morphology to their American ancestors (see Fig. 9). They have shortened nepionic coils and embryonic chambers that are vertical at the apex of the test (Fig. 9D; Plate 5, Fig. 25). Assemblages are composed only of microspheric generations, closely linked morphologically to the American *M. gunteri* which ranges from the latest Rupelian to the Chattian (Late P20 to P22), with uniserial coils surrounding the proloculus. However, they exhibit the unique characteristic of multiserial growth, which results in irregular oblique rows of equatorial

chamberlets. The development of this multiseriate growth and the persistent apical fringe of their American ancestors differentiates these forms from their counterparts in Tethys (Figs 5 and 9). They also seem to have evolved more slowly than those of the Tethys or the Americas, as by the Burdigalian they are less evolved than their contemporary Tethyan or American counterparts. The miogypsinid sequence developed can be characterised morphometrically as: *Miogypsina mcmillania* – 11 - *M. africana* – 9 - *M. southernia* – 6 - *M. ianmcmillania* (Fig. 9A to Fig. 9D). American and Tethyan miogypsinids evolved at a more rapid pace losing completely their uniseriate coil by the Burdigalian, but this advanced stage does not occur in South Africa. No South African miogypsinids older than the Burdigalian have been found.

>>>Fig. 9

3. THE PALAEOGEOGRAPHIC EVOLUTION OF THE MIOGYPSINIDS

We have previously demonstrated that the miogypsinids originated in the Americas from *Neorotalia* in the Early Oligocene (Rupelian, P18) (see BouDagher-Fadel and Price, 2010a). It is apparent that during the Early Oligocene (P18 – P19) a series of sea level regressions (Miller *et al.*, 2011; Katz *et al.*, 2008) reduced the effective width of the early Atlantic Ocean sufficiently to facilitate transoceanic migration of *Neorotalia* from the American province to the North African coast and into the Mediterranean. During this time, Tethyan shallow water niches were still occupied by the Paleogene *Nummulites*. However, towards the end of the Early Oligocene (Early P1, around 31 to 29Ma), an environmental stress, perhaps associated with cooling and the large flood basalt event in Ethiopia and Yemen (see Courtillot and Renne, 2003), contributed to the disappearance of the last Tethyan *Nummulites*. The Tethyan

Neorotalia (*N. tethyana*) had by this stage become distinct from its American counterparts by having lost the strong marginal fringe, and the disappearance of the *Nummulites* provided an opportunity for a new phylogenetic lineage of miogypsinids derived from *N. tethyana* to fill the warm reefs of the Mediterranean. As the morphology of American and Tethyan miogypsinids are seen to be crucially different, it follows that their evolutionary development was independent but closely parallel. There appears to be no occurrence of fringed, American miogypsinids in the Mediterranean, so we conclude that after the last major regression in the Early Chattian (P21), the rising sea level and the ongoing oceanic rifting eventually isolated the West African shelf from the American province (around 28 Ma) ending the any flow of *Neorotalia* or miogypsinids from America to Tethys. It should be noted that during this time, there was also a major change in oceanic circulation that resulted from the reversal of the direction of flow through the Panama Seaway (von der Heydt and Dijkstra, 2006). This reversal of flow was due to the tectonically driven widening of the Drake Passage and the narrowing of the seaway between the Mediterranean and Indo-Pacific, and we infer this may have also mitigated against further trans-Atlantic miogypsinid migration to the Mediterranean Tethys after P21 (Fig. 10).

>>> Fig. 10

In the Late Oligocene and Early Miocene (P22-Early N8), successive forms of miogypsinid continued their migration eastward through the open seaway from the Mediterranean and into the Indo-Pacific, where they typically arrive a million years or so after their first Mediterranean appearance (Fig. 11).

>>>Fig. 11

Once in the tropical setting of the Indo-Pacific, with its diverse palaeogeography, the migrants gave rise to richer diversity of local species than seen in the Mediterranean. However, in the Late Burdigalian (Early N8, around 17 Ma) this eastward migration between the Mediterranean and the Indo-Pacific was interrupted by the closure of the tectonically narrowed seaway between the Mediterranean and Indian Ocean (Rögl, 1998) during a significant sea level drop (Fig. 12). Prior to this first closure of the Eastern Tethys seaway in the Burdigalian (17 Ma), the miogypsinids had thrived in the warm climates of the Mediterranean reaching their peak diversity, with a maximum number of species, in the Early Burdigalian. However, with the first closure of the Tethys seaway in the Late Burdigalian, the miogypsinids became isolated with limited ecological diversity and many species (86%) died out at the Burdigalian - Langhian boundary (Early N8, 15.9 Ma), but a few species, such as *M. mediterranea* persisted into the Early Langhian. The first closure of the Tethyan sea was short-lived however, as a major global transgressions in the Early Langhian (15.5 – 16.5 Ma), flooded the Mediterranean from the Indo-Pacific. This transgression led to the extinction of the remaining Mediterranean miogypsinids within the Early Langhian (N8), as they were replaced by algal-coral patch reefs, tropical mollusc fauna and flat forms of LBFs, such as *Amphistegina* (BouDagher-Fadel and Clark, 2006; BouDagher-Fadel, 2008). This transgression coincided with a Mid-Miocene (14 – 16.5 Ma) global warming (Fig. 12), which by contrast stimulated the development of further diversity of the miogypsinids in the Indo – Pacific sub-province (Figs 6 and 8). In the Late Langhian-Early Serravallian (13 – 14 Ma), a time of several regressions (Fig. 12), the short-lived marine reconnection between the Mediterranean and Indian Ocean closed again (Rögl, 1998). This final closure coincided with the onset of global cooling (Fig. 12) and by the time the East Antarctic Ice Sheet was established (12 Ma), the miogypsinids had become extinct from the Indo-Pacific sub-

province (Late Serravallian, Early N13/Early Tf3). This final miogypsinid extinction was also globally accompanied by the extinction of 60% of all other LBF forms (BouDagher-Fadel, 2008).

In contrast to the apparent isolation of Tethys from the Americas from the Early Chattian onwards, it seems that trans-Atlantic migration to South Africa remained possible up to the Late Chattian (P22, see Fig. 12), thus enabling the direct migration of the early American miogypsinids (not just the *Neorotalia* seen in Tethys) to South Africa. Subsequently, sea-level rises isolated the South African miogypsinids, which then evolved lineages that were independent from their American ancestors. In the Burdigalian (N5 – Early N8) South African species (see Fig. 9) were still morphologically close to their American ancestors, but never evolved into the advanced forms of the megalospheric generations seen in the American and Tethyan *Miogypsina*. This comparatively slow rate of evolution might reflect the lack of environmental diversity and the more temperate conditions in which the South African miogypsinids found themselves. Eventually, however, the rapid sea level change between the Burdigalian and Langhian (Fig. 12) and global tectonic events, such as the eruption of the Columbia River Flood (15 – 17 Ma), seem to have triggered the extinction of the South African miogypsinids and they were replaced by other forereef LBF, such as *Operculina* and *Heterostegina*. On the other hand, in the American province, the rapid deepening of the carbonate facies, coeval with a global warming event (Fig. 10), the so-called mid-Miocene Climatic Maximum, resulted in the replacement of the reefal facies, dominated by miogypsinids, by pelagic environments containing planktonic foraminifera (see BouDagher-Fadel and Price (2010a) and BouDagher-Fadel *et al.* (2010)).

>>>Fig. 12

4. CONCLUSION

Detailed comparative biostratigraphy has been combined with tectonic, sea-level and climatic data to infer the phylogenetic and palaeogeographic evolution and eventual extinction of the Tethyan and South African miogypsinids. We conclude that the miogypsinids of Tethys evolved from a rotaliid ancestor independently from the miogypsinids of the Americas. In contrast miogypsinids of South Africa evolved, but again independently, from American miogypsinid ancestors. These processes are an example of “parallel speciation” by Schluter *et al.* (2004). As species became geographically isolated, colonising however new areas environmentally similar to each other, they thrive and evolve similar but distinct parallel lineages, taking advantages of empty niches and optimum conditions. This processes probably reflects that they all share a genetic pre-disposition to develop mutations of a specific, advantageous type, inherited from their last common ancestor.

The new understanding of the phylogenetic evolution of the Tethyan and South African miogypsinids presented in this paper, when combined with the improved understanding of their biostratigraphic ranges and facies relationships, enhances the usefulness of the miogypsinids as a tool for the study of Cenozoic warm-water carbonate platforms, which are so important in today’s hydrocarbon exploration. However, work is still needed on the Oligocene-Early Miocene of West Africa to understand better the exact timing and details of the trans-Atlantic migration event, and on the Late Chattian and Aquitanian of South Africa to establish the details of the phylogenetic evolution of the Burdigalian forms described in this paper.

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Appendix A

SYSTEMATIC DESCRIPTION OF THE MYOGYPSININDS

Class FORAMINIFERA Lee, 1990

Order ROTALIIDA Delage and Hérouard, 1896

The tests of members of this order are multilocular and have a calcareous wall, of perforate hyaline lamellar calcite (Fig. 1). They have apertures that are simple or have an internal toothplate. They range from Triassic to Holocene.

Superfamily ROTALIOIDEA Ehrenberg, 1839

Tests are involute to evolute, initially trochospiral or planispiral, commonly with many chambers in numerous whorls. As new chambers are added, septal flaps attach to the previous apertural face and enclose radial canals, fissures, umbilical cavities, and intraseptal and subsutural canals. The wall is made of perforate hyaline calcite, and is generally optically radial in structure. Primary apertures occur singly or as multiples. Small opening into the canal system may occur along the sutures. Late Cretaceous (Coniacian) to Holocene.

Family Rotaliidae Ehrenberg, 1839

Tests are trochospiral with umbilical plugs and radial canals throughout, or with fissures and intraseptal and subsutural canals. Apertures are umbilical, basal, single to multiple. Late Cretaceous (Maastrichtian) to Miocene.

Genus: *Pararotalia* Le Calvez, 1949

Type species: *Pararotalia inermis* (Terquem, 1882)

Loeblich and Tappan (1988), in their new description of the genus *Pararotalia*, reported the presence of a septal flap partially doubling each of the septa. They describe the aperture as interiomarginal, extending obliquely into the apertural face, and the intercameral foramen as areal, due to the attachment of an imperforate toothplate that extends to the distal margin of the aperture. Hottinger *et al.* (1991) emended the description of the Pararotaliinae to include the canal system. It is also distinguished from *Neorotalia* by the lack of the closed interocular spaces (“enveloping canal system”, Hottinger *et al.*, 1991). Late Cretaceous (Coniacian) to Middle Eocene.

Pararotalia sp. A

Plate 1, Figure 1

Figured specimen: UCL MF154.

Dimensions: Maximum measured length 1.5 mm.

Remarks: *Pararotalia* cannot be identified to its species because all the validly named species are described as solid specimens and all we have are very distinctive thin sections. *Pararotalia* sp. A is characterised by a biconvex, low trochospiral, smooth test, with a simple plug that fills the umbilicus.

Distribution: Early Eocene, Laki Formation, Sakesar Limestone, Bhadrar beds, Salt Range, Pakistan.

Genus: *Neorotalia* Bermúdez, 1952

Type species: *Rotalia mexicana* Reiss, 1963

Low trochospiral, with a simple umbilical boss and pillared walls, both ventrally and dorsally. Aperture: single, areal, with no complicated umbilical canal system. Early

Oligocene (P18) in the Americas (see BouDagher-Fadel and Price, 2010a), (P19/Late Tc) in the Mediterranean and the Indo-Pacific, to Early Miocene, Burdigalian (Lower Tfl letter stage, N6 planktonic foraminiferal zone, see BouDagher-Fadel, 2008)

Neorotalia tethyana BouDagher-Fadel and Price, new species

Plate 1, Figs 2-4, Plate 4, Fig. 1

2008 *Neorotalia* sp. BouDagher-Fadel, p. 451, Plate 7.14, Figs 1-2.

Figured specimens: UCL MF155.

Dimensions: Maximum measured length 1.5 mm.

Remarks: A *Neorotalia* with pillared walls, almost rectangular high chambers narrowing towards the interior of the test; sutures straight, slightly curved near the periphery. 13 to 15 Chambers in the last whorl, increasing gradually in size.

Distribution: Latest Early Oligocene - earliest Miocene (Aquitanian) of Indonesia and Cyprus.

Family Miogypsinidae Vaughan, 1929

Test: flattened to biconvex. The microspheric form has a trochospiral or planispiral early spire, while the megalospheric form has a bilocular embryonal stage followed by a fan of median chamberlets. Middle Oligocene to Middle Miocene.

Genus: *Paleomiogypsina* Matsumaru, 1996

Type species: *Paleomiogypsina boninensis* Matsumaru, 1996

Paleomiogypsina differs from *Pararotalia* (Plate 1, Fig. 2) and *Neorotalia* (Plate 1, Fig. 6) in having a few scattered chambers on the dorsal side of the test and a strong umbilical plug. This is the evolutionary beginning of the fan of chambers which was to develop in

Miogypsinella (see BouDagher-Fadel 2008) . Oligocene (P19 to P21) in the Americas (see BouDagher-Fadel and Price, 2010a), latest Early Oligocene to latest Late Oligocene (P21) in the Mediterranean, Late Oligocene (Late P21, Te1) in the Indo-Pacific.

Paleomiogypsina boninensis Matsumaru, 1996

Plate 1, Fig. 5, Plate 4, Fig. 2

1996 *Paleomiogypsina boninensis* Matsumaru, p. 56-58, pl. 8, figs.1-2; pl. 9, figs. 1-14; pl. 32, fig. 7; text-fig. 23-2 .

2000 *Paleomiogypsina boninensis* Matsumaru. BouDagher-Fadel, Lord and Banner, p. 144, pl. 1, figs. 12-13.

2010 *Paleomiogypsina boninensis* Matsumaru. Matsumaru, Sari, and Özer, p.448, pl. 1, Figs 1-4.

Figured specimens: UCL MF156.

Dimensions: Maximum measured length 1.50mm.

Remarks: This species is characterised by few advanced equatorial chambers, ogival to rhombic shaped, present on the equatorial side of spiral chambers.

Distribution: *P. boninensis* Matsumaru was first described from the Early Chattian of Minamizaki Limestone, Chichi-Jima, Ogasawara Islands (Matsumaru 1996). It was also reported from the Early Chattian of the Gomantong Limestone, North Borneo (Bou-Dagher-Fadel *et al.* 2000), Christmas Island (Adams and Belford, 1974), and of the Andaman Basin (Mishra 1996; Govindan 2003), Bey Dağlari Autochton, Menderes-Taurus Platform, Turkey. In the present study it is found in the latest Rupelian to Early Chattian of Cyprus (P21) and Chattian of Borneo (Late P21).

Genus: *Miogypsinella* Hanzawa, 1940

Type species: *Miogypsinella borodinensis* Hanzawa, 1940

Miogypsinella differs from *Paleomiogypsina* in having a fan of equatorial chambers, producing a broad equatorial layer of ogival chambers and differs from *Miogypsinoides* in having a weak trochospiral initial coil, and the lateral walls of the initial spire and the succeeding fan of ogival median chambers are much thinner with no solid outer laminae. Middle to Late Oligocene (P19-P22 planktonic foraminiferal zones) in the Americas (see BouDagher-Fadel and Price, 2010a), Late Oligocene (P21, Te1) to Early Miocene (Early N4, Early Te5) in Tethys.

Miogypsinella bornea BouDagher-Fadel and Price, new species

Plate 1, Figures 9-15

Holotype: UCL MF160, Plate 1, fig. 10.

Paratypes: UCL MF161 -6, Plate 1, figs 11-16.

Dimensions: Maximum measured length 1.3mm.

Description: A biconvex test with a small protoconch followed by 11 nepionic chambers in the megalospheric forms, 17 to 19 in the megalospheric forms. The nepionic chambers are almost subquadrate in the coiled whorl, increasing gradually in size. In equatorial section the fan of equatorial chambers is narrow with chambers being arcuate to pointed. and rudimentary ogival fan of chamberlets. In axial section the median layer is formed by large thick-walled chambers covered on both sides with pustules and strong pillars. The shape of the chambers and the pillars and rudimentary chambers distinguish this species from other *Miogypsinella*. The subquadrate chambers of the embryonic coil, which are followed by a narrow fan of small irregular chambers, distinguish this species from other species of *Neorotalia* and give it a primitive appearance. This species shows clearly the evolutionary

beginning of the fan of chamberlets that develop in *Miogypsinella* and separate it from *Paleomiogypsina*.

Distribution: Late Oligocene (Early Chattian).

Miogypsinella borodinensis Hanzawa, 1940

Plate 1, Fig. 8

1940 *Miogypsinella borodinensis* Hanzawa, p.779, pl.39, figs 1-9, p.767, tf.2.

2000 *Miogypsinella* cf. *borodinensis* Hanzawa, Boudagher-Fadel, Noad and Lord, 2000, p.144, pl.2, fig.3.

2008 *Miogypsinella borodinensis* Hanzawa. BouDagher-Fadel, 2008, p. 451, fig. 3.

Figured specimens: UCL MF159.

Dimensions: Maximum measured length 1.2mm.

Remarks: This species is characterised by a biconvex test with conical pillars embedded in the dorsal side as seen in axial section. The early, coiled stage in equatorial section is composed of 7 quadrate chambers followed by 6 ogival-formed chambers.

Distribution: This species was first described from the "Oligocene" of North Borodino Island. It is here found in the Late Oligocene of Borneo (P22).

Miogypsinella cyprea BouDagher-Fadel and Price, new species

Plate 4, Figures 4-8

Holotype: UCL MF229.

Paratypes: UCL MF230-33

Description: A tightly coiled *Miogypsinella* with a small protoconch followed by 11 elongate arcuate nepionic chambers. In equatorial section, the arcuate chambers produce an ogival appearance. Chambers become pointed and irregular in shape towards the distal end of the

test. In axial section, the median layer is composed of subrectangular, large chambers. Fissures are mainly present at the apex of the test. The periphery has a thick wall traversed by pillars (Plate 4, Figs 3A, 7C). However, the thickening in the microspheric forms is mainly in the centre of the test, (Plate 4, Figs 3B, 4). The elongate arcuate chambers and the thickening of the centre of the test distinguish this form from other species of *Miogypsinella*. Microspheric and megalospheric specimens are often found next to each other in the same sample (see Plate 4, 3, 8).

Distribution: Late Oligocene to Early Miocene, Aquitanian, Terra Limestone, Cyprus

Miogypsinella ubaghsi (Tan Sin Hok, 1936)

Plate 1, Figures 6-7

1936 *Miogypsinella ubaghsi* (Tan Sin Hok), p. 47, figs 1-7.

2008 *Miogypsinella ubaghsi* (Tan Sin Hok). BouDagher-Fadel, 2008, p. 437, pl. 7.8, fig. 5, pl. 7.14, fig. 4,8.

Figured specimens: UCL MF159.

Dimensions: Maximum measured length 1.5mm.

Remarks: The uniserial embryonic coils of *Mlla ubaghsi* is composed of 13 to 16 small chambers followed by a narrow fan of thick-walled ogival chambers with thick walls. In axial section, the chambers are broad and irregular in shape.

Distribution: This species was first described from the “Tertiary” of Borneo. It is figured here from the Miocene (Early Aquitanian), Darai Limestone, Papua New Guinea.

Genus: *Miogypsinoides* Yabe and Hanzawa, 1928

Type species: *Miogypsinoides dehaarti* Van der Vlerk 1924

A miogypsinid with planispiral embryonic coils and only one whorl around the megalospheric proloculus. A weak septal canal system is present. It differs from other miogypsinids in having very thick and solid lateral walls of the initial spire and the succeeding fan of ogival median chambers. The septa of all the chambers of *Miogypsinoides* also possess a clear intraseptal canal system. latest Early Oligocene (Middle Oligocene) to Late Oligocene (late P20 to P22 planktonic foraminiferal Zone) in Americas (see BouDagher-Fadel and Price, 2010a), Late Oligocene to Miocene (Chattian, P21b to Burdigalian N7) in the Mediterranean, (P22 to Early Langhian N8 in the Indo-Pacific province)

Miogypsinoides dehaarti (van der Vlerk, 1924)

Plate 1, Figs 16-23, Pl. 2, Figs 1-2, 14, Plate 4, Figs 18-19, Plate 5, Fig. 4

1924 *Miogypsina dehaartii* van der Vlerk 1924, p. 429-432, text-figs. 1-3

1969 *Miogypsina dehaarti* van der Vlerk, Cole, p. C10, pl.1, figs 1-20.

1953 *Miogypsina dehaarti* van der Vlerk, Drooger, p. 110-114, figs. 15-19.

1984 *Miogypsina dehaarti* van der Vlerk, Chaproniere, p. 46-47, pl. 7, fig. 7a-b; pl. 8, figs. 1-3; pl. 17, figs. 15-17; text-fig. 17-1b, 2e.

2000 *Miogypsina dehaarti* van der Vlerk, Boudagher-Fadel, Noad and Lord, 2000, p.145, pl. 2, fig. 5.

2008 *Miogypsina dehaarti* van der Vlerk, BouDagher-Fadel, p. 451, Pl. 7.14, figs 10, 14-18, Pl.7.19, figs 1-2.

2010 *Miogypsina dehaarti* van der Vlerk, Matsumaru, Sari, and Özer, p.454, pl. 2, figs 7-10, pl. 3, fig. 6.

Figured specimens: UCL MF167-72, 175-6, 236-7; NHM 6764 1295; Ferr. Coll. 241.

Dimensions: Maximum measured length 2.50mm.

Remarks: *M. dehaarti* has very thick lateral walls and is smooth exteriorly lacking pillars. The equatorial chambers are ogival in shape. The large spherical proloculus is followed by an equally large deuteroconch and 6 to 7 nepionic chambers.

Distribution: This species was first described from the Early Miocene of Larat, Moluques, Netherlands Indies. It was subsequently found in the Late Aquitanian and Burdigalian of Borneo and the Late Oligocene (Late Chattian) to Early Miocene (Burdigalian) of Cyprus (BouDagher-Fadel and Lord, 2006) and Turkey (Matsumaru *et al.*, 2010). This form is figured here from the Early Miocene, Middle Burdigalian, Subis formation in Borneo, Late Burdigalian of Northern Sardinia area in Castlesardo section and Late Aquitanian of Sulawesi.

Miogypsinoides complanatus (Schlumberger, 1900).

Plate 6, Figures 1-3

1900 *Miogypsina complanata* Schlumberger, p. 300, pl. 2, figs. 13-16; pl. 3, figs. 18-21.

1940 *Miogypsinella complanata* (Schlumberger) - HANZAWA, p.766-767, fig. 1.

1959 *Miogypsina (Miogypsinoides) complanata* Schlumberger – Drooger and Magne, p. 273-277, pl. 2, figs. 1-3.

1962 *Miogypsinoides complanatus* Schlumberger - Hanzawa, p.153-154, 157, pl. 7, fig. 11, text-fig. 5.

2010 *Miogypsinella complanata* (Schlumberger 1900) - Matsumaru, Sari, and Özer, p.450, pl., 1, figs 5-7.

Figured specimens: UCL MF262-264

Dimensions: Maximum measured length 2.50mm.

Remarks: The embryonic chambers near apex consist of protoconch and deuteroconch, followed by subquadrate 9 to 20 nepionic chambers, disposed in planispiral coil typical of a *Miogypsinoides*.

Distribution: This form was first described from the Early Aquitanian of France. It was also found in the Late Oligocene (Late Chattian) of Morocco, France, India, Late Oligocene of Bey Dağları Autochthon, Menderes-Taurus Platform, Turkey. In the present study, it is found in the Late Oligocene of Borneo and the Early Miocene of Terra Limestone, Cyprus.

Miogypsinoides formosensis (Yabe and Hanzawa, 1928)

Plate 4, Figs 11, 12, 17.

1928 *Miogypsina* (*Miogypsinoides*) *dehaartii* van der Vlerk var. *formosensis* Yabe and Hanzawa, p. 536, Fig. 1.

1957 *Miogypsinoides formosensis* Yabe and Hanzawa - Hanzawa, p. 92, pl. 15, figs. 10, 20-21.

1974 *Miogypsina* (*Miogypsinoides*) *formosensis* Yabe and Hanzawa - Raju, p. 79, pl. 4, fig. 1, pl. 111, fig. 3.

Figured specimens: Ferr. Coll. MF252

Dimensions: Maximum measured length 2.3mm.

Remarks: The embryonic chambers consist of protoconch and deuteroconch, followed by 16 to 17 planispiral nepionic chambers followed by a wide, irregular fan with ogival chambers.

Distribution: This form was first described from the "Tertiary" of the coal bearing Arisan Formation, Taiwan. It has been reported from the Late Chattian to Early Aquitanian of Corsica (Ferrandini *et al.* (2011) and of Turkey (Matsumaru *et al.*, 2010), and from Late Chattian-Earliest Aquitanian of the Far East (BouDagher-Fadel, 2008). It is here figured from

the Early Aquitanian, Nerthe area, near Marseille, Petit Nid section, Formation pararécifale du Cap de Nautes.

Miogypsinoides bantamensis (Tan Sin Hok, 1936)

Plate 4, Figs 13-16

1936 *Miogypsinoides complanata* (Schlumberger) *forma bantamensis* Tan

Sin Hok 1936, p. 48-50, pl. 1, fig. 13.

1957 *Miogypsinoides bantamensis* (Tan Sin Hok) - Hanzawa, p.91,pl. 15, figs. 4-6.

2008 *Miogypsinoides bantamensis* (Tan Sin Hok). – BouDagher-Fadel, p. 451, pl. 7.14, fig. 12.

Figured specimens: Ferr. Coll. MF253-6.

Dimensions: Maximum measured length 2mm.

Remarks: The embryonic chambers consist of protoconch and deuterococonch followed by 12 to 13 planispiral nepionic chambers, and later equatorial ogival chambers are arranged toward the distal margin.

Distribution: This form was first described from the “Tertiary” of Borneo. It was reported from the Late Chattian – Aquitanian of Turkey (Matsumaru *et al.*, 2010), Early Aquitanian to Late Burdigalian of Corsica (Ferrandini *et al.*, 2011) and Aquitanian of the Far East (BouDagher-Fadel, 2008). It is here illustrated from the Late Burdigalian of Northern Sardinia area, Castlesardo section and Early Aquitanian, the Nerthe area, near Marseille, Petit Nid section, Formation pararécifale du Cap de Nautes.

Genus: *Miogypsinodella* BouDagher-Fadel, Noad and Lord, 2000

Type species: *Miogypsina primitiva* Tan Sin Hok, 1936

The embryonic coil is similar to that of *Miogypsinoides*, it is virtually planispiral, but there is only one whorl around the megalospheric proloculus, and a septal canal system is present. However, the lateral walls have gaps between the lamellae, which begin to split apart and form the beginnings of lateral chambers. This splitting results in thick-walled irregular chambers, unlike the regularly formed, stacked chambers of *Miogypsina*. Late Oligocene (Chattian, P22) to Early Miocene (Aquitanian, N4) in Americas (see BouDagher-Fadel and Price, 2010a), Early Miocene (Burdigalian, N5) to Middle Miocene (Early Langhian/Early N8) in Tethys.

Miogypsinodella primitiva (Tan Sin Hok, 1936)

Plate 2, Figs 15-17

1936 *Miogypsina primitiva* Tan Sin Hok, p. 50, 52-53, pl. 1, figs. 14-16, 17

1940 *Miogypsinopsis primitiva* (Tan Sin Hok) - Hanzawa, p. 776.

2000 *Miogypsinodella primitiva* (Tan Sin Hok) - BouDagher-Fadel, Lord and Banner, p. 145-146, pl. 2, figs. 8-11.

Figured specimens: UCL MF200-3

Dimensions: Maximum measured length 2mm.

Remarks: Embryonic chambers consisting of protoconch and deuterococonch, followed by planispiral and single whorl of 9 to 10 nepionic. Lateral walls thick with irregular chambers; pillars traversing lateral walls.

Distribution: This form was first described from the "Tertiary" of Borneo. It has been reported from the Early Miocene (Burdigalian) to Middle Miocene (Early Langhian) of the Far East (BouDagher-Fadel *et al.*, 2000, 2008), Turkey (Matsumaru *et al.*, 2010) and Corsica (Ferrandini *et al.*, 2011). It is figured here from the Burdigalian of Sumatra.

Miogypsinodella pillaria Ferrandini *et al.*, 2011

Plate 4, Figs 22-23

2011 *Miogypsinodella pillaria* Ferrandini *et al.*, pl. 2, fig. 8, pl. 7, figs 1A, 2.

Figured specimens: UCL MF238-9.

Dimensions: Maximum measured length 2mm.

Remarks: A *Miogypsinodella* with a biconvex test and pillars between the irregular gaps of the lamellae. The equatorial chambers are almost rectangular with thick walls.

Distribution : This form was first described from the Late Burdigalian to the Early Langhian of the southern Corsica. It is here figured from Bonifacio area, southern Corsica, Cala di Labra Est section, R1 of Cala di Labra Formation.

Genus: *Miogypsina* Sacco, 1893

Type species *Nummulina globulina* Michelotti, 1841

The embryont in *Miogypsina* is near the apex with microspheric specimens possessing a uniserial coil around the proloculus, and megalospheric embryont having no coil around the proloculus, but two bidirectional coils around the proloculus, with lateral chambers regularly stacked on each side of the median layer, but lacking a canal system. Older species have megalospheric nepionts in which two series of chambers surround the deuteroconch unequally. In advanced forms the series become equal, and both surround the megalospheric deuteroconch by means of equal half whorls. Latest Early Oligocene (late P20) to Early Miocene (Burdigalian, early N8) in Americas (see BouDagher-Fadel and Price, 2010a), Late Oligocene (Chattian, P22), in Mediterranean, Early Miocene (Aquitanian, N4), in the Far East) to Middle Miocene (Langhian, Early N8) in the Mediterranean, (Middle Serravallian, Early N13) in the Indo-Pacific province.

Miogypsina africana BouDagher-Fadel and Price, new species

Plate 5, Figs 19-21

Name: This species is named *africana* to illustrate its type locality.

Holotype: UCL MF250, Plate 5, fig. 19

Paratypes UCL MF270-71, Plate 5, figs 20-21

Dimensions: Maximum measured length 1.5 mm.

Description: A *Miogypsina* with biometric factors: $X=9$ to 8 , $V=0$, megalospheric forms (Pl. 3, fig. 7). The circular protoconch is followed by a semicircular deuteroconch and 7 to 8 semicircular to spatulate periembryonic chambers, arranged so they extend completely around the first protoconch but just reaching half of the deuteroconch. The first chamber, with two stolons, generates two spirals, only one of which creates the fan shaped test. On the other hand, the fourth embryonic chamber always generate a small chamber with two stolons within the thick fibrous layer. The equatorial chambers are of regular size and shape. They are broadly spatulate, lacking the pointed ends of *M. gunteri* Cole, later becoming hexagonal in shape. In vertical section the equatorial layer is thick throughout the test with rectangular chambers almost equal in size throughout the test. It is overlaid on either by stacks of regular lateral curved chambers. Pillars are missing. This species differ from *M. gunteri* in the shape of chambers and embryonic chambers. It differs from *Miogypsina irregularis* in lacking pillars between the lateral chambers and possessing a more definite coil of chambers surrounding the initial embryonic chambers. It differs from *M. maxmilliana* in the shape and numbers of the embryonic chambers and the shape of the equatorial chambers.

Distribution: Burdigalian, Childs Bank Burdigalian, Ka1, South Africa.

Miogypsina antillea (Cushman, 1919)

Plate 6, Figures 4-5

1919 *Heterosteginoides antillea* Cushman, p.5, pl.5, figs. 5,6.

2010 *Miogypsina antillea* (Cushman) - BouDagher-Fadel, p.573, pl.3, fig.22.

Figured specimen: UCL MF265-8.

Dimensions: Maximum measured length 1.8mm.

Remarks: A *Miogypsina* with a biometric factor between 90 and 95. The embryonic chambers are bilocular with a large circular proloculus (~ 0.16mm), surrounded by almost rectangular chamberlets. Equatorial chambers are diamond in shape.

Distribution: This species was first described from the Late Oligocene of Anguilla, Venezuela. It was later reported from the Late Oligocene of Florida, Early Miocene offshore Brazil (Sousa *et al.* 2003), (latest P22), the Early Miocene (Burdigalian) offshore Brazil (BouDagher-Fadel and Price, 2010a), the Middle Miocene (Langhian) of Corsica (Ferrandini *et al.*, 2011) and from the Late Langhian to Serravallian of the Far East (BouDagher-Fadel, 2008). Here it is figured from the Late Burdigalian of Cyprus.

Miogypsina bifida Rutten, 1912

Plate 3, Figure 8

1912 *Miogypsina bifida* Rutten, p. 209, pl. 12, figs 10-11.

2008 *Miogypsina bifida* Rutten, BouDagher-Fadel, p. 485, pl. 7.19, fig. 14.

Figured specimen: NHM. Van Vesseem, coll. BB 469 – 1913.

Dimensions: Maximum measured length 2.3mm.

Remarks: An advanced *Miogypsina* with a symmetrical nepiont of a biometric factor close to 100 with two or more periembryonic spirals.

Distribution: This form was first described from East Borneo. It is widely reported from the Middle Miocene (Serravallian) of the Far East (BouDagher-Fadel, 2008). It is here recorded from the Miocene (Serravallian) of Sungai, Boengaloen, East Borneo.

Miogypsina borneensis Tan Sin Hok, 1936

Plate 1, Figs 24-25

1936 *Miogypsina borneensis* Tan Sin Hok, p. 50, 53-54, pl. 1, figs. 18-19.

2008 *Miogypsina borneensis* Tan Sin Hok – BouDagher-Fadel, p. 485, pl. 7.19, figs 9-13.

2010 *Miogypsina borneensis* Tan Sin Hok 1936, Matsumaru *et al.*, Pl. 3, figs 9-10, Pl. 4, figs 1-2.

Figured specimens: UCL MF173-4

Dimensions: Maximum measured length 2mm.

Remarks: The protoconch and deuteroconch are followed by planispiral and uniserial coil composed by 11 to 12 nepionic chambers. Equatorial chambers are ogival to irregular in shape. Lateral chambers, well developed and occurring in regular tiers between pillars.

Distribution: This species is first described from the “Tertiary” of Borneo. It was reported from the Aquitanian and Early Burdigalian of France (Cahuzac and Poignant, 1993), Latest Chattian to Burdigalian of Turkey (Matsumaru *et al.*, 2010) and Aquitanian of the Far East (BouDagher-Fadel, 2008). It is figured here from the Aquitanian of the Darai Limestone, Papua New Guinea.

Miogypsina cushmani Vaughan, 1924

Plate 5, Figure 8, Plate 6, Figures 14-15

1918 *Heterosteginoides panamensis* Cushman, pars, p. 89, pl. 43, figs. 1, 2.

1924 *Miogypsina cushmani* Vaughan, pp. 802, 813.

2008 *Miogypsina cushmani* Vaughan – BouDagher-Fadel, p. 485, pl. 7.19, fig. 16.

2010a *Miogypsina cushmani* BouDagher-Fadel and Price, p. 573, Text-Figure 1c.

Figured specimen: Ferr. Coll. MF244, UCL MF259-60

Dimensions: Maximum measured length 1.6mm.

Remarks: A *Miogypsina* with biometric factors V between 80 and 90, megalospheric forms with a circular protoconch followed by a larger semi-circular deutoconch. Equatorial chambers are diamond in shape.

Distribution: This species was first described from the latest Oligocene-Early Miocene of Venezuela. This form was reported from the latest Oligocene to Early Miocene (Burdigalian) of offshore Brazil (BouDagher-Fadel, 2008), the Late Burdigalian of Corsica (Ferrandini *et al.*, 2011) and the Langhian of the Far East (BouDagher-Fadel, 2008). It is here figured from Late Burdigalian of Castlesardo section (Northern Sardinia), Corsica.

Miogypsina globulina (Michelotti, 1841)

Plate 2, Figs 11-13, 21; Plate 5, Fig.5; Plate 6, Figs 3-5, 13

1841 *Nummulites globulina* Michelotti 1841, p. 297, pl. 3, fig. 6.

1841 *Nummulites irregularis* Michelotti 1841, p. 297, pl. 3, fig. 5.

1952 *Miogypsina irregularis* (Michelotti) - Drooger p. 54-55, pl. 2, figs. 25-29.

2008 *Miogypsina globulina* (Michelotti 1841) – BouDagher-Fadel, p.485, Fig. 20.

2010 *Miogypsina globulina* (Michelotti) - Matsumaru *et al.*, p. 17-26, pl. 1, figs. 1-4

Figured specimens: UCL MF196-9, Ferr. Coll. MF242, UCL MF258, UCL MF265-8.

Dimensions: Maximum measured length 2.30mm.

Remarks: A *Miogypsina* with a biometric factor V is between 42 and 45. The protoconch is globular followed by a large deutoconch (~ 0.14mm) and two principal auxiliary chambers of unequal size. The protoconchal spiral is composed of 7 spiral nepionic chambers. The deutoconchal spiral is short with V values of 20. The equatorial chambers are ogival and rhombic in shape with curved edges.

Distribution: *M. irregularis* and *M. globulina* are Aquitanian - Burdigalian species with a world-wide geographic distribution (from Central America to the Indo–West Pacific area and Europe). They were first described from the Early Miocene (Late Burdigalian) of Italy. They were subsequently described from the Early Miocene (Burdigalian) of Angola (Raju, and Meijer, 1977), Turkey (Matsumaru *et al.*, 2010), Late Burdigalian of Corsica (Ferrandini *et al.*, 2011), Burdigalian and Early Aquitanian of the Far East (BouDagher-Fadel, 2008). Offshore Brazil *M. globulina* has been found in the Late Oligocene (Chattian) to the Burdigalian (BouDagher-Fadel and Price, 2010a). It is figured here from the Burdigalian of Borneo, Cyprus and from Corsica.

Miogypsina gunteri Cole, 1938

Plate 4, Figs 20-21

1938 *Miogypsina gunteri* Cole, 42, pl. 6, figs. 10-12, 14.

2008 *Miogypsina gunteri* Cole – BouDagher-Fadel, p. 485, pl. 7.19, figs 3-5.

2010a *Miogypsina gunteri* Cole - BouDagher-Fadel and Price, p. 574, pl. 3, figs 1-5, 7; Pl. 4, figs 1, 2; Pl. 5, figs 6, 7.

Figured specimens: NHM coll MF257

Dimensions: Maximum measured length 3 mm.

Remarks: A *Miogypsina* with biometric factors: X= 10 to 12, V=0, megalospheric forms (Pl. 4, Fig. 20) with a circular protoconch followed by a subrectangular deuterioconch. These two chambers are succeeded by 10 to 12 wedge-shaped chambers which completely surround them. The equatorial chambers are diamond in shape. *M. gunteri* differs from *M. irregularis* in possessing a more definite coil surrounding the initial embryonic chambers and from *M. praegunteri* BouDagher-Fadel and Price, 2010a) in having fewer chambers in the first coil.

The equatorial chambers are more regularly shaped than those of *M. praegunteri*. All Tethyan *M. gunteri* have a smaller fissured edge than those of the American forms.

Distribution: *M. gunteri* was first described from the Upper Oligocene Swanee limestone of Florida. It is recorded in the Late Oligocene of offshore Brazil, Chattian (BouDagher-Fadel and Price, 2010a). It is common in the Aquitanian of the Mediterranean (Özcan *et al.*, 2009), and the Far East (BouDagher-Fadel, 2008). It is here figured from the Miocene (Aquitanian), top of Superga Mountain, Aman.

Miogypsina ianmcmillania BouDagher-Fadel and Price, new species

Plate 5, Fig. 25-26

2008 *Miogypsina* sp. BouDagher-Fadel, p. 441, fig. 7, p.445, fig. 6,

Name: In honour of Prof. Ian McMillan.

Holotype: UCL MF276, Plate 5, fig. 25.

Paratype: UCL MF277, Plate 5, fig. 26.

Dimensions: Maximum measured length 1.5 mm.

Description: Test broadly biconvex with biometric factors: $X=5$, $V=0$, megalospheric forms (Pl. 3, fig. 7) with a large circular protoconch followed by a smaller circular deuterococonch and 5 to 6 thick-walled periembryonic subtriangular chambers increasing gradually in size, arranged so they extend completely around the protoconch. The first chamber with two stolons generate multiple spires. The equatorial chambers are of regular size and shape, broadly spatulate with almost the pointed. In vertical section the equatorial layer is overlaid on either by stacks of regular lateral chambers. Pillars are missing. This species differ from other species of South African *Miogypsina* described here in having a vertically positioned embryont and in the shape, number and size of embryonic chambers.

Distribution: Burdigalian, Childs Bank, Late Burdigalian, Ka1, South Africa.

Miogypsina indonesiensis Tan Sin Hok, 1936

Plate 2, Figures 19-20

1936 *Miogypsina (Miogypsina) indonesiensis* Tan Sin Hok, p. 54, pl. 2, figs 3-4.

2008 *Miogypsina indonesiensis* Tan Sin Hok – BouDagher-Fadel, p.444, pl. 7.12, fig. 12.

Figured specimens: UCL MF204.

Dimensions: Maximum measured length 2.5mm.

Description: This species is distinguished in having a biserial embryont with bilateral symmetry of 98 to 100 biometric factor. Two protoconchal spirals of the same length are developed, whereas PA-I and PA-II are almost equal in size. The equatorial chambers are spatula and arranged in oblique stacks.

Distribution: This species was first described from the “Tertiary” of Borneo. It was widely reported from the Middle Miocene (TF3) of the Far East (BouDagher-Fadel, 2008). It is figured here from the Miocene (Serravallian), Nias.

Miogypsina kotoi Hanzawa, 1931

Plate 2, figs 3-4; Plate 3, Figures 1-2.

1931 *Miogypsina kotoi* Hanzawa, p. 154, pl. 25, figs 14-18.

2000 *Miogypsina kotoi* Hanzawa - BouDagher-Fadel and Wilson, p. 157, pl. 3, figs 1-2.

2008 *Miogypsina kotoi* Hanzawa - BouDagher-Fadel, p. 484, pl. 719, figs 6,8.

Figured specimens: UCL MF179-8; UCL MF206-7

Dimensions: Maximum measured length 2 mm.

Remarks: This species has a biserial nepiont which is strongly asymmetrical, with biometric factor between 30 and 40. It distinguished in having ogival median chambers, small thick-walled, but strongly convex chambers.

Distribution: *Miogypsina kotoi* was first described from the Burdigalian of Japan. It has been reported from the Late Burdigalian to Langhian, of eastern Borneo, Kalimantan and in the Tf1 (Upper Burdigalian) and Early Tf2 (Early Serravallian) of Djatirago, the Gunung Sewu area of South Central Java (BouDagher-Fadel and Wilson, 2000; BouDagher-Fadel, 2008). It is figured here from the Early Miocene (Middle Burdigalian) of Kalimantan and Borneo.

Miogypsina mediterranea Bronnimann, 1940

Plate 5, Figs 6-7, Plate 6, Figs 8-12

1940 *Miogypsina (Miogypsina) mediterranea* Bronnimann, p. 94, pl. 6, figs 5, 10-11.

2008 *Miogypsina mediterranea* Bronnimann, BouDagher-Fadel, p. 485, pl. 7.19, fig. 18.

Figured specimens: Ferr. Coll. MF244; UCL MF252-5

Dimensions: Maximum measured length 3mm.

Remarks: This species has an almost symmetrical nepiont with a biometric factor between 90 and 95. Equatorial chambers are ogival to rhombic in shape.

Distribution: This species was first described from the Late Burdigalian of Morocco. It is widely reported from the Late Burdigalian of the Mediterranean (BouDagher-Fadel, 2008, Ferrandini *et al.*, 2010). It is here figured from the Late Burdigalian, Bonifacio area, southern Corsica, Cala di Ciappili section, R1 of Cala di Labra Formation and from the Burdigalian of Morocco.

Miogypsina mcmillania BouDagher-Fadel and Price, new species

Plate 5, Figs 9-18

2008 *Miogypsina* sp. BouDagher-Fadel, p. 441, fig. 7, p.445, fig. 6,

Name: In honour of Prof. Ian McMillan.

Holotype: UCL MF239, Plate 5, fig. 9

Paratypes: UCL MF240-49, Plate 5, figs 10-18

Dimensions: Maximum measured length 1.5 mm.

Description: A *Miogypsina* with biometric factors: $X=11$, $V=0$. Test flattened to biconvex with a planispiral early spire. The embryonic chamber is near the apex but is surrounded from one side with pronounced fissures on the periphery of the initial whorls typical of the American *Miogypsina* and with a uniserial coil around the proloculus. The latter is followed by 11 periembrionic curved to broadly spatulate chambers, arranged so they extend completely around the first chamber. The first chamber with two stolons generate three spirals; two become discontinuous at the apex of the test within a thick fibrous layer, while the third spiral extends to create the fan shaped test. The equatorial chambers are originally of regular size and shape, broadly spatulate, lacking the pointed ends of *M. gunteri* Cole. However, they might become hexagonal in shape. In vertical section the equatorial layer is thick throughout the test with rectangular chambers almost equal in size throughout the test. It is overlaid on either by stacks of regular curved thick-walled lateral chambers. Pillars are scattered over the test. This species differs from *M. gunteri* in the shape of chambers and embryonic chambers. It differs from *Miogypsina irregularis* in lacking pillars between the lateral chambers and possessing a more definite coil of chambers surrounding the initial embryonic chambers. It differs from other typical miogypsinas in having the first chamber with two stolons generating multiple spires, instead of just two and the hexagonal shape of the chambers seen only in genera such as *Lepidosemicyclina* in the Far East.

Distribution: Burdigalian, Childs Bank, Early Burdigalian, Ka1, South Africa.

Miogypsina niasiensis BouDagher-Fadel and Price, new species

Plate 2, Figures 22-25

Name: This species is named *niasiensis* to illustrate its type locality.

Holotype: UCL MF205, Plate 2, fig. 22.

Paratypes : UCL MF206-8, Plate 2, figs. 23-25

Dimensions : Maximum measured length 1.3mm.

Description: A *Miogypsina* with a biometric factor of 75 with a large embryont with large protoconch and deutereconch placed at the extreme apex of the test. In equatorial section the chambers are arcuate like those of *M. subiensis* but they are smaller with much thinner walls and not in lateral contact. In vertical view, they are stacked in 3 to 4 regular rows on the equatorial layer. Pillars are absent. The chambers of the median layer are much narrower than those of *M. subiensis* as seen in axial section.

Distribution: This species is found in the Early Langhian, Middle Tf1 “letter stage” limestone, Gawo Formation, Nisua, Nias, east of Sumatra, Indonesia.

Miogypsina regularia BouDagher-Fadel and Price, new species

Plate 3, Figures 3-7

Name: This species is named *regularia* to illustrate the regular stacking of the lateral chambers.

Holotype: UCL MF208, Plate 3, fig. 3.

Paratypes : UCL MF209-12, Plate 3, figs. 4-7

Dimensions : Maximum measured length 2mm.

Description: A *Miogypsina* with a biometric factor of 50. Embryonic apparatus is composed of a large spherical protoconch and slightly rectangular deuteroconh surrounded by thick walls. The equatorial view shows rhombic to elongate arcuate chambers, producing ogival appearance. The lateral chambers are small, arcuate, narrow and stacked obliquely in regular rows on the equatorial layer.

Distribution: This species is found in the Early Langhian, Middle Tfl, Gawo Formation, Nisua, Nias, east of Sumatra, Indonesia.

Miogypsina samuelia BouDagher-Fadel and Price, new species

Plate 3, Figs 9-16

Name: In honour of Dr. Andy Samuel.

Holotype: UCL MF221, Plate 3, fig. 16.

Paratypes: UCL MF214-20, Plate 3, figs 9-15.

Dimensions: Maximum measured length 2mm.

Description: A *Miogypsina* with a biometric factor of 70. Embryonic apparatus placed at the apex of an elongated test with protoconch and deuterococonch almost of equal size. Equatorial chambers are initially elongate arcuate, producing a familiar ogival appearance but followed with rhombic and diamond-shaped chambers. Axial view show small arcuate chambers sperated by pillars and stacked in three rows on either side of the equatorial layer.

Distribution: Late Aquitanian, Gawo Formation, 27B, Nisua, Nias, east of Sumatra, Indonesia.

Miogypsina subiensis BouDagher-Fadel and Price, new species

Plate 2, Figures 6-10

Name: This species is named *subiensis* to illustrate its type locality.

Holotype: UCL MF192, Plate 2, fig. 8.

Paratypes: UCL MF190-191, 193-5, Plate 2, figs. 5-7. 9-10.

Dimensions: Maximum measured length 2mm.

Description: Test: small, broadly biconvex. The equatorial section show a miogypsinid coil with a biometric factor between 5 and 8. This species is distinguished be having broadly

arcuate, thick-walled chambers, in lateral contact. In vertical sections the lateral chambers are irregular in shape and size, stacked in 4 to 5 rows. Pillars are absent to rare. The median layer is broad, almost of uniform breadth throughout, occupying almost half of the test toward the edges and fifth of it in the centre. It is formed of rectangular chambers, almost equal in size, but becoming slightly narrower towards the edges.

Distribution: This form co-occurred with *Miogypsinoides dehaarti* in the Early Miocene, Middle Burdigalian, Subis formation, Borneo.

Miogypsina tani Drooger, 1952

Plate 2, Fig. 5

1952 *Miogypsina tani* Drooger, p. 26, 51, 52, pl. 2, figs. 20-24.

2008 *Miogypsina tani* Drooger - BouDagher-Fadel, p.437, pl. 7.8, fig. 1.

2010a *Miogypsina tani* Drooger - BouDagher-Fadel and Price, p. 574, Pl. 3, figs 19 – 21.

Figured specimens: UCL MF189.

Dimensions: Maximum measured length 2mm.

Remarks: A *Miogypsina* with an $X = 8$; V between 0 and 10. This species is distinguished by having a long megalospheric nepionic coil of auxiliary chambers, low cubicalae with inflated roofs and many scattered pillars.

Distribution: This species was first described from the “Middle Oligocene” of east-central Costa Rica. Similar forms have a wide distribution in the American, Mediterranean and Indo-Pacific regions. It was recorded from the Aquitanian stage, Upper Te, of Italy and southern Spain (Raju 1974). Similar specimens were found by BouDagher-Fadel *et al.* (2000) in the upper Upper Te (Burdigalian) of Borneo and by Sharaf *et al.* (2005) the Lower Tf1 “letter stage” of the Burdigalian of East Java and Early Langhian of Sumatra (BouDagher-Fadel, 2008). This species was also reported from the Late Burdigalian of Corsica (Ferrandini *et al.*,

2011; Early Miocene (Aquitanean) of the Foz do Amazonas, Brazil (Mello e Sousa *et al.* 2003) and from the middle Early Oligocene (P21) to Early Miocene of offshore Brazil (BouDagher-Fadel and Price, 2010a). It is here figured from the Early Miocene, Middle Burdigalian, Subis formation, Borneo.

Miogypsina southernia BouDagher-Fadel and Price, new species

Plate 5, Figs 22-24

2008 *Miogypsina* sp. BouDagher-Fadel, p. 441, fig. 7, p.445, fig. 6,

Name: In order to illustrate its geographic occurrence.

Holotype: UCL MF273, Plate 5, Fig. 22.

Paratypes UCLMF274-275, Plate 5, Figs 23-24.

Dimensions: Maximum measured length 1.5 mm.

Description: A *Miogypsina* with biometric factors: $X=7$ to 6 , $V=0$, megalospheric forms (Pl. 3, fig. 7) with a circular protoconch followed by a semicircular deuteroconch and 7 to 8 periembryonic with a very thick fissured peripheral fringe, increasing slowly in size but rapidly after the fourth chambers, arranged so they extend completely around the protoconch, reaching just the beginning of the deuteroconch. The first chamber with two stolons generate two spirals; one become discontinuous at the apex of the test within a thick fibrous layer, while the second spiral extend to create the fan shaped test. As with *M. Africana*, the fourth chamber generates a small chamber within the fibrous layer. Chambers are very thick in equatorial layers; the first rows are made up with chambers almost diamond in shape followed by rows of broadly spatulate chambers. In vertical section the equatorial layer is overlaid on either by stacks of regular curved, thick-walled lateral chambers. Pillars are missing. This species differ from *M. gunteri* in the shape of chambers and embryonic chambers. It differs from *Miogypsina irregularis* in lacking pillars between the lateral

chambers and possessing a more definite coil of chambers surrounding the initial embryonic chambers. It differs from *M. Africana* in shape and size of the embryonic chambers, the thicker fibrous layer and the shape of the equatorial chambers.

Distribution: Late Burdigalian, Childs Bank Burdigalian, Ka1, South Africa

Genus *Lepidosemicyclina* Rutten, 1911

Type species: *Orbiloides (Lepidosemicyclina) thecideaformis* Rutten, 1911

A roughly circular test, with an embryonic apparatus made of a spherical protoconch and a reniform deuteroconch, has a tendency to become enlarged in most advanced forms. Two sets of planispiral periembryonic chambers surround the embryo, the larger primary spiral and three unequal secondary spirals. The equatorial chamberlets are at first ogival, then rhombic and finally distinctly hexagonal. Early Miocene (Burdigalian, N4 to Early N8) in the Indo-Pacific.

Lepidosemicyclina banneri BouDagher-Fadel and Price, new species

Plate 3, Figures 17-23

Name: In honour of Prof. Fred Banner.

Holotype: UCL MF239, Plate 6, fig. 20A

Paratypes: UCL MF222, Plate 6, fig. 17; UCL MF240-51, Plate 6, figs 17-19, 21-22.

Dimensions : Maximum measured length 6 mm.

Description: An elongated *Lepidosemicyclina* with a circular protoconch occupying a place between centre and edge of the test, and a smaller reniform deuteroconch which lines up with the protoconch closer to the apex of the test. In axial view chambers are very small,

supported by pillars and stacked in irregular rows on the median chambers. In equatorial view, chambers are hexagonal in irregular and hexagonal in shape.

Distribution: Early Miocene (Burdigalian), Borneo and Java.

Lepidosemicyclina excentrica Tan Sin Hok, 1937

Plate 6, Figure 16

1937 *Miogypsina (Miolepidocyclina) excentrica* Tan Sin Hok, p.40, pl.1, fig. 12, pl. 2, figs 1-9.

Figured specimen: UCL MF263

Dimensions: Maximum measured length 4mm.

Remarks: Embryonic chambers consist of large protoconch and deuterococonch eccentric in their position. Test elongated in axial section with thick small chambers arranged in regular tiers and traversed by thin pillars. Equatorial chambers, ogival, rhombic and short hexagonal in shape.

Distribution: This species was first described from the Burdigalian of Indonesia. It is figured here from Late Burdigalian of Java.

Lepidosemicyclina thecidaeformis (Rutten, 1911)

Plate 2, figure 18

1911 *Orbitoides (Lepidosemicyclina) thecidaeformis* Rutten, p. 1157-1158.

1912 *Miogypsina thecidaeformis* (Rutten), p. 204, pl. 12, figs. 1-5.

1974 *Miogypsina (Lepidosemicyclina) thecidaeformis* (Rutten). – Raju, p. 84-85, pl. 6, figs. 2-4.

1984 *Miogypsina (Lepidosemicyclina) thecidaeformis* (Rutten) – Chaproniere, p. 44-46, pl. 7, figs. 3-6; pl. 17, figs. 1-11; pl. 25, fig. 14; Text-fig. 17-3-5.

2008 *Lepidosemicyclina thecidaeformis* (Rutten) – BouDagher-Fadel, p. 445, pl. 7.12, fig. 8.

Figured specimen: NHM P22849

Dimensions: Maximum measured length 3mm.

Remarks: Embryonic chambers consist of protoconch and deuteroconch and are followed by two principal auxiliary chambers of unequal size with biometric factors ranging from 45 to 70. Equatorial chambers, ogival, rhombic and short hexagonal in shape; lateral chambers are well developed and occur in regular tiers between thin pillars .

Distribution: This form was first described from the Miocene of Borneo. It was reported from the Burdigalian of the Far East (BouDagher-Fadel, 2008). The authors here do not consider the forms figured by Matsumaru *et al.*, 2010, from the Late Chattian to Burdigalian of Turkey p. 460, pl. 4, figs 3-4, as *Lepidosemicyclina thecidaeformis* (Rutten 1911). The figured specimens have irregular chambers, not the typical hexagonal shape of *Lepidosemicyclina* genus. *Lepidosemicyclina thecidaeformis* is figured here from the Burdigalian of Tanzania.

Genus *Miolepidocyclina* A. Silvestri, 1907

Type species: *Orbitoides (Lepidocyclina) burdigalensis* Gümbel, 1870

The embryonic apparatus, consisting of large protoconch and deuteroconch, is surrounded by a thick wall. The megalospheric nepiont is similar to that of *Miogypsina*, with no coil around the proloculus but 2-bidirectional coils around the proloculus. However, the nepiont is centrally placed, instead of being at the edge of the test, as in *Miogypsina*. Late Rupelian (Late P20) to Early Miocene (Burdigalian, Early N8) in Americas (see BouDagher and Price, 2010), Early Miocene, Burdigalian (Late N5 to Early N8) in the Mediterranean, Late Burdigalian (N6 to Early N8) in the Indo-Pacific.

Miolepidocyclina burdigalensis (Gümbel, 1870)

Plate 6, figures 6-7

1870 *Orbitoides (Lepidocyclina) burdigalensis* Gümbel, p. 719.

1900 *Miogypsina burdigalensis (Gümbel)* - Schlumberger, p.330, pl. 2, figs. 11-12; pl. 3, figs. 22, 25.

1952 *Miogypsina (Miolepidocyclina) burdigalensis* Gümbel - Drooger, p. 58, 61, pl. 1, figs. 30-34.

2010 *Miolepidocyclina burdigalensis (Gümbel 1870)* - Matsumaru *et al.*, p. 460, pl.4, fig. 9.

Figured specimens: UCL MF256-57

Dimensions: Maximum measured length 1.50mm.

Remarks: Embryonic chambers eccentric in position and consisting of protoconch and deuterioconch, followed and surrounded by two spiral of 11 nepionic chambers. Equatorial chambers, ogival to short spatulate shaped toward the periphery.

Distribution: This form was first described from the Miocene of Germany. It has been reported from the Burdigalian of the Mediterranean (BouDagher-Fadel, 2008; Ferrandini *et al.*, 2011). It is here figured from the Burdigalian of Cyprus.

Miolepidocyclina excentrica Bronnimann, 1940

Plate 5, Figures 1-3

1940 *Miogypsina (Miogypsina) mediterranea* Bronnimann var. *excentrica* Bronnimann, pl. 6, figs 12-16, pl. 8, fig.25.

2008 *Miolepidocyclina excentrica* Tan Sin Hok – BouDagher-Fadel, p.444, pl. 7.12, fig. 11, pl. 7.19, fig. 21.

Figured specimens: UCL MF256-57

Dimensions: Maximum measured length 2.5mm.

Remarks: Embryonic chambers eccentric to almost central in position and consisting of two large protoconch and deuteroconch, occupying almost third of the test. Equatorial chambers are with thick walls and ogival in shape.

Distribution: This species was first described from the Burdigalian of Morocco. It was reported from the Late Burdigalian of Corsica and the Mediterranean (BouDagher-Fadel, 2008; Ferrandini *et al.*, 2011). It is here figured from the Late Burdigalian, Bonifacio area, southern Corsica, Cala di Labra Est section, R1 of Cala di Labra Formation.

Fig. 1. SEM images of *Miogypsina borneensis* Tan Sin Hok showing: (A) embryonic apparatus, and equatorial chambers; (B) and (C) the internal surface of equatorial chamber wall bearing 'eggholders'.

Fig. 2. The generic phylogenetic evolution of Tethyan miogypsinids.

Fig. 3. (A). A sketch showing the earliest chamber of a late *Miogypsinoides*, such as *Miogypsinoides complanatus*. There are 18 spirally coiled nepionic chambers (biometric index X). The angle of rotation between the apical line of symmetry and the central line crossing the protoconch and deuterocoel is around -330° . (B) *Miogypsinoides bantamensis* Tan Sin Hok from Castlesardo section (Northern Sardinia) with a biometric index X = 10 and γ of approximately -290° . (C) A sketch of the early chambers of an early *Miogypsina*, such as *M. cushmani*, with 2 auxiliary chambers (ax) with a biometric index V ($= 200\alpha/\beta$). γ , the positive angle of deviation of the line of symmetry of the adult test is approximately 78° . (D) *Miogypsina cushmani* Vaughan, from Castlesardo section (Northern Sardinia), equivalent of Cala di Labra formation. (E) *Miogypsina mcmillania* new sp., Burdigalian, South Africa.

Fig. 4. Range chart of miogypsinid species in the South African and Tethyan provinces.

Fig. 5. (A) a Mediterranean *Miogypsinoides* (*Mdes bantamensis* Tan Sin Hok), (B) An American *Miogypsinoides* (*Mdes praegunteri* BouDagher-Fadel and Price, 2010a), (C) the Mediterranean *Miogypsina mediterranea* Bronnimann, and (D) the South Africa *Miogypsina mcmilliana* new sp.

Fig. 6. The phylogenetic evolution of the Tethyan *Neorotalia*, *Paleomiogypsina*, *Miogypsinella* and *Miogypsinoides* spp.

Fig. 7. The phylogenetic evolution of the Mediterranean *Miogypsina* spp. and *Miolepidocyclina* spp.

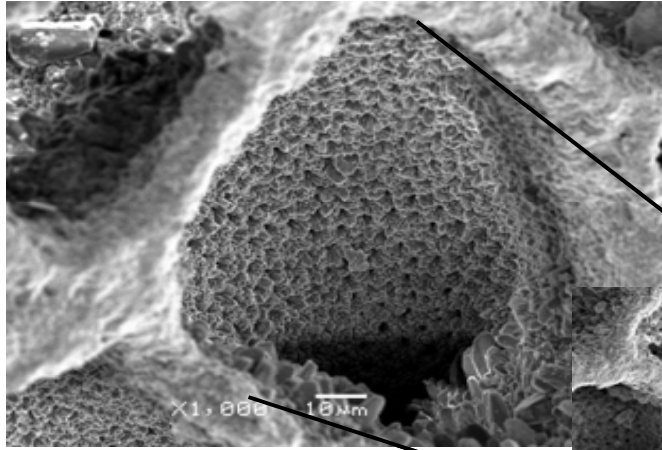
Fig. 8. The phylogenetic evolution of the Indo-Pacific *Miogypsina* spp., *Miolepidocyclina* spp. and *Lepidosemicyclina* spp. Dotted arrows show forms thought to have migrated from the Mediterranean sub-province.

Fig. 9. Evolution of South African miogypsinids during the Burdigalian.

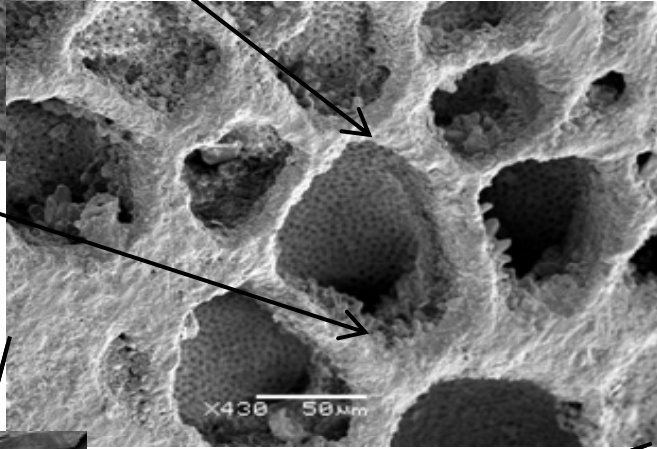
Fig. 10. The major tectonic, oceanic and climatic events affecting miogypsinid migration, evolution and extinction.

Fig. 11. The migration of miogypsinids during Early Oligocene, shown by black arrows, from the Americas (1), to the Mediterranean (2), and on to the Indo-Pacific (3), or to South Africa (4).

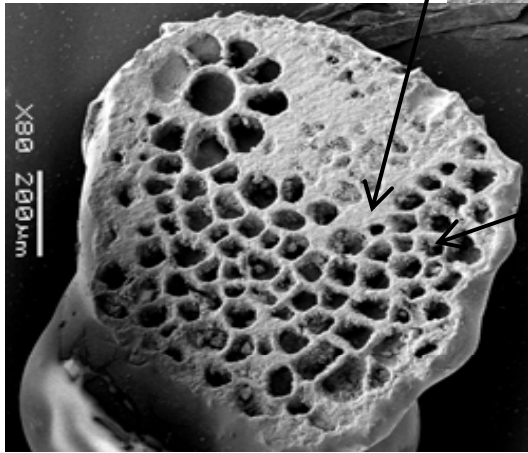
Fig. 12. Variation in sea level and temperature during the Oligocene and Mid-Miocene based on Miller *et al.* (2011) and Zachos *et al.* (2001).



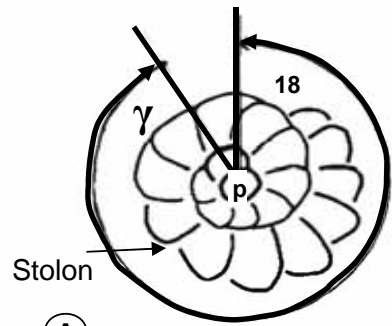
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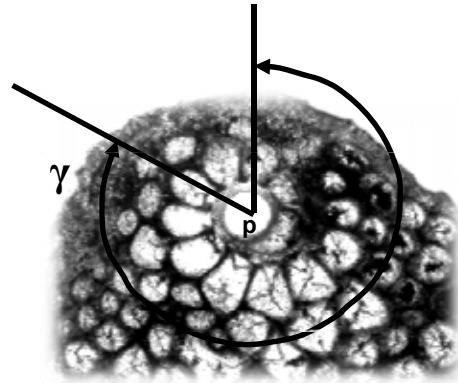
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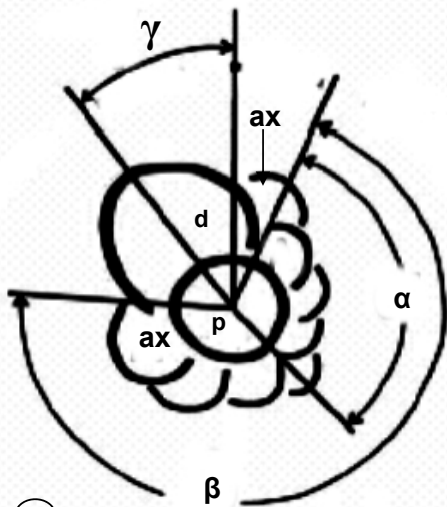
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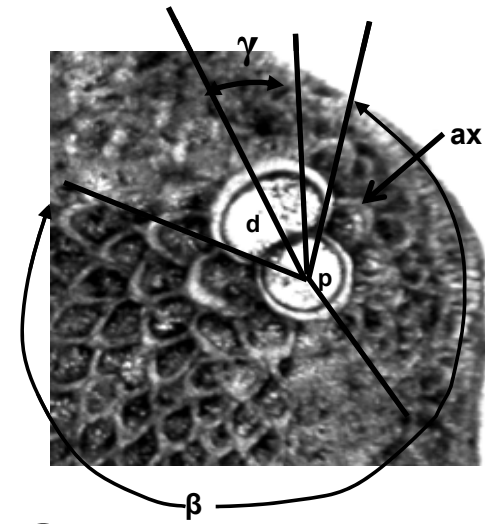
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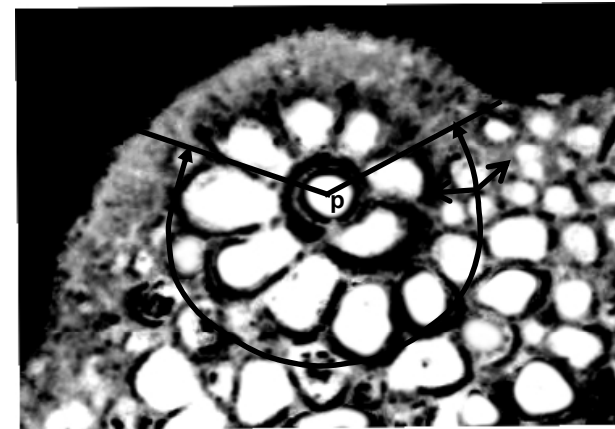
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(C)



(D)



(E)

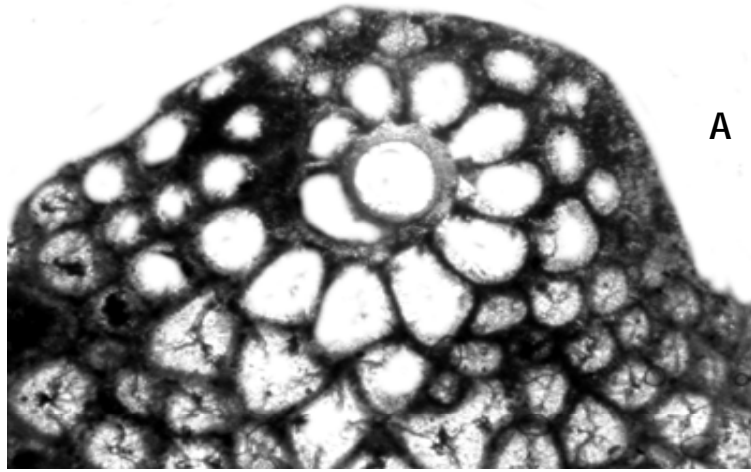
OLIGOCENE				EARLY MIOCENE				MIDDLE MIOCENE				Epoch			
RUPELIAN		CHATTIAN		AQUIT.		BURDIG.		LANGHIAN		SERRAVALLIAN		Stage			
P18	P19	P20	P21	P22	N4	N5	N6	N7	N8	N9	N10	N11	N12	N13	Planktonic Zone
															<i>Neorotalia tethyana</i>
															<i>Paleomioegypsinina boninensis</i>
															<i>Mioegypsinella bornea</i>
															<i>Mioegypsinoides complanatus</i>
															<i>Mioegypsinoides formosensis</i>
															<i>Mioegypsinella cyprea</i>
															<i>Mioegypsinella borodinensis</i>
															<i>Mioegypsinoides bantamensis</i>
															<i>Lepidosemicyclina thecideaeformis</i>
															<i>Mioegypsinina borneensis</i>
															<i>Mioegypsinoides dehaarti</i>
															<i>Mioegypsinina gunteri</i>
															<i>Mioegypsinina globulina</i>
															<i>Mioegypsinodella primitiva</i>
															<i>Mioegypsinodella pillaria</i>
															<i>Miolepidocyclina burdigalensis</i>
															<i>Miolepidocyclina excentrica</i>
															<i>Mioegypsinina tani</i>
															<i>Lepidosemicyclina banneri</i>
															<i>Mioegypsinina macmillania</i>
															<i>Mioegypsinina africana</i>
															<i>Mioegypsinina cushmani</i>
															<i>Miolepidocyclina</i> sp. 1
															<i>Mioegypsinina subiensis</i>
															<i>Mioegypsinina mediterranea</i>
															<i>Mioegypsinina niastensis</i>
															<i>Mioegypsinina regularia</i>
															<i>Mioegypsinina kotoi</i>
															<i>Mioegypsinina lanmcmilliana</i>
															<i>Mioegypsinina southernia</i>
															<i>Mioegypsinina samuelia</i>
															<i>Mioegypsinina antillea</i>
															<i>Mioegypsinina bifida</i>
															"Letter Stages"
															Tf3
															Tf2
															Upper Tf1
															Middle Tf1
															Lower Tf1
															Upper Te (Te5)
															Te4
															Te3
															Te1
															Td
															Tc



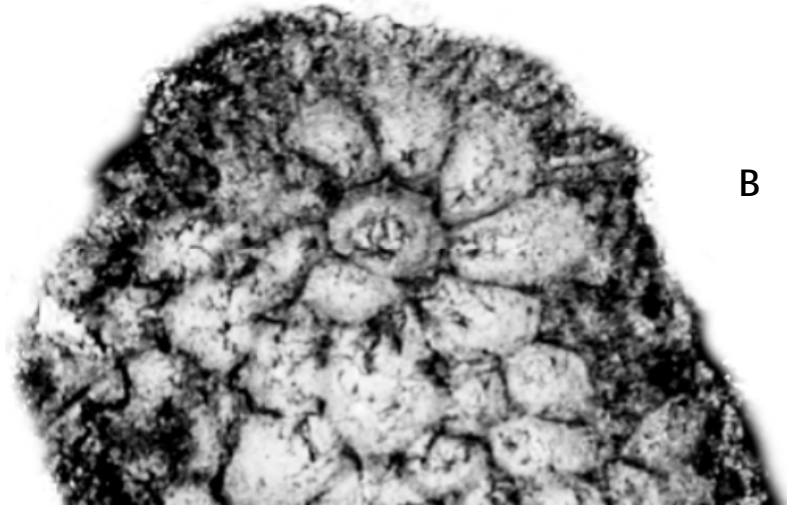
 South Africa

 Indo-Pacific

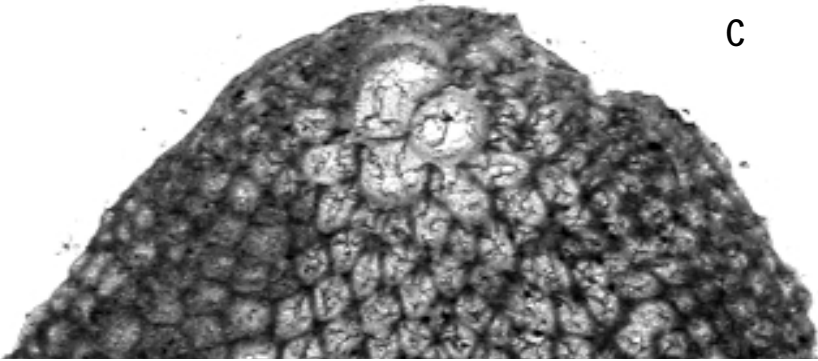
 Mediterranean



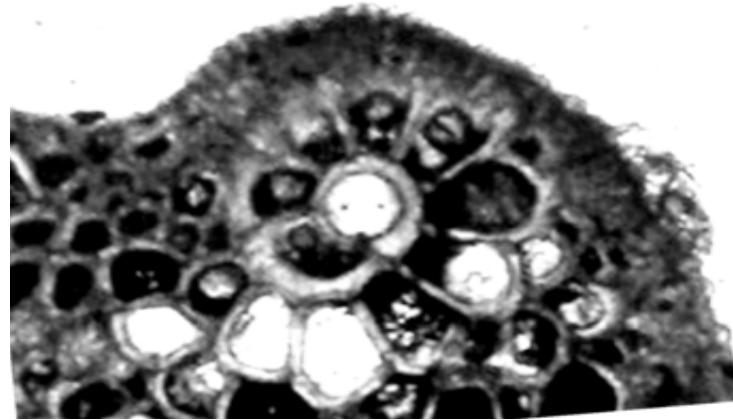
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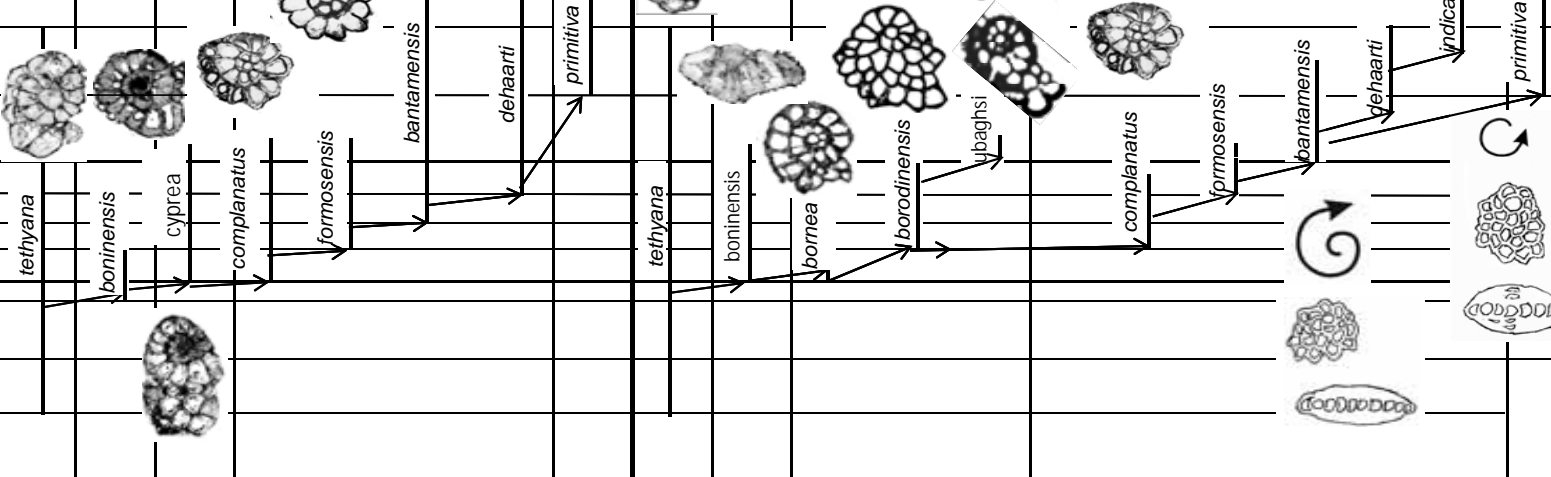
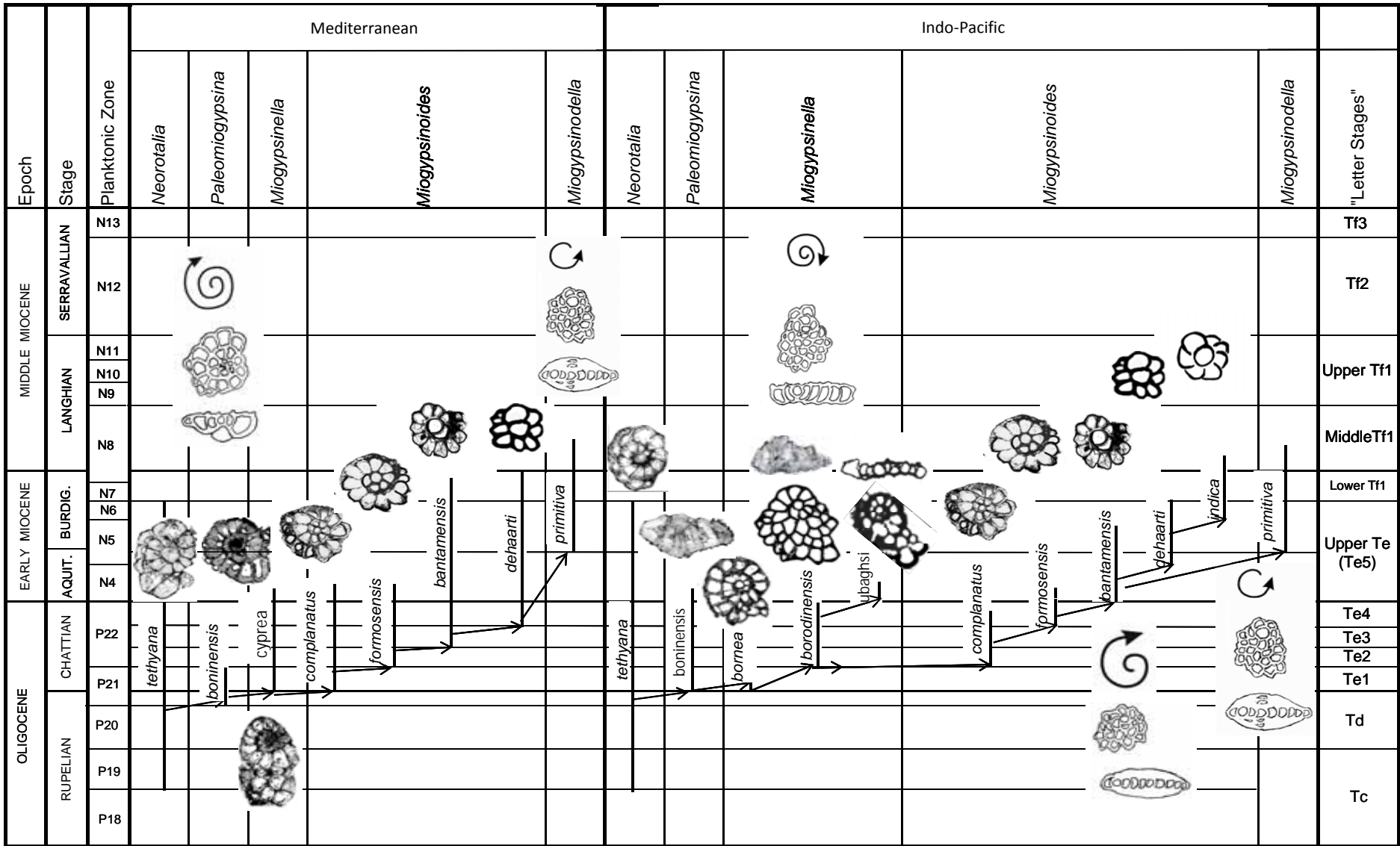
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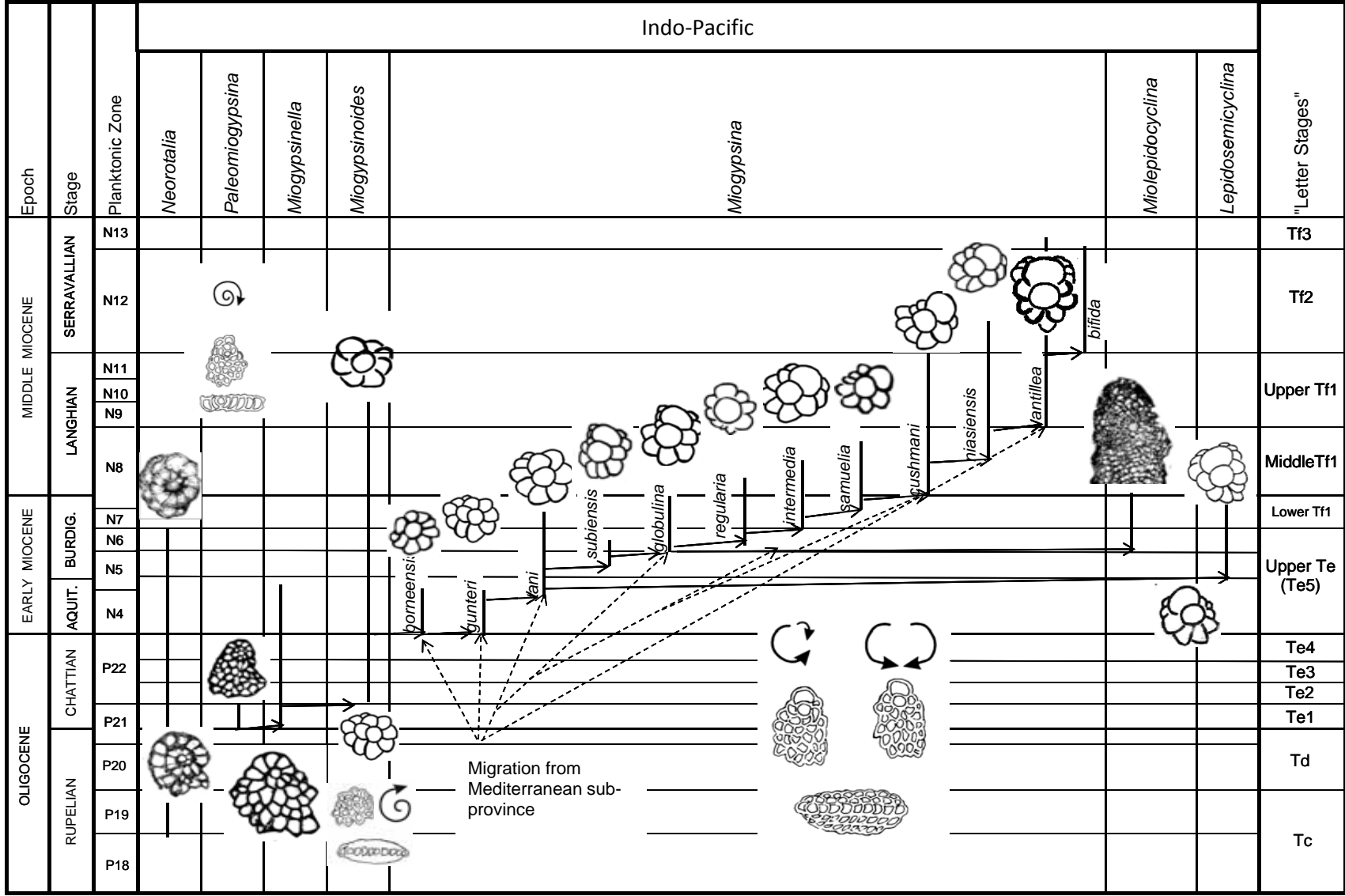


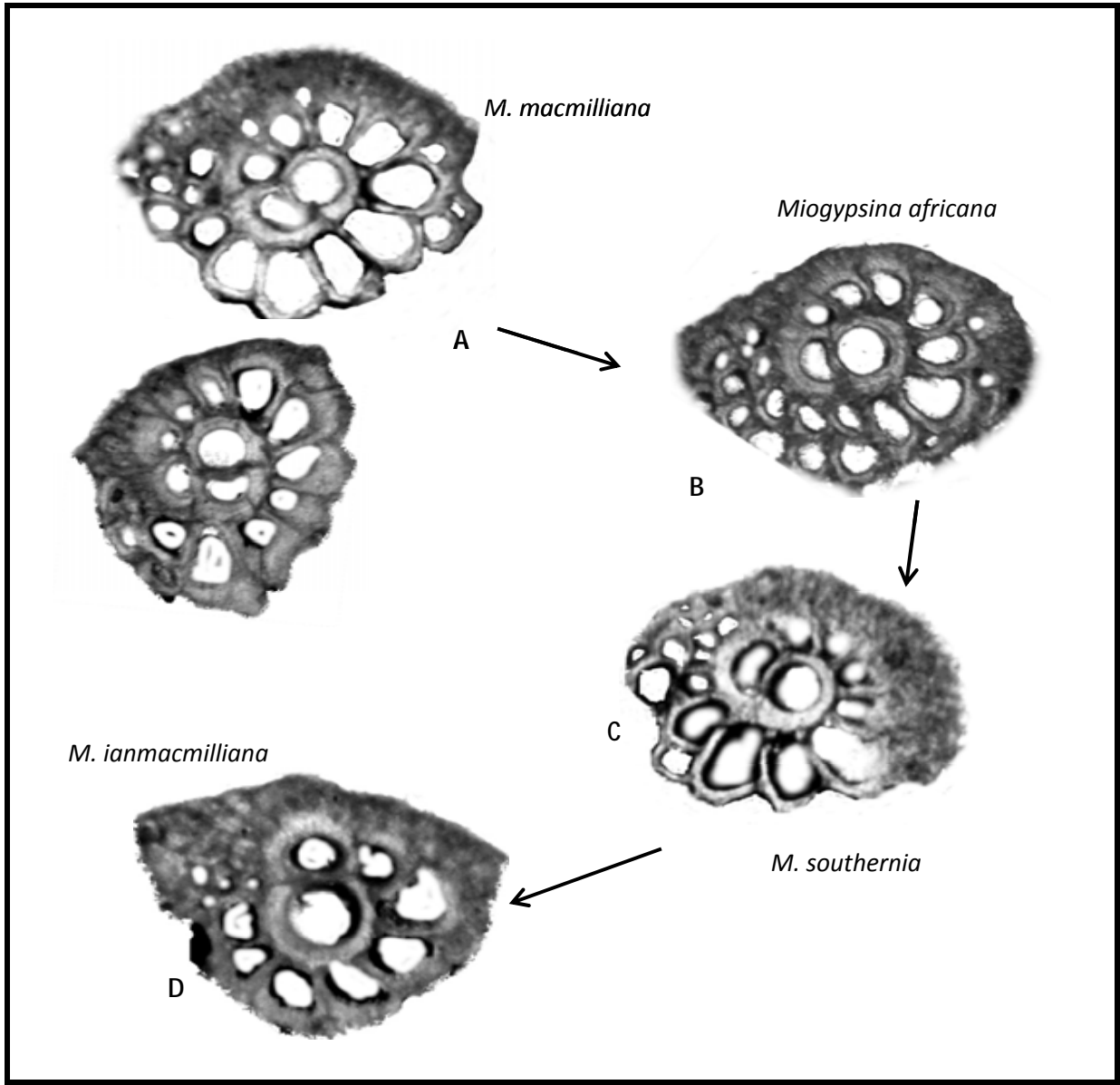
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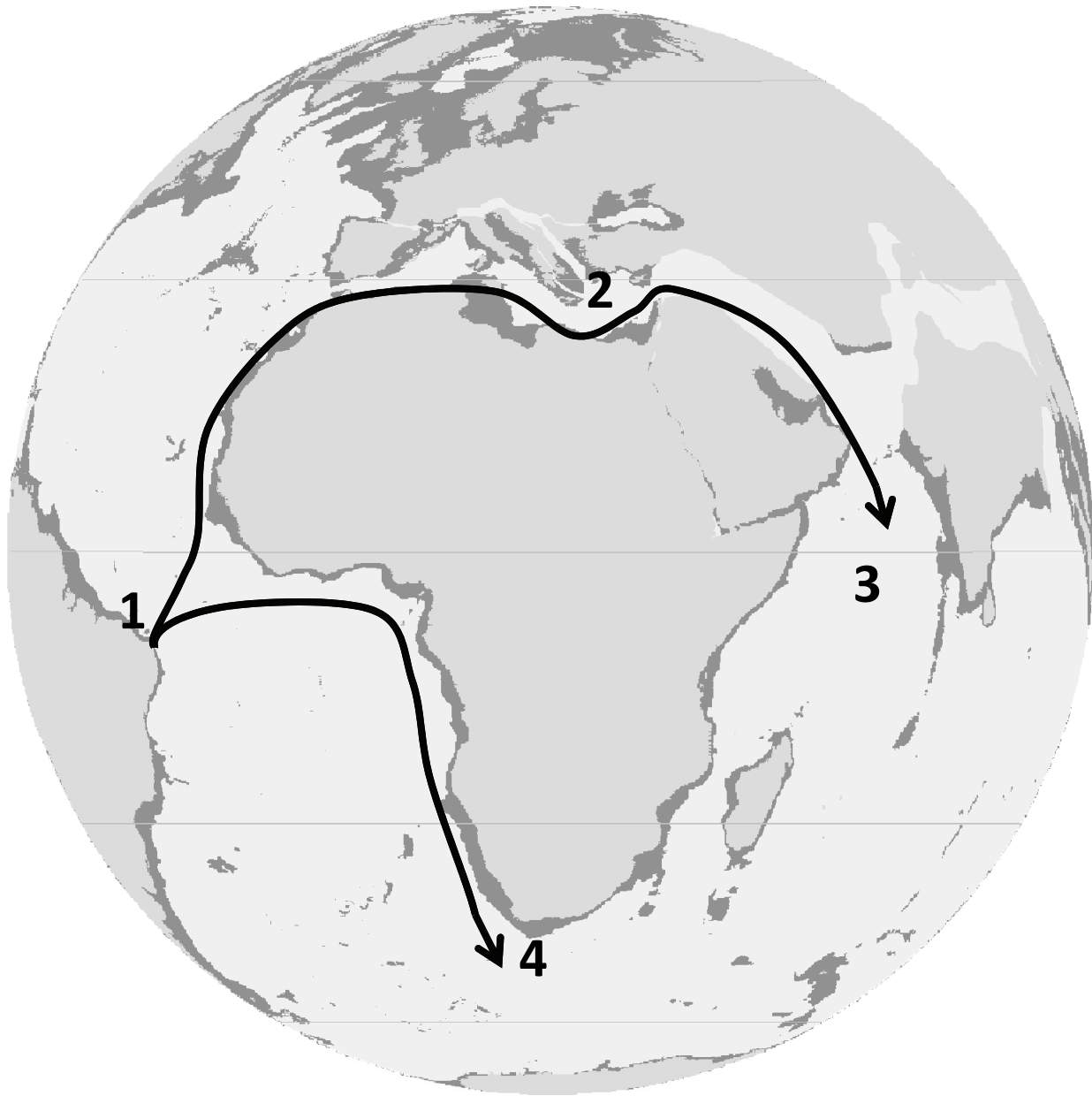
D







Epoch	Stage	PZ	Miogypsinid Events	Tectonic and Oceanic Events	Climatic Events
MIDDLE MIOCENE	SERRAVALLIAN	N13	<p>Extinction of miogypsinids from the Indo-Pacific subprovince (N13).</p> <p>Final extinction of miogypsinids from the Mediterranean subprovince, replaced by Indo-Pacific non-miogypsinid forms (N8). Extinction of miogypsinids from the American and South African provinces, and significant diversity reduction in Med. (End Burdigalian).</p> <p>Migration of miogypsinids to South Africa (N4-N5).</p> <p>Miogypsinids colonize Indo-Pacific (P22).</p> <p>Migration of miogypsinids to Med.(P21). End of migration of <i>Neorotalia</i> (P21).</p> <p>Eastward transoceanic migration of early American <i>Neorotalia</i> to West Africa/Tethyan (P18-P19).</p>	<p>Final closure of the connection between the Mediterranean and the Indian Ocean (13-14Ma).</p> <p>Major global transgressions (15.5-16.5Ma). Eruption of the Columbia River Flood basalts (15 - 17Ma). First closure of Eastern Mediterranean (17Ma).</p> <p>Red Sea Rifting (21Ma).</p> <p>Reversal of flow through the Panama Seaway (20 to 30 Ma).</p> <p>Rising sea level isolated the West African shelf from the American province (28Ma).</p> <p>Ethiopian Flood Basalts(31-29 Ma).</p> <p>Sea level low stands (29 - 33Ma). Drake passage opened (33Ma) .</p>	<p>East Antarctic Ice Sheet established (12Ma).</p> <p>Global cooling (10-14Ma).</p> <p>Mid-Miocene Climatic Optimum (14-16.5Ma).</p> <p>Late Oligocene Warming, global temperature rise (26-27Ma).</p> <p>Significant global cooling (33-34Ma).</p>
		N12			
	LANGHIAN	N11			
		N10			
		N9			
EARLY MIOCENE	BURDIG.	N8			
		N7			
		N6			
	AQUIT.	N5			
N4					
OLIGOCENE	CHATTIAN	P22			
		P21			
	RUPELIAN	P20			
		P19			
		P18			



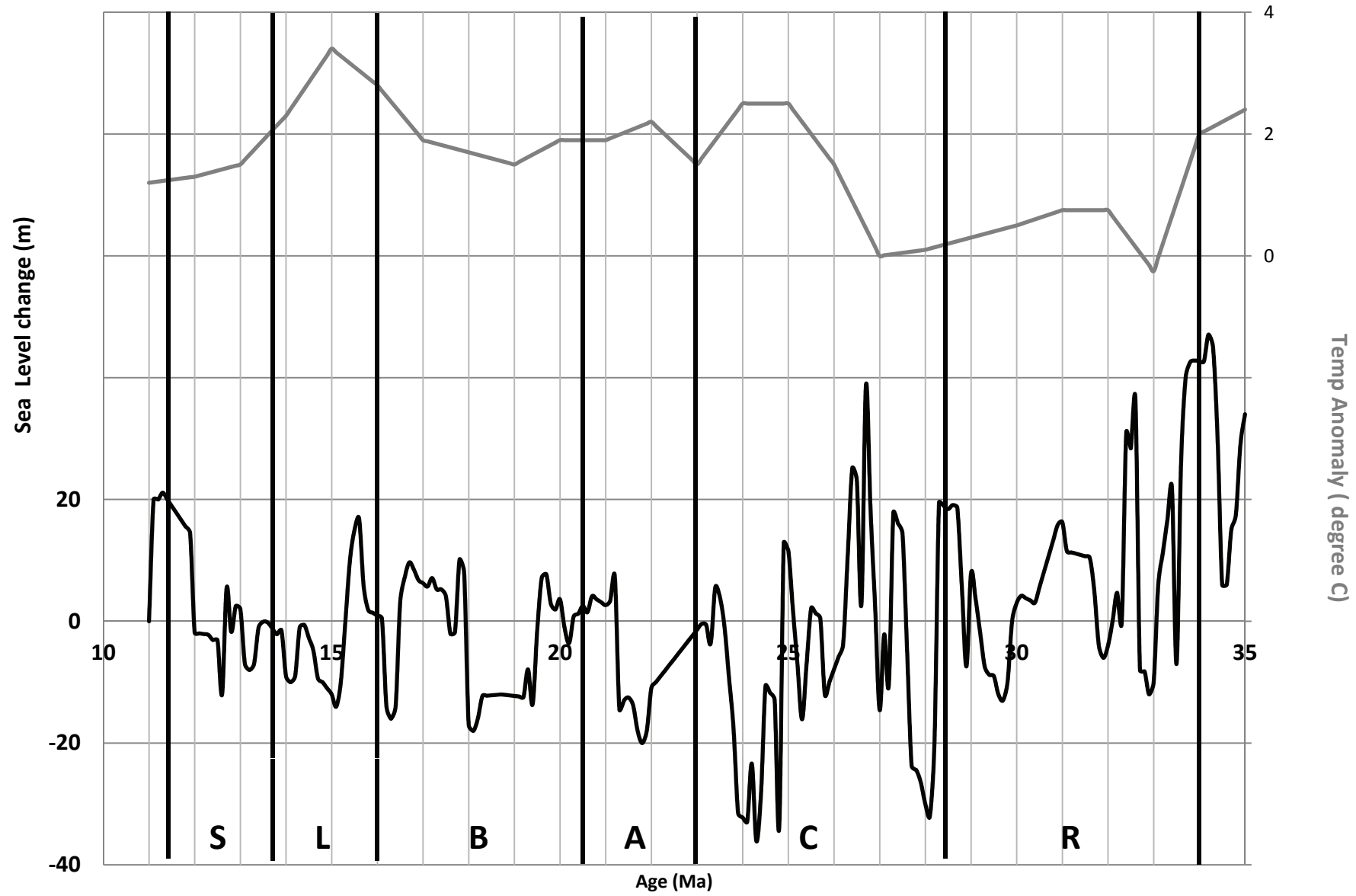


Plate 1

Fig. 1. *Pararotalia* sp. A. Early Eocene, Laki Formation, Sakesar Limestone, Bhadrar Beds, Salt Range, Pakistan, UCL MF154, x38.

Fig. 2-4. *Neorotalia tethyana* new species. (2-3) Late Oligocene-earliest Miocene, JBC3, Java, x40; (4) Miocene (Aquitania), Loc. 621/3, Borneo, UCL MF155, x50.

Fig. 5. *Paleomiogypsina boninensis* Matsumaru. Late Oligocene, Chattian, P21, Loc. 621/3, Borneo, UCL MF156, x70.

Figs 6-7. *Miogypsinella ubaghsi* (Tan Sin Hok). Miocene (Early Aquitania), Darai Limestone, UCL MF157; UCL MF158, x54.

Fig. 8. *Miogypsinella borodinensis* Hanzawa. Late Oligocene, Loc. 204, Borneo, UCL MF159, x45.

Figs 9-15. *Miogypsinella bornea* new sp. Late Oligocene (Early Chattian - Early Aquitania), Java, holotype UCL MF160, 9, x45; paratypes UCL MF161 -6, 10, x50; 11, megalospheric form, x42; 12, x45; 13, x34; 14, x29; 15, x20.

Figs 16-23. *Miogypsinoides dehaarti* (van der Vlerk). 16-17, 23, Late Aquitania, Sulawesi, 16, UCL MF167-72, x21; 17, x20; 23, x30. 18-19, Miocene (Burdigalian), Waterfall Section, Christmas Island, Indian Ocean, NHM 6764 1295, 18, x24; 19 x27. 20-22, Miocene, Late Aquitania, Loc. 251, Borneo, 20, x17; 21, x15; 22, x19.

Fig. 24-25. *Miogypsina borneensis* Tan Sin Hok. Miocene (Aquitania), Darai Limestone, Papua New Guinea, UCL MF173-4, 24, x45; 25, x30.

Plate 2

Figs 1-2, 14. *Miogypsinoides dehaarti* (van der Vlerk), 1-2, Miocene (Burdigalian), Nias, Sumatra, 201, UCL MF175-6, x50; 14, Early Miocene, Middle Burdigalian, Subis Formation, Borneo, UCL MF178, x24.

Figs 3-4. *Miogypsina kotoi* Hanzawa. Early Miocene, Middle Burdigalian, Subis Formation, Borneo, S21, UCL MF179-8, 3, x22; 4, x18.

Figs 5. *Miogypsina tani* Drooger, Early Miocene, Middle Burdigalian, Subis Formation, Borneo, UCL MF189, SB8, x25.

Figs 6-10. *Miogypsina subiensis* new sp. Early Miocene, Middle Burdigalian, Subis Formation, Borneo, holotype UCL MF192, paratypes 190-91, 193-5. 6, S15, x28; 7, 8, SB6, x29; 9, 10, SB8, x32.

Figs 11-13, 21. *Miogypsina globulina* (Michelotti). Burdigalian, Borneo. Loc. 251, UCL MF196-9, 11, 13, x29; 12, x23; 21, Nias, x40.

Figs 15-17. *Miogypsinodella primitiva* BouDagher-Fadel and Lord, Miocene (Burdigalian), Nias, Sumatra, UCL MF200-3, 15, x29; 16, x24; 17, x32.

Fig. 18. *Lepidosemicyclina thecideaeformis* Rutten, Miocene (Burdigalian), Upper Chake Beds, Pemba, Tanzania, NHM P22849, x39.

Figs 19-20. *Miogypsina indonesiensis* Tan Sin Hok. Miocene (Serravallian), Nias, UCL MF204, x19.

Figs 22-25. *Miogypsina niasiensis* new species. Gawo Formation, Nias Island, N161, Early Langhian, Middle Tfl, holotype UCL MF205, N192, Late Burdigalian, lower Tfl, paratypes UCL MF206-8, 22, x35; 23, x44; 24, x33; 25, x39.

Plate 3

Figs 1-2. *Miogypsina kotoi* Hanzawa. Early Miocene, NHM coll. 1981/3 Borehole, 075A, 245.4m Sakakanan Kalimantan, UCL MF206-7, 1, x45; 2, x22.

Figs 3-7. *Miogypsina regularia* new species. Nias, Indonesia, Gawo Formation, 25, Tf1, Holotype, UCL MF208, 3, x15; paratypes UCL MF209-12, 4, x20; 5, x33; 6, x22; 7, x24.

Fig. 8. *Miogypsina bifida* Rutten, Miocene (serravallian), Sungai, Boengaloen, East Borneo, NHM. Van Vessem, coll. BB 469 – 1913, x19.

Figs 9-16. *Miogypsina samuelia* new species. Nias, Indonesia, Gawo Formation, 27B, paratypes UCL MF214-20, 9, x32; 10, x20; 11, x21; 12, x24; 13, x28; 14, x24; 15, x30; holotype UCL MF221, 16, x26.

Fig. 17. A) *Lepidosemicyclina banneri* new species, B) *Heterostegina (Vlerkina) borneensis* van der Vlerk. Early Miocene (Burdigalian), Borneo, Loc. 203, UCL MF222, x12.

Figs 18-23. *Miolepidocyclus banneri* new species. Early Miocene (Burdigalian), Java, Indonesia, holotype 20A, UCL MF223; paratypes UCLMF224-27, 18,19, x5; 20, x3; 21, x4; 22, x4; 23, x7;

Fig. 24. *Miolepidocyclus* sp.1, Late Burdigalian, Borneo, Loc 130, UCL MF269, x12.

Plate 4

Figs 1. *Neorotalia tethyana* new species. Rupelian, Cyprus, Geroskipou, UCL MF266, x44.

Fig. 2. *Paleomiogypsina boninensis* Matsumaru, Late Chattian, Cyprus, Geroskipou, UCL MF228, x43.

Figs 3-8. *Miogypsinella cyprea* new species. Early Miocene, Aquitanian, Terra Limestone, Cyprus, holotype UCL MF229, 6, x27; paratypes UCL MF230-33, 3A, 4, x42; 5, x43; 7A, x40; 8, x36.

Figs 9-10. *Miogypsinoides complanatus* (Schlumberger). Early Miocene, Aquitanian, Terra Limestone, Cyprus, UCL MF234-5, 9, x32; 10, x40.

Figs 11-12, 17. *Miogypsinoides formosensis* Yabe and Hanzawa. Early Aquitanian, Nerthe area, near Marseille, Petit Nid section, Formation pararécifale du Cap de Nautes, Ferr. Coll. MF252, 11, x48; 12, 17, x38.

Figs 13-16. *Miogypsinoides bantamensis* Tan Sin Hok. Late Burdigalian, Ferr. Coll. MF253-6, 13-14, Northern Sardinia area, Castlesardo section, 13, x29; 14, x32; 15, Early Aquitanian, the Nerthe area, near Marseille, Petit Nid section, Formation pararécifale du Cap de Nautes, x30; 16, Late Burdigalian, Northern Sardinia area, Castlesardo section, x40.

Figs 18-19. *Miogypsinoides dehaarti* (van der Vlerk). Miocene (Burdigalian), Cyprus, UCL MF236-7, 18, x 33; 19, x27.

Figs 20-21. *Miogypsina gunteri* Cole. Miocene (Aquitanian), top of Superga Mountain, Aman, about 2km S.E. of Superga, NHM coll MF257, x19.

Figs 22-23. *Miogypsinodella pillaria* Ferrandini *et al.*. Miocene (Burdigalian), 22, Cyprus, UCL MF238, x23; 23, Bonifacio area, southern Corsica, Cala di Labra Est section, R1 of Cala di Labra Formation, Ferr. Coll. MF239, x28.

Plate 5

Figs 1-3. *Miolepidocyclina excentrica* Bronnimann. Late Burdigalian, Bonifacio area, southern Corsica, Cala di Labra Est section, R1 of Cala di Labra Formation, Ferr. Coll. MF240, 1, x30; 2, x28; 3, x30.

Fig. 4. *Miogypsinoides dehaarti* (van der Vlerk). Miocene (Late Burdigalian), Northern Sardinia area, Castlesardo section, Ferr. Coll. MF241, x31.

Fig. 5. *Miogypsina globulina* (Michellotti). Balistra section (R2), Bonifacio area, southern Corsica, Cala di Labra Formation, Ferr. Coll. MF242, x30.

Figs 6-7. *Miogypsina mediterranea* Bronnimann. Late Burdigalian, Bonifacio area, southern Corsica, Cala di Ciappili section, R1 of Cala di Labra Formation, Ferr. Coll. MF243, x24.

Fig. 8. *Miogypsina cushmani* Vaughan. Miocene (latest Burdigalian), Castlesardo section (Northern Sardinia), equivalent of Cala di Labra formation, Fernandini coll., Ferr. Coll. MF244, x32.

Figs 9-18. *Miogypsina mcmillania* new species, Burdigalian, Childs Bank Burdigalian, Ka1, 400m, South Africa, McMillan coll., 9, holotype UCL MF239, 10-18; paratypes UCL MF240-9, x29.

Figs 19-21. *Miogypsina africana* BouDagher-Fadel and Price, new species. Burdigalian, Childs Bank Burdigalian, Ka1, 360m, South Africa, McMillan coll., 19, holotype UCL MF250; 20-21, paratypes, UCL MF270-71, x25.

Figs 22-24. *Miogypsina southernia* BouDagher-Fadel and Price, new species. Burdigalian, Childs Bank Burdigalian, Ka1, 360m, South Africa, McMillan coll. 22, holotype UCL MF273; 23-24, paratypes UCLMF274-275, x20.

Fig. 25-26. *Miogypsina ianmcmillania* BouDagher-Fadel and Price, new species. Burdigalian, Childs Bank Burdigalian, Ka1, 360m, South Africa, McMillan coll., 25, holotype UCL MF276; 26, paratype, UCL MF277, x17.

Plate 6

Figs 1-3. Packstone of *Miogypsinoides cyprea* new species. Late Oligocene, Chattian, Terra Limestone, Cyprus, UCL MF262-264, x20.

Figs 4-5. *Miogypsina antillea* (Cushman). Late Burdigalian, Cyprus, Terra member, UCL MF265-8, x27.

Figs 6-8. *Miolepidocyclus burdigalensis* (Gümbel). Burdigalian, Cyprus, UCL MF256-57, x28.

Figs 9-13. *Miogypsina mediterranea* Bronnimann. Late Burdigalian, Morocco, UCL MF252-5, x8.

Fig. 14. *Miogypsina globulina* (Michellotti). UCL MF258, x10.

Figs 15-16. *Miogypsina cushmani* Vaughan. Miocene (latest Burdigalian), Castlesardo section (Northern Sardinia), equivalent of Cala di Labra formation, Fernandini coll., Ferr. Coll., UCL MF259-60, 15, x17; 16, x30.

Fig. 16. *Lepidosemicyclus excentrica* Tan Sin Hok. Late Burdigalian, Java, JBC3KAL197, UCL MF263, x5.

