The phylogenetic and palaeogeographic evolution of the nummulitoid larger benthic foraminifera

Marcelle K. BouDagher-Fadel[1] and G. David Price[1]

[1]*Department of Earth Sciences, University College London, Gower Street, London, WC1E 6BT, UK*
Corresponding author (e-mail: m.fadel@ucl.ac.uk)

ABSTRACT

Nummulitoidea are larger benthic foraminifera, and were major reef-forming organisms from the Middle Paleogene to the Early Neogene. Today, porous nummulitoid limestones, which occur globally from the Atlantic to the Indo-Pacific, form potentially valuable oil reservoirs. Until now the origin, evolution and palaeogeographic development of the nummulitoids have not been fully articulated, but new material allows here the first systematic, global biostratigraphic comparison and correlation of the nummulitoids to be made. It is found that the nummulitoids originated in the Americas during the Middle Paleocene (Selandian). These early nummulitoids are inferred to have migrated across the Atlantic in the Late Paleocene (Thanetian) following two paths: south towards SW Africa, and north-eastwards through the Tethyan corridor. The Tethyan forms evolved during the Eocene into many lineages, which in turn migrated, within a few million years of their first appearance, into the Indo-Pacific, where they became isolated and diversified further. Meanwhile the SW African forms remained small and similar to the original American stock until the Early Miocene (Burdigalian), when assemblages were augmented by forms that migrated from Tethys, an event established by the discovery of new Mediterranean-derived species of *Planostegina* in SW Africa: *africana, mcmillania, southernia, langhiana.* Climatic and tectonic processes contributed to the Middle Oligocene disappearance of *Nummulites* and the Early Miocene global extinction of *Spiroclypeus* and of *Cycloclypeus* in the Mediterranean. Morphologically small nummulitoids persisted however, and are still present in all provinces to this day.

INTRODUCTION

Members of the planispirally coiled superfamily Nummulitoidea are larger benthic foraminifera (LBF) that belong to the suborder Rotaliina; as such they are single-cell, marine protozoa. Many are restricted to the Indo-Pacific Province and are still extant, but fossilized, extinct forms are abundant from the Paleogene in the American, the Western Tethyan, Southwest African and Indo-Pacific provinces. Large nummulitoids were rock-forming and were often supported on sea-grasses and similar substrates (BouDagher-Fadel, 2008). They are thought to have hosted photosynthesizing symbionts (Langer and Hottinger, 2000; Beavington-Penney and Racey, 2004). The latitudinal global distribution of present day nummulitoids, and therefore by inference their fossil relatives, is mainly controlled by

temperature (they are limited to tropical and subtropical reefal waters), and their distribution and morphological adaptations are also dependent upon the light requirements of their endosymbionts and substrates (Beavington-Penney and Racey, 2004; Murray, 2006; BouDagher-Fadel, 2008).

Morphologically, living nummulitoids seldom exceed 2mm in size, but fossil nummulitoids range from small, millimetre sized forms to gigantic, centimetre-sized forms. Gigantic forms (>100mm) evolved twice, first during the Paleogene, in species within the genus *Nummulites,* and later in the Neogene within the genus *Cycloclypeus*. The largest reported *Nummulites* is the Mediterranean *N. millecaput* (Nemkov, 1962), which existed in the Middle Eocene (Lutetian) during a globally significant warm climatic episode (Cramer and Kent, 2005), and grew, despite being a single-cell organism, to have a diameter of up to 160mm. After the acme of such forms in the Middle Eocene, large *Nummulites* declined in size and diversity, but later in the Miocene, gigantic forms developed again, with the Indo-Pacific *Cycloclypeus carpenteri* developing a maximum diameter of up to 150mm in the Langhian (BouDagher-Fadel, 2008), during the Neogene thermal high (usually referred to as Middle Miocene Climate Optimum (Zachos *et al.* 2001)). It has been demonstrated that there is a correlation between photosynthesis and calcification in coral reefs (Gattuso, and Buddemeier, 2000) and it would seem reasonable to infer that the development of gigantism in nummulitoids might be related to climatically determined activity of their algal symbionts (Cowen, 1983). The presence of symbionts in fossilised nummulitoids is inferred from microstructures within the fossilised tests that are similar to those observed in present-day LBF, and which provide shelter for the symbionts and allow respiration (Bartholdy, 2002; Jorry *et al.*, 2006). The large sizes of some fossil forms are also credited to multispiral growth, documented by authors such as Ferràndez-Cañadell (2012), who deduced that the gigantic sizes reached by *Nummulites* are produced mainly by the increase in growth rate provided by multispiral growth, and only secondarily by an increase in longevity that is thought to be of less than 6 years.

Nummulitoids exhibited relatively rapid evolutionary rates, and developed complex tests, which make them a very important index fossil group for the shallow-marine environments of the Late Paleocene through to (in the Indo-Pacific at least) the Early Miocene (Schaub, 1981; Pignatti, 1998; Serra-Kiel *et al.*, 1998). Their large sizes were made achievable as a result of the evolutionary development of a variety of different morphological structures that had the effect of mechanically strengthening the nummulitoid test, including for example the in-filling of the umbilical area with pillars, the subdivision of chambers into small chamberlets, and the development of suspended lamellae from a thickened marginal cord (BouDagher-Fadel, 2008).

Today nummulitoid limestones, which occur globally from the Atlantic, through the Mediterranean and the Gulf, to the Indo-Pacific, form potentially valuable oil reservoirs. The study of nummulitoid species and the definition of their stratigraphic ranges are therefore of considerable economic importance. As such, they have been the subject of many regional micropalaeontological investigations (see Barnett, 1974; Blondeau, 1972; Schaub, 1981;

Adams, 1988; Racey, 1995; Jorry *et al.*, 2006; BouDagher-Fadel 2008; Haynes *et al.*, 2010). However, until now, it has not been possible to develop an effective global view of their evolution, since in the past, the systematic study of the relationship between the American, African, Western Tethys and Indo-Pacific lineages has been hampered by the lack of biostratigraphic correlation between the geographically scattered nummulitoid assemblages described in the literature, and by the scarcity of described material from West and SW Africa. In addition, the lack of a consistent phylogenteic framework and the limited taxonomic consensus on some forms, even at the generic level, has in the past made global correlation very difficult. Furthermore, correlating the stratigraphic ranges of Western Tethyan and Indo-Pacific genera in particular has been hampered by the occasional misidentification or confusion between similar species (discussed in, for example, Renema, 2002).

Fossil nummulitoids of the Western Tethys (now found in the Mediterranean region), especially members of the genera *Nummulites* and *Assilina,* have been intensively studied (e.g. De la Harpe 1877; Blondeau, 1972; Hottinger 1977; Schaub 1981; Adams, 1988; Serra-Kiel *et al.*, 1998; Beavington-Penney and Racey, 2004; Less and Özcan, 2008; Less *et al.*, 2008; Hohenegger, 2011), and various species have been used to zone and date Western Tethyan Paleogene and Neogene sediments (Serra-Kiel et al 1998; Cahuzac and Poignant, 1998). However, information about forms from SW Africa relies on only a very few papers (e.g. Vaughan, 1933), and those from the American province rely on papers such as Cole (1952). Likewise, relatively few nummulitoid species have been described from Tibet and the Indo-Pacific (e.g. Krijnen, 1931; Tan Sin Hok, 1937; Blondeau, 1972; Matsumaru, 1996; Saraswati *et al.*, 2000; Renema 2002; Matsumaru and Sarma, 2010) and there have only been a few attempts to define a taxonomy within the Indo-Pacific and to provide biostratigraphic correlation with forms from the Western Tethys (e.g. Renema, 2002). The earliest major overview of the occurrences of nummulitoids in Indonesia was published by Doornink, (1932) and dealt only with Java. A recent comprehensive study published by Renema (2002) dealt with the entire Indo-West Pacific, focussing on Indonesia. Racey (1995) and Haynes *et al.* (2010) described nummulitoids from Oman and integrated these with the zonal scheme of Schaub (1981).

In this paper, we present new findings from material recently obtained as a result of various explorations of LBF-bearing carbonate facies from some Atlantic basins from offshore Brazil (Campos Basin), Venezuela (Matacaibo Basin), and SW Africa (from Kudu boreholes, offshore Namibia; from the Benguela Basin near Dombe Grand, Angola; and from the Childs Bank (Hole X-A1), offshore South Africa). These are augmented by studies of new material from several localities in Spain (shallow marine sequences within the Ainsa Basin), Cyprus (the Circum-Troodos Massif Sedimentary Succession in northern Cyprus), Northwest Syria (Latakia), South Tibet (Tingri and Gamba regions), and from the Sarawak Basin (onshore carbonates, Tinjar Province).

As a result, by combining our new observations with those in the literature, we are able to put forward, for the very first time, a comprehensive, global, systematic analysis of the

biostratigraphic, phylogenetic and palaeogeographic evolution of the nummulitoids. We infer that the nummulitoids originated in the Americas during the Middle Paleocene (Selandian) from, we suggest, a simple rotaliid ancestor that survived the global End Maastrichtian extinction event. We contend that these early nummulitoids migrated across the Atlantic in the Late Paleocene following two paths: one to the south towards SW Africa; the other to the north and east, through the Western Tethyan corridor and on to the Indo-Pacific.

The Western Tethyan forms evolved during the Eocene into many lineages (that included the development of gigantic forms) and migrated, within a few million years of their first appearance, into the Indo-Pacific, where they became isolated and often diversified further. Meanwhile the SW African forms remained small (with sizes not exceeding 2mm) and similar to the original American stock until the Miocene, when the SW African assemblages were augmented by forms that migrated from Tethys. This event is defined by our discovery of four new Mediterranean-derived species in SW Africa, *Planostegina africana, Pl. mcmillania, Pl. southernia* and *Pl. langhiana,* all of which are described below. The tectonically driven partition of the Western Tethys seaway into Proto-Mediterranean and Parathethys, and environmental stresses, perhaps associated with global cooling and the large flood basalt event in Ethiopia and Yemen (Courtillot and Renne, 2003), are likely to have contributed to the extinction in the Oligocene (Chattian) of the last Mediterranean and Indo-Pacific species of *Nummulites*. In addition, the continued global cooling and the tectonically driven closure in the Early Miocene (Burdigalian) of the seaway between what is today the Mediterranean and the Indo-Pacific can be correlated with, and we suggest drove, the subsequent extinction of the Mediterranean *Cycloclypeus* (Early Miocene, Burdigalian) and the subsequent global cooling which coincided with the global extinction of *Spiroclypeus* (Early Miocene, Burdigalian). Morphologically small (millimetre-scale) nummulitoids persisted however, and are still present in all provinces to this day.

In our definitions of stratigraphic ranges, we primarily use the planktonic foraminiferal zonal scheme of BouDagher-Fadel (2013), which is tied to the time scale of Gradstein *et al.* (2012). This scheme is developed from the calibration of the N-zonal scheme of Blow (1979), and the M-zonal scheme of Berggren (1973), which has been recently revised by Wade *et al.* (2011). In this paper, the planktonic foraminiferal zonal scheme is also correlated with the larger benthic foraminiferal 'Letter Stages' of the Far East, as defined by BouDagher-Fadel and Banner (1999) and later revised by BouDagher-Fadel (2008), and with the biogeographic zonation of shallow benthic larger foraminifera as defined by Serra-Kiel, *et al.* (1998), which incorporates a series of biozones proposed for the Paleogene of Western Tethys based on species of *Nummulites* and *Assilina* (Schaub, 1981). These biozones have been integrated into the shallow benthic zones (SBZ) covering the Paleocene to Eocene of the Mediterranean region by Serra-Kiel *et al.* (1998), as a system of numbered units for the "Tertiary" with SBZ 1-23 covering the Paleogene.

MORPHOLOGY AND TAXONOMY OF THE NUMMULITOIDS

Morphology

Nummulitoids usually have a flattened to stoutly lenticular or even globular test, with a periphery that varies from being sharp to being rounded or somewhat undulose (Beavington-Penney and Racey, 2004). Fig. 1 shows outer shell surface specimens and thin sections of various nummulitoid species, and highlighted in this figure are their main morphological features, including the presence of chambers, septa, septal pillars, the canal systems in the marginal cords and septa, and the proloculus. Many authors have studied the morphology of the nummulitoid tests, with some detailed descriptions as early as d'Archiac (1850), Carpenter (1850), Galloway (1933), Davies (1935), and Glaessner (1945). Among the more recent studies are those of Hottinger (1977; 1978), Adams (1988), Hottinger *et al.* (2001), Racey (1995), BouDagher-Fadel (2008), and Haynes *et al.* (2010).

The morphological details of the nummulitoids are of importance because they are the basis of the taxonomy of the superfamily. The key features of this taxonomy are dominated by:

- the degree of the involution or evolution of the test;
- the degree of the development of the marginal cord;
- the extent of the opening of the spire;
- the division and subdivison of the chambers;
- the overall size of the microspheric forms (i.e. the forms produced by sexual reproduction), which increases over geological time for most lineages;
- the size of the proloculus, which increases with time in the megalospheric forms (i.e. forms produced by asexual reproduction) for most lineages;
- the development of embryonic chamber complexity, which tends to increase with time;
- the shape of the septa (see Adams, 1988; Racey, 1995). There are three orders of septal filaments in *Nummulites*: primary filaments, which arise directly from the septa and are present in all species; secondary filaments, which are merely the distal walls of blister-like chamberlets and are largely restricted to the subreticulate and reticulate groups; and tertiary filaments, which originate as spiral ridges and are all clearly canaliculated. The septal complexity generally increases during time, thus:
  - simple radiating (striate), falciform or curved septal filaments in Late Paleocene–Early Eocene species (see Fig. 1a,c);
  - meandriform and complex branching in Middle Eocene forms (see Fig. 1b);
  - reticulate septal filaments in Late Eocene forms (Figs 1d,e);
  - in the Early Oligocene the reticulate septa are still widespread, but there is a tendency to the return to simple structures.

One of the characteristic features of the nummulitoids is that they exhibit a complex three-dimensional canal system within the thickened peripheral keel (marginal cord) and well-developed spiral and subsutural septal canals (Fig. 1f-l). The development of the canaliculate

marginal cord, which replaced the primary aperture of the nummulitoid ancestor, is essential for growth, locomotion, reproduction, excretion and protection (Röttger, 1984). It permits the extrusion of the pseudopodia from any point of the marginal cord, providing the nummulitoid with radial symmetry, and enables the disposal of waste products. During sexual reproduction, it enables the release of gametes, and during asexual reproduction it allows the extrusion of the cytoplasm and symbionts to the ambient seawater (Röttger, 1984; BouDagher-Fadel, 2008). This complex canal system is characteristic of all living and fossil nummulitoids (Hottinger, 1977). They have canal systems within the walls of their plurilocular calcareous tests. Such constructions are called supplemental skeletons, representing infolded outer lamellae. The biological function of the canals has been investigated by many authors (Röttger, 1984; Hottinger *et al.*, 2001). They became very complicated in the Eocene, with forms such as *Pellatispira* (see Hottinger *et al.*, 2001). In extant nummulitoids, they are found filled with protoplasm containing permanently differentiated microtubules (Hottinger and Dreher, 1974; Leutenegger, 1977; Hottinger and Leutenegger, 1980; Hottinger *et al.*, 2001).

In involute spiral forms, the lumina of the chambers (the cavities of the shell filled with protoplasm) in one coil cover laterally those of the preceding coil (e.g. *Nummulites,* Figs 1c, d), which develop, in some cases, wing-like extensions from the lumen to the poles (alar prolongation, Figs 1c). However, when the chamber lumina do not cover laterally those of the preceding coil, the test becomes spirally coiled in evolute genera (e.g., *Assilina*, Fig. 1n). The characteristic lamination of the nummulitid tests are formed during the process of chamber construction, in which each outer lamella covers the entire test, including all former chambers (Hoheneger, 2001).

Taxonomy
In the past, there has been much confusion over the classification and taxonomy of the nummulitoids. Several studies (e.g. Cole, 1964) have associated (or combined) together many genera as they considered characteristics, such as degrees of evolution and involution, or the thickness of the marginal cord to be gradational and not definitive at the generic level, leading to loss of resolution, which subsequent studies have reversed (see discussion in Haynes *et al.*, 2010).

The current nummulitoid taxonomy is based on works such as that of Hottinger (1977), Haynes (1980), Schaub (1981), and Haynes *et al* (2010), who noted that certain features visible in axial section (as seen in petrographic thin section), such as the alar prolongations (chevron-shaped cavities on each side of the test) in involute forms, characteristic of *Nummulites*, and the presence of thick lamellar walls on each side of the equatorial layer, as in *Cycloclypeus*, are useful in classification at the generic level (Fig. 1).

Hottinger (1977) proposed a generic classification based on the type of canal and stolon system, and the absence or presence of trabeculae ("imperforate shell material extending from an imperforate sutural zone into the perforate lateral chamber wall and housing oblique, ramified trabecular canals opening between the pores on the surface of the lateral chamber

wall", Hottinger (2006); see Fig. 1g). He considered the chamber formation and the type of stolon and canal system of greatest importance in the taxonomy of nummulitoids. Hottinger considered the stolon system and the canal structure as progressive, since they appear to become more complex with time.

BouDagher-Fadel (2008) presented an analysis of the history of nummulitoid taxonomy, and suggested that the Nummulitoidea should be divided into four families:

- Family Pellatispiridae Hanzawa, 1937 (genera without a marginal cord, but with radial and vertical canals or fissures: including genera *Biplanispira, Bolkarina, Miscellanea, Pellatispira, Serraia* and *Vacuolispira*),
- Family Nummulitidae de Blainville, 1827, which includes the
  - Subfamily Heterostegininae Galloway, 1933 (genera with true secondary septa, developed right across the chamber, forming chamberlets: including the genera *Grzybowskia, Heterostegina, Planostegina, Spiroclypeus* and *Tansinhokella*), and the
  - Subfamily Nummulitinae de Blainville, 1827 (genera without secondary septa forming chamberlets: including *Assilina, Chordoperculinoides, Nummulites, Operculina, Operculinella, Palaeonummulites, Planocamerinoides* and *Ranikothalia*),
- Family Cycloclypeidae Galloway, 1933 (genera with concentric annular, wholly evolute chambers, each chamber being divided into numerous chamberlets along the median plane, and with each chamberlet separated from adjacent chamberlets by straight, canaliculated walls. Members of this family have no marginal cord, except in the early stages of the microspheric generation: including the genera *Cycloclypeus* and *Katacycloclypeus*),
- Family Orthophragminidae Vedekind, 1937 (the development of which is not considered in this paper, but will be described separately in a subsequent study).

Haynes *et al.* (2010) introduced the subfamily Palaeonummulitinae Haynes *et al.*, 2010, for the simple nummulitoid genera with primary septa only (*Assilina, Caudrina* (a Late Paleocene new genus in which they included sub-evolute forms with coarse vertical canals), *Chordoperculinoides, Nummulitoides, Operculina, Palaeonummulites, Planocamerinoides,* and *Ranikothalia*). However, in our opinion the criteria that define the subfamily Palaeonummulitinae are so similar to those of the Nummulitinae as defined by de Blainville (1827) and later emended by BouDagher-Fadel (2008), which include all forms with simple undivided chambers, that we here consider the subfamily Palaeonummulitinae to be a synonym of the subfamily Nummulitinae.

Further confusion over the assignment of the genera within the Nummulitinae/Palaeonummulitinae has resulted from lumping or separating similar forms. Arni (1965) designated *Chordoperculinoides* (Pl. 1, Figs a-c) as including the moderately tightly coiled, involute nummulitids with thick, coarse vertical canals and a massive marginal cord with ramifying marginal canals. Loeblich and Tappan (1964, 1987) and Hottinger (1977) mistakenly assigned *Operculinella cumingii* (type species of *Amphistegina cumingii*,

Carpenter 1860, Pl. 1, Fig. g) to *Nummulites* (Fig. 1a-l) on the basis that the former possessed trabeculae (a feature that Hottinger considered wholly restricted to the genus *Nummulites*). However, Eames *et al.* (1962) had noted the strong dimorphism seen between microspheric and megalospheric forms of Oligocene specimens of *Nummulites,* and they differentiated them from *Operculinella* (where the microspheric and megalospheric generations are externally identical). The megalospheric *Operculinella* (e.g. *Operculinella cumingii*, Pl. 1, Fig. g) persists to the Holocene, but the large protoconch seen in the true *Nummulites* does not occur after the Early Oligocene (Fig. 1f). *Palaeonummulites* (type species of *Nummulina pristina* Brady 1874, see Pl. 1, Figs r-s) are here attributed to all involute forms, but having a tight spire and lacking the developed, highly extended later chambers of *Operculinella* (see Haynes *et al.*, 2010).

On the other hand, the American *Operculinoides*, with rapidly widening coils in the adult stage such as the *O. ocalanus* group (see Pl. 1, Figs d-e), were included by Nagappa (1959) as belonging to *Operculina*, on the grounds that involution is a gradational character. The coiling of *Operculina* is distinguishingly evolute (see Fig. 1m-n), and all involute forms with the rapidly widening coils in the adult stage, assigned previously to *Palaeonummulites* or *Operculinoides,* should in fact be included in *Operculinella* (see Plate 1, Figs d-i). Therefore, by comparing the American small involute forms, which only have simple primary septa, with those found in the Mediterranean and Indo-Pacific, we conclude that these small involute nummulitoids (up to 3mm in size) belong in fact to two genera, the tightly to moderately coiled *Palaeonummulites* (Pl. 1, Fig. k-s), and the loosely coiled *Operculinella* (see Pl. 1, Figs d-i). Therefore, we consider the American genus *Operculinoides* (type species of *Nummulites willcoxi* Heilprin, 1883, see Pl. 1, Fig. l) as a synonym of *Palaeonummulites,* and for the first time therefore, we report the presence of *Operculinella,* in the American province (see Pl. 1, Figs d-f).

Following the above taxonomic revision, the respective biostratigraphic and palaeogeographic evolution of the nummulitoids from the American, Western Tethyan, Indo-Pacific and SW African provinces are outlined below. At the end of this paper, in the Appendix (Comments on New Taxa), we provide the systematic taxonomic description of the new SW African species of *Planostegina, Pl. africana* and *Pl. mcmillania, Pl. southernia, Pl. langhiana* (illustrated in Plates 2-4) that have been used to differentiate and define some of the phylogenetic and biogeographical evolution outlined below.

BIOSTRATIGRAPHY AND PALAEOGEOGRAPHIC DISTRIBUTION OF THE NUMMULITOIDS

Traditionally, in the Paleogene the LBF were considered to define three major, distinct palaeogeographic realms; namely, the American, the Western Tethys, and the Indo-Pacific provinces. On the basis of this current study, however, we are able to establish for the first time that there was in fact a fourth distinct palaeogeographic nummulitoid province, namely the newly defined SW African realm. This follows a similar discovery of a fourth SW African province for the Neogene LBF family Miogypsinidae (BouDagher-Fadel and Price,

2013). From Plate 1 it can be seen that the nummulitoid forms found in the Americas are very small (with diameters no more than 2mm), and different from those of Western Tethys and the Indo-Pacific. Those found in the Paleogene of SW Africa are also small and similar to those described in the Americas. We show below however that in the Neogene, the SW African assemblages contain forms of *Planostegina* (see Plates 2-4), previously only found in the Western Tethyan and Indo-Pacific provinces. We will conclude that after defined, occasional migration events between provinces, the nummulitoids in the four provinces developed independently of each other, but exhibit parallel evolutionary trends (see Fig. 3).

The American province

In studying new samples from Paleogene carbonate succession from offshore Brazil (see BouDagher-Fadel and Price, 2010a, 2010b; Boudagher-Fadel *et al.*, 2010), we recorded the first occurrence of *Chordoperculinoides bermudezi* in the Middle Paleocene of the Campos Basin (Pl. 1, Fig. a). It was also found no earlier than the Selandian (P3) in the Caribbean and the Americas by previous researchers, *e.g.* Butterlin (1987); Mello e Sousa (2003). We suggest that this form was derived from a pre-existing rotaliid, but the species linking the two forms are still ambiguous. *Chordoperculinoides* (Pl. 1, Figs a-c), characterised by coarse vertical canals and a massive marginal cord, is found throughout the Selandian (P3) and the Thanetian (P4), and gave rise to the sub-evolute *Caudrina* in the Late Thanetian (P5). *Caudrina* did not survive the Paleocene-Eocene boundary, while *Chordoperculinoides* died out at the top of the Early Eocene (End Ypresian, P9). *Caudrina* has not been recorded so far from the Eastern Hemisphere, but as we will see below we infer that the other forms migrated eastward from the Americas, to populate the Eastern realms.

The first completely evolute form, with a moderately thick marginal cord, is found in the Thanetian (P4b) and is represented by the long-ranging, cosmopolitan, *Operculina*. During the same period, *Operculina* appears to have given rise to the evolute tightly coiled *Assilina* and the involute tightly coiled extant genus, *Palaeonummulites*. The latter had given rise to "lax" forms (*i.e.* as defined by Haynes *et al.*, 2010) by the beginning of the Lutetian (P10), as seen in *Operculinella*. In a separate lineage, the Middle Eocene (P12b) also witnessed the development of an early involute test in some operculine species, which subsequently became fully involute, having chambers divided into chamberlets with secondary septa, giving rise to *Heterostegina* (Fig. 2).

The Western Tethyan province

In the Western Tethyan province (which includes the modern day regions of West Africa, the Mediterranean and Tibet), forms similar to the American *Pararotalia, Chordoperculinoides* and *Operculina* first appeared in West Africa in the Thanetian (P4b); this is later than their first appearance in the Americas. The first so called "*Nummulites*" of West Africa is "*N.*" *ewekoroensis* Sachs and Adegoke, as yet recorded only from its type locality, the Ewekoro Limestone in Nigeria (Sacks and Adegoke, 1975). This form is characterized by its small size (1.0 to 1.4mm) and a poorly developed marginal cord in the megalospheric generation, as in *Palaeonummulites*. On these grounds, it is considered here that it should in fact be designated *Palaeonummulites ewekoroensis,* and is in fact of Late Thanetian age (P4c-P5a) on the basis

of its co-existence with the planktonic foraminifera *Morozovella acuta, M. velascoensis* (see BouDagher-Fadel, 2013).

The Western Tethyan nummulitids have no apparent indigenous Tethyan ancestors, but from their morphological similarity we suggest that they were derived from American ancestors presumably by trans-Atlantic migration (a processes previously inferred (BouDagher-Fadel and Price 2010a; 2010b; 2013) also to have occurred at a later geological epoch to explain the global dispersal of two other LBF groups, the lepidocyclinids and the miogypsinids). The involute *Chordoperculinoides* remained very rare in the Tethyan province, and they have only been recorded from Oman (Haynes *et al.*, 2010), from Senegal (Blondeau, 1982) and Algeria (Amard and Blondeau, 1979) as '*Ranikothalia bermudezi*', and in Turkey (see Butterlin and Monod, 1969) as '*Ranikothalia savitriae*'. The new Tethyan forms, in contrast to the American forms which have coarse vertical canals, are characterised by fine perforations as seen in *Ranikothalia* (P4b). Both *Chordoperculinoides* and *Ranikothalia* disappeared from Western Tethys at the end of the Paleocene (early P5) (BouDagher-Fadel, 2008; Haynes *et al.*, 2010; Renema, 2002).

Apparently contemporaneous with their appearance in West Africa, nummulitoids are also found in the region of the modern day Mediterranean. In Europe and in the Mediterranean Tethys, the first unambiguous Nummulitidae are also from the Early Thanetian (P4b), e.g. *"Operculina" heberti* from the Pyrenees, which occurs along with *Palaeonummulites*, *Chordoperculinoides, Assilina* and the uniquely Tethyan form *Ranikothalia*, (see Fig. 3). The lineages evolved rapidly, but independently and in parallel to their American ancestors, suggesting that the migration of nummulitoids across the Atlantic was only possible for a limited period around the Thanetian, and that thereafter the American nummulitoids remained small, rare and isolated from those in the East for a geologically significant period, as the exclusively Tethyan large species of *Nummulites* and *Ranikothalia* never appeared in the Americas.

We here suggest that following the migration of *Operculina* into the Tethys during the Thanetian, there was an immediate radiation of forms with simple, numerous, equatorial (median) chambers and a moderate marginal cord, such as the quasi-evolute *Planocamerinoides*. The short-lived (Late Thanetian, P4c-P5a) sub-evolute genus *Nummulitoides* evolved from *Ranikothalia,* and was similar to, but significantly different from, the American *Caudrina*, as it had finely perforate walls (see Haynes *et al.*, 2010). *Nummulitoides* and *Ranikothalia* both disappear from the Tethyan record by the onset of the Eocene (see Fig. 3).

As would be expected, the Tethyan *Palaeonummulites* were similar in shape to the involute American *Palaeonummulites*, but it is our inference that they evolved independently of them. The most significant example of this independent evolution being the development of the uniquely Tethyan *Nummulites*. We suggested above that the West African "*Nummulites*" *ewekoroensis* Sachs and Adegoke, should be designated *Palaeonummulites ewekoroensis,* and so we infer that crucially, Tethyan *Palaeonummulites* gave rise in the Thanetian (P5a) to a form not found in the Americas, the unique, frequently large, involute

Nummulites. Nummulites itself developed many evolutionary lineages in the Paleogene of the Western Tethys (see Fig. 3, and Serra Kiel *et al.*, 1998), and it became the most common constituents of Late Paleocene-Early Eocene carbonate platforms, filling the empty niches left by the decline of the Cretaceous rudist-coral assemblages.

Despite the difference in evolutionary development that restricted the *Nummulites* to the Eastern hemisphere, the Tethyan *Palaeonummulites* like its American counterpart did give rise to a loosely coiled form, the Tethyan *Operculinella.* This form, however, did not develop in Tethys before the Bartonian (P12b), whereas the American forms had evolved by the End Ypresian (P9).

Although the Late Paleocene-Early Eocene witnessed the diversification of the nummulitoids in the Western Tethys, it was during the Eocene that they fulfilled their unique rock-forming potential. During that time, *Nummulites* and *Assilina* witnessed a major radiation and increase in test size, which persisted up to the major extinction of the last large species at the Middle-Late Eocene (End Bartonian) boundary (see Fig. 3). At approximately this boundary, a major faunal change occurred in the Western Tethyan nummulitoids; the large-sized *Nummulites* and *Assilina* disappeared and were replaced by *Spiroclypeus* and *Heterostegina* in the Late Eocene. These forms were joined by forms that survived the Middle Eocene boundary, such as *Pellatispira*, and some morphologically small reticulate and radial *Nummulites*, such as *N. striatus, N. fabianii* (see Romero *et al.*, 1999; Less *et al.*, 2008; Less and Özcan, 2012).

In the Chattian, nummulitoids with cyclic chambers developed to give rise to *Cycloclypeus.* In the Western Tethys, this form persisted until the end of the Early Miocene (Özcan and Less, 2009).

The Indo-Pacific province
In the Indo-Pacific, *Pararotalia* and *Chordoperculinoides* reach the province by the Thanetian (P4c), while *Ranikothalia, Planostegina, Nummulitoides* and *Operculina* made their first appearance in the Late Thanetian (P5a), about 2 million of years after they first appeared in Western Tethys (see BouDagher-Fadel, 2008; Renema, 2002). As in Western Tethys, *Ranikothalia* did not survive the Paleocene-Eocene boundary, however *Operculina* and *Planostegina* are still living today. The morphological similarity between Western Tethyan forms and Indo-Pacific forms suggests that they are in fact the same genera, and it is to be inferred that the forms seen in the Indo-Pacific migrated along the coastal regions from the Western Tethys a few millions years after their first appearance there. *Planocamerinoides* appeared in the Indo-Pacific in the Late Thanetian (P5a) (Haynes *et al.,* 2010), soon after its first appeared in the Western Tethys at the base of the Thanetian (P4b) (Renema, 2002), while in contrast *Assilina* did not appear in the Indo-Pacific before the Late Ypresian (P8), about 10 million years after their first appearance in Western Tethys (Boudagher-Fadel, 2008). *Palaeonummulites* made its first appearance in the earliest Ypresian (P5b), which locally defines the top of Ta1 Letter Stage (e.g. *P. thalicus,* see Haynes *et al.*, 2010).

The establishment of *Nummulites* in the Indo-Pacific occurred in the Ypresian (P7), compared with the Late Thanetian (P5a) in Western Tethys, which is locally placed within the lower part of Ta2 Letter Stage (e.g. *N. atacicus*, see Racey, 1995). In the Middle and Late Eocene, many of the long established species of *Nummulites* migrated from Western Tethys into the Indo-Pacific Pacific, where they again typically arrived a million years or so after their first appearance. *Nummulites beaumonti,* which first appeared in Western Tethys in the Middle Lutetian (P11), did not reach the Indo-Pacific before Late Lutetian (P12), whereas *Nummulites striatus* first occurred in the Middle Bartonian (latest P14-earliest P15) of the Western Tethys, did not reach the Indo-Pacific before the Priabonian (Tb Letter Stage) (see Fig. 4). Similarly, the reticulate nummulitids were abundant and widespread in the Priabonian of the Western Tethys (see Blondeau, 1972; Schaub, 1981), but did not arrive to the Indo-Pacific province before the end of the Eocene or the beginning of the Rupelian (*N. fichteli,* see Fig. 4). However, on arrival they became widely distributed in the islands of Java, Sumatra, Borneo, Sulawesi, Sumba and Irian Jaya (Renema, 2002), in Mindanao (Hashimoto and Matsumaru, 1984), in Mindoro and Luzon (Philippines; Cosico *et al.,* 1989) and in Papua New Guinea (Bain and Binnekamp, 1973).

As soon as forms of *Nummulites* were established in the Indo-Pacific, however, most species appear to have become isolated and evolved into local lineages. New endemic species evolved separately from, but in parallel with, those of the Western Tethys, with some of them appearing in geographically isolated areas. (e.g. *Nummulites djokdjokartae,* is only found in Indonesia and Western India). Many of them had features similar to those exhibited by Western Tethyan species, which caused initial misidentification in the literature, but they have subsequently been identified as distinct species. For example, *Nummulites boninensis* Hanzawa occurring in Indonesia was attributed to *N. gizehensis* (Forskål), but differs from *N. gizehensis* (Forskål) by its more regular coiling and thicker marginal cord (see Renema, 2002).

The last large *Nummulites* (*N. fichteli*) became extinct at the same time in both the Western Tethyan and the Indo-Pacific provinces in zone P21a.

Cycloclypeus appeared in the Indo-Pacific in the Early Oligocene (Late Rupelian, Td), and seems to have followed the same evolutionary patterns as related forms from the Western Tethys. However, while *Cycloclypeus* went extinct in the Early Miocene in the Mediterranean, it thrived in the Indo-Pacific and reached maximum sizes of up to 150mm in the Middle Miocene. By the Serravallian it had developed distinct inflations along the test, as in *Katacycloclypeus*. The division of the median chambers of *Cycloclypeus* and *Katacycloclypeus* has evolutionary parallels with the division of the lateral chamberlets of the LBF *Miogypsina* (see BouDagher-Fadel and Price, 2013), where the illuminated chambers are also inferred to have been nests for diatoms (see BouDagher-Fadel *et al.*, 2000). *Cycloclypeus* ranges from the Oligocene to Holocene, whereas *Katacycloclypeus* is confined to the Tf1–Tf2 stages, of the upper Early Miocene to Middle Miocene of the Indo-Pacific.

The SW African province

In the SW African province, which includes South Africa, Namibia and Angola, the Paleogene nummulitoids that have been found are similar to the Americas stock, and are distinct from those of the Tethys. No true *Nummulites* have been found in South Africa prior to the Early Oligocene (Rupelian), when very small numbers of *Nummulites* are found in material from the Kudu boreholes (see Fig. 5). The Paleogene offshore *Nummulites* and *Assilina* found in the Kudu boreholes are very small and quite unlike those of the tropical Tethys (McMillan *pers. comm.*). Chapman (1930) reported *Nummulites* spp. from the Birbury, just inland of the SE coast of South Africa, but these are very small and are likely to be ?*Lenticulina* spp. (e.g. Pl. 2, Figs a-b). From their occurrence with *Morozovella aequa,* a latest Middle Paleocene-Early Eocene age (Late Selandian, P4a, to Ypresian, P9) is indicated (see BouDagher-Fadel, 2013).

Although the Western Tethyan and SW African provinces may have been isolated one from another in Middle and Late Paleogene, we infer that there was a migration of Tethyan nummulitoids to SW Africa in the Miocene. This migration also brought with it miogypsinids, (see BouDagher-Fadel and Price, 2013), which first appeared in S Africa in the Burdigalian (N5b). This sudden migration towards SW Africa might be linked to the reported cooling of the Mediterranean (Karami *et al.*, 2011) as a result of the tectonic narrowing and eventual closing of the seaway between the Mediterranean and Indian Ocean (see Fig. 6).

In material studied here from Namibia, Angola and West Africa (see details below), we have identified the first occurrence of *Planostegina* spp. in the Burdigalian (N5b) of the SW African province (a form never found in assemblages from the Americas). However, the Tethyan genus, *Planostegina* occurs much later in SW Africa than its first appearance in Western Tethys or the Indo-Pacific provinces, where its first occurrence is in the Late Paleocene (P4b) of Somalia (Eames and Clarke, 1967).

After its arrival in the Burdigalian, it seems that the SW African *Planostegina* again became isolated from their Mediterranean ancestors, and evolved lineages that were independent from them. As described below, *Planostegina* spp. occurs at three different stratigraphic levels in the Burdigalian and Langhian section of offshore SW Africa. *Pl. africana, Pl. mcmillania, Pl. southernia* and *Pl. langhiana* are thin, compressed, and lenticular in shape, but their internal structures become increasingly complicated, with incomplete secondary septa branching separately from the primary septa. Their chambers increase in height (to become almost equidimentional (see Plate 2-4), as in primitive *Cycloclypeus),* or the last chambers becomes almost fully divided with septal partitions, as in primitive *Heterostegina* (see Pl. 2, Fig. p). We have not found in our samples tests with fully divided chambers, as in the cosmopolitan *Heterostegina*, but the latter is found living today with *Operculina* and *Planostegina* offshore SW Africa (Langer and Schmidt-Sinns, 2006).

THE PHYLOGENETIC RELATIONSHIPS OF THE NUMMULITOIDS

Until now, there has been no clear articulation of the evolutionary origins of the superfamily Nummulitoidea (see BouDagher-Fadel, 2008). However, the spatial and temporal palaeogeographic evolution of the nummulitoids described above enables us to link their phylogenetic evolution (described below), with known global plate tectonic, sea-level and climate changes (see Fig. 6). In previous studies (see BouDagher-Fadel and Price 2010a; 2010b; 2013), we have found that other families of LBF (the lepidocyclinids and miogypsinids) originated in the Americas only to migrate to the Tethyan, Indo-Pacific and SW Africa provinces. The trans-Atlantic migrations of the lepidocyclinids and miogypsinids were inferred to correlate with global sea-level falls, which in these cases occurred during the Middle Eocene and Early Oligocene respectively. We suggest that a similar conclusion can be drawn for the development of the Nummulitoidea.

In looking for the beginning of the nummulitoids as a superfamily, many researchers have focused upon seeking a parochial origin for the major Tethyan and Indo-Pacific genus *Nummulites*. Thus, Boukhary and Scheibner (2009) claimed that *Urnummulites* (based on *U. schaubi*), from the Late Paleocene of Egypt, was the ancestor of *Nummulites*. However, *Urnummulites* is trochospiral and has no marginal chord. It is similar to the rotaliid *Lockhartia,* and the degree of convexity and the shape of their pustules, which according to Boukhary and Scheibner (2009) separated the two genera, are specific characteristics and do not separate them at a generic level. We therefore suggest *Urnummulites* should be placed in the synonymy of *Lockhartia.*

From the material described in this study, however, we suggest (see Fig. 2) that the first nummulitoid may have evolved in the Americas from a pre-existing rotaliid form with a trochospiral test and intraseptal passages of a canal system, typified by a genus such as *Pararotalia* (Pl. 1, Fig. a). Analyses of molecular data from extant forms show a close relationship between the nummulitids and the rotaliids (Holzmann *et al.,* 2003). However, the proposed development of the nummulitids from a rotaliid, such as *Pararotalia,* would have been complicated and involved a series of coupled morphological changes. The trochospiral chambers of *Pararotalia* are arranged to expose the umbilical region that creates direct access to the ambient environment. The test possesses a spiral umbilical canal, formed by interconnected toothplates, with a free edge (Hottinger *et al.,* 1991). We suggest that the Nummulitinae may have evolved from a simple rotaliid test through forms that developed a moderately thick marginal cord and a rapidly widening coil leading to, in the Late Paleocene (P4a), the long-ranging completely planispiral evolute *Operculina* (see Fig. 2). The detailed description of these early gradational forms is still tentative, but the South Africa small forms, which resembles *Lenticulina* (*?Lenticulina* sp., Pl. 2, Figs a-b), may be the link, but not enough material is currently available to unambiguously prove this claim. We therefore suggest that the first true nummulitid to evolve in the Americas was *Chordoperculinoides* in Selandian (P3), and subsequently in the Thanetian (P4b) further development led to *Operculina, Assilina* and *Palaeonummulites.*

We have inferred that in the Thanetian (P4b) *Chordoperculinoides, Palaeonummulites, Assilina* and *Operculina* migrated eastward from the Americas and became cosmopolitan. Their arrival in Tethys in the Thanetian (P4b) was immediately followed by a radiation of forms with simple numerous equatorial (median) chambers, such as *Nummulites* (P4c) and *Planocamerinoides* in the latest Paleocene (P5a) (see Fig. 3). From our observations reported here, *Nummulites* subsequently migrated into the Indo-Pacific, much later than their first appearance in Western Tethys, in the Early Eocene (P7) (see Figs 3 and 4, and Matsumaru and Sarma, 2010). Quite separately, *Chordoperculinoides,* with coarse vertical canals in its marginal cord (Pl. 1, Figs a-c), gave rise to *Ranikothalia,* with a finely perforate marginal cord, in the Late Paleocene (P4b in Western Tethys, P5a in the Indo-Pacific).

We suggest that the trans-Atlantic migration of the nummulitoids in or around the Thanetian coincided with, and was enabled by the notable major sea-level regressions inferred to have occurred around 57Ma in the Late Paleocene (see Fig. 7). We suggest that for a short period, these major sea-level falls would have reduced the effective width of the early Atlantic ocean sufficiently to facilitate the trans-oceanic migration (probably during their embryonic stage) of the first nummulitoids from the American province to the closest coastline of West Africa, from where they were able to spread both to the north and to the south (see Fig. 8). By the end of the Late Paleocene, several genera that had originated in the Americas had reached the Western Tethys, but already by this stage several Tethyan forms were developing and becoming distinct from their American counterparts. For examples, Western Tethyan species of *Chordoperculinoides* had a thinner marginal cord and a more rapid rate of coil opening, which resulted in them having higher chambers in both the microspheric and megalospheric generations than their American counterparts.

As the morphologies of American and Western Tethyan nummulitoids are seen to be crucially different, it follows that their evolutionary development was independent (albeit closely parallel), and so it is to be inferred that after the initial trans-Atlantic migration of the American stock had occurred, the province again became isolated as sea-levels rose to a record high stand around 53Ma (see Fig. 7). This isolation was maintained until the sea-levels again fell globally in the Middle Eocene, at which stage new LBF stock from the Americas reached the Africa and eventually the Western Tethys and the Indo-Pacific. During this time of isolation, the American nummulitoids remained small in size, and they never developed the gigantisms seen in two of the eastern provinces. Indeed in the Americas, nummulitoids remained relatively rare in the Eocene and Oligocene, with no new genera appearing after the Middle Eocene. Instead of being dominated by nummulitoids, the shallow foraminifera assemblages in the Americas were in fact dominated by other, larger, apparently more robust and more successful LBF forms such as *Eulepidina, Lepidocyclina* and *Miogypsina*, which only evolved in the Americas in Early Eocene (see BouDagher-Fadel *et al.*, 2010) after the inferred re-isolation of this province. On the other hand, the absence of the lepidocyclinids from the Early Eocene in Western Tethys provided an opportunity for the nummulitoids to thrive with minimal completion and to fill the reef-forming niche left vacant after the End Maastrichtian global crisis.

At the end of the Paleocene, the Earth's climate went through the warmest period of the entire Cenozoic (see Fig. 7), the Paleocene-Eocene Thermal Maximum (PETM). From Early to Middle Eocene, the average global sea-water temperatures rose by 6°C (Macleod, 2013). Western Tethyan species of the *Nummulites* increased rapidly in size, reaching a few centimetres by Middle Eocene, and evolved into many new phylogenetic lineages completely different in size and shape from their American ancestors. Successive forms of nummulitoids continued their migration eastward through the open seaway from the Western Tethys into the Indo-Pacific, where they typically arrived a million years or so after their first Tethyan appearance (see Fig. 4 for examples). Once in the tropical setting of the Indo-Pacific, with its diverse palaeogeography, the migrants gave rise to similar, but local species, which evolved into isolated lineages parallel to yet distinct from those seen in Western Tethys.

Global temperatures fell dramatically at the Eocene-Oligocene boundary (see Fig. 7). During this time the Tethyan seaway narrowed (Macleod, 2013) as sea-level dropped, and the Western Tethys was partitioned into the Mediterranean and the Paratethys by the rise of the Alps (Rögl, 1999; Piller and Harzhauser, 2005). These changes correlate with, and probably drove the significant End Eocene extinction of nummulitids in the Western Tethyan province, where a third of nummulitid species went extinct while only 9% disappeared from the Indo-Pacific (see BouDagher-Fadel, 2008). Finally, however, as global temperatures remained low and other environmental stresses developed (such as the eruption of the extensive Ethiopian flood basalts, Fig. 6), the *Nummulites* that had continued into the Oligocene, eventually went extinct globally towards the end of the Early Oligocene (around 31–29 Ma).

The extinction of the *Nummulites* from Western Tethys and the Indo-Pacific at the end of the Chattian provided the opportunity for the recently arrived lepidocyclinids and miogypsinids to occupy the newly empty niches. They replaced the nummulitids as major reef-forming forms and evolved along many parallel lineages (see BouDagher-Fadel and Price, 2010a; 2010b). They also (like the nummulitoids before them) continued their migration eastward through the open seaway from the Mediterranean into the Indo-Pacific, where they also typically arrived a million years or so after their first Mediterranean appearance.

We suggest that the continued global cooling and the tectonically driven closure of the seaway between the Mediterranean and the Indo-Pacific in the Early Miocene (Burdigalian) triggered the subsequent extinction of many Mediterranean LBF. Many lepidocyclinids (e.g. *Eulepidina* spp.) and miogypsinids were wiped out from the Mediterranean at the top of the Burdigalian (N6). We further suggest that the remaining nummulitoids were also casualties of this closure, as *Cycloclypeus* and *Spiroclypeus* disappeared completely from the Mediterranean in the Early Miocene (N5 and N6 respectively). On the other hand, *Cycloclypeus* continues to thrive up to the present day in the deep photic zone of the Indo-Pacific.

The development of the nummulitoids and the LBF assemblages in the SW African province was, however, quite different from that of Western Tethys and the Indo-Pacific.

Following the first wave of trans-Atlantic Paleocene (P4b) migration, the SW African nummulitoids remained very small and never evolved the large sizes and diversity of the Tethyan *Nummulites.* This comparatively slow rate of evolution might reflect the lack of environmental diversity and the relatively temperate conditions in which the SW African nummulitoids found themselves. The rising sea-level and the continuing oceanic rifting finally isolated the American from the SW African province (around the End Rupelian). In the Early Miocene (Burdigalian), forms of the nummulitoid *Planostegina,* similar to those of the Mediterranean and Indo-Pacific provinces, appeared in SW Africa. The presence of *Planostegina* in the Miocene of SW Africa differentiates the assemblages of this province from those of the Americas, where *Planostegina* is never found.

CONCLUSION

Analysis of new material, combined with a synthesis of the published literature, has allowed the understanding of the palaeobiogeographic development and evolution of the nummulitoids of the four LBF provinces of the Americas, the Western Tethys, the Indo-Pacific and SW Africa to be defined.

We conclude that, like previously studied LBF forms such as the lepidocyclinids and the miogypsinids, the nummulitoids evolved first in the Americas and then migrated eastward to Western Tethys (and then eventually on to the Indo-Pacific) and to SW Africa. As species became geographically isolated, they evolved parallel and distinct lineages. Eocene to Oligocene nummulitoids of Southern Africa evolved directly from American ancestors and were distinct from the Tethyan and Indo-Pacific forms, but a wave of nummulitoid migration occurred in the Miocene from the Mediterranean into the SW African province.

The new understanding of the phylogenetic evolution of the Western Tethys, Indo-Pacific and SW African nummulitoids presented in this paper, when combined with the improved understanding of their biostratigraphic ranges and facies relationships presented here, provides the first global-scale understanding of their development and so enhances their usefulness as a tool for the study of Cenozoic warm-water carbonate platforms, which are so important in today's hydrocarbon exploration.

APPENDIX: COMMENTS ON NEW TAXA

As in BouDagher-Fadel and Price (2013), we follow Lee's (1990) elevation of the Order Foraminiferida to Class Foraminifera, and the concomitant elevation of the previously recognized suborders to ordinal level. Throughout, 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).

All materials relating to the new species described below are deposited in the UCL Geology Collection (http://www.ucl.ac.uk/museums/geology).

Below we describe new material from SW Africa (from locations shown in Fig. 5). All the newly discovered *Planostegina* species of South West Africa have smooth, very compressed and fragile tests (as seen in Plate 4). We were only able to separate them on a specific levels by studying them in thin section. In order to characterise the new material, we have used a morphometric description. The qualitative feature is the presence/absence of granulation on the test's surface. The smooth tests and the absence of granulation on all tests distinguish the SW African species from most of the Tethyan species. The second qualitative feature is the shape of the chambers, which are mainly narrow and strongly or slightly curved, the arrangement (irregular or regular) of the septula, which divide the complete or incomplete sub-rectangular chamberlets. All the other characteristics are described quantitatively based on the morphometric system introduced by Drooger and Roelofsen (1982) (see Fig. 9):

P: The largest diameter of the proloculus in μm, excluding the thickness of the wall.

D: The largest diameter of the deuterconch in μm, excluding the thickness of the wall.

X: The number of undivided, operculinid chambers before the appearance of the first partly divided, planosteginid chamber, excluding the embryon (the first two chambers, protoconch and deuteroconch). This parameter indicates the degree of operculinid reduction. (see for example Fig. 9, in which X = 8).

l: the maximum diameter of the first whorl as measured in μm, along the common symmetry axis of the embryon (including the protoconch and deuteroconch).

L: the maximum diameter of the first whorl and the subsequent half whorl, measured in μm, along the common symmetry axis of the embryon (including the protoconch and deuteroconch).

K: the index of spiral opening, where $K = 100 \times (L-l)/(L-P)$.

The taxonomic descriptions of the new species described here are as follows:

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. They have apertures that are simple or have an internal toothplate. They range from Triassic to Holocene.

Superfamily NUMMULITOIDEA de Blainville, 1827
Tests are planispiral or cyclic, lenticular multicamerate, with septal flaps and canaliculated septa. A spiral marginal cord and a spiral canal system are present in early forms, but this is modified in advanced forms or replaced by intraseptal canals. Paleocene to Holocene.

Family NUMMULITIDAE de Blainville, 1827
Tests are planispiral involute or evolute with septal, marginal and vertical canals. Paleocene to Holocene.

Subfamily HETEROSTEGININAE Galloway, 1933
Tests are planispiral, with a canaliculate marginal cord, and septal canal trabeculae, but they have true secondary septa, developed right across the chamber, forming chamberlets. Paleocene to Holocene.

Genus *Planostegina* Banner and Hodgkinson, 1991

Type species: *Heterostegina costata* d'Orbigny
A totally evolute form, with chambers divided by septula into complete or incomplete subrectangular chamberlets, connected by Y-shaped intercameral stolons. The test is smooth or has strong ornamentation and undivided sutural canals. Forms have fine to moderately thick marginal cords, with fine vertical canals. Eocene to Holocene.

Planostegina africana BouDagher-Fadel and Price, **new species.**
Plate 2, Figs c-l, Plate 4, Figs j-k.

Name derivation: This species is named *africana* to illustrate its type locality.
Type locality: Namibia, Kudu borehole, line -940, sample 80-01, 940/8000, 6.6-6.7m (see Fig.5c).
Holotype: UCL MF283, Plate 2, Fig. c.
Paratypes: UCL MF284-92, Plate 2, Figs d-l.
Dimensions: Maximum measured longest diameter (MMLD) 5mm.

Description: Tests are flat, compressed and smooth. The proloculus is large (85 to 86μm in the megalospheric forms) and circular, making up about 67% of the embryonic apparatus and is followed by a reniform deuteroconch. Chambers are numerous, long and narrow, increasing slowly in size, and occur in up to three whorls. The index of spiral opening in the megalospheric (K=29) (see Fig. 9) is almost half of that of the micropsheric forms (K=46), where the last whorl becomes rectilinear (see Plate 2, Figs f-h). The total number of spirally coiled operculine stage chambers is 7 to 8, separated by slightly curved thin septa. The rest of the chambers have, in the early part, incomplete divisions, while in the later part the septa are complete, dividing the chambers in an irregular way (see Plate 2, Figs j-k). Most chambers are rectangular in shape, whereas others are irregular hexagonal.

Remarks: The irregular nature of the divisions of the chambers near the periphery distinguishes this species from other species of *Planostegina*. The irregular shape of the chamberlets, the irregular shape of the complete septa separate this species from *P. mcmilliana, P. southernia* and *P. langhiana. Planostegina africana* is abundant in it type locality (see Fig Plate 4, Figs j-k). The tests are fragile and mainly broken and shell material is common. The presence of *Catapsydrax dissimilis, Globigerina praebulloides* and *Globoquadrina dehiscens* indicate an Early Burdigalian age (see BouDagher-Fadel, 2013).

Distribution: This species occurs in the Early Burdigalian (N5b-N6), in Kudu boreholes offshore Namibia, near Dombe Grande (Benguela Basin) in Angola and Childs Bank Hole X-

A1, offshore South Africa. Assemblages contain abundant *Planostegina* and rare planktonic and small benthic foraminifera (e.g. *Eponides*, ?*Lenticulina* spp.).

Planostegina mcmillania BouDagher-Fadel and Price, **new species.**
Plate 2, Figs m-af, Plate 4, Fig. l.

Name derivation: This species is named in honour of Professor Ian McMillan.
Type locality: Namibia, Kudu borehole, 1130/14500, at sample 1, base of core DN 1624 (see Fig. 5c).
Holotype: UCL MF294, Plate 2, Fig. n.
Paratypes: UCL MF293, MF295-310, Plate 2, Figs m-w.
Dimensions: MMLD 4.5mm.

Description: Tests are flat, lenticuline in shape, compressed and smooth with two slightly raised knobs on both sides. The proloculus is large (approximately 117μm) and circular, followed by a semi-circular, slightly larger deuteroconch, which makes up 60% of the embryonic apparatus. Chambers are long and narrow, increasing slowly in size with up to three whorls. The index of spiral opening in the megalospheric form (K=60) is larger than that of the microspheric forms (K=56), where the last whorl may become rectilinear (see Pl. 2, Fig. ad) or extend backwards so that it makes up more than half of the equatorial test, making the tests of some microspheric forms almost circular (see Pl. 2, Fig. p). The total number of operculine stage chambers is 4 to 5, which are separated by strongly curved thick septa. The latter are just curved near the periphery in the planostegine stage. The subdivisions in the planostegine stage are partially developed, short in length and sporadic throughout the last two whorls, except near the end of growth, where some complete partitions might be present forming irregular small rectangular chamberlets.

Remarks: The thickness of the embryonic wall and the shape of the chambers distinguish this species from *Planostegina africana, P. southernia* and *P. langhiana.* The large embryon and the lack of a costate periphery and granular surfaces differentiate this form from those already described from the Miocene of Tethys, such as *Pl. costata* and *Pl. granulatatesta.*

Distribution: This species occurs in the Late Burdigalian (N7-8a), in Kudu boreholes from offshore Namibia, near Dombe Grande (Benguela Basin) in Angola, and the Childs Bank Hole X-A1, offshore South Africa. It is also present offshore of Orange Banks 1929, sample 1 DN 350/19300, Depth below sea-floor 3.88m, present day water depth +/- 200m, approximately 29^0 south, 14^0 30^0 east.

Planostegina southernia BouDagher-Fadel and Price, **new species.**
Plate 3, Figs a-t, Plate 4, Figs m-n.

Name derivation: This species is named *southernia* to illustrate its type locality.
Type locality: Namibia, Kudu borehole, 1130/14500, at sample 1, base of core DN 1624 (see Fig. 5c).

Holotype: UCL MF310, Plate 2, Fig. a.
Paratypes: UCL MF311-24, Plate 3, Figs b-n.
Dimensions: MMLD up to 7mm.

*Description***:** Tests are flat, lenticuline in shape, compressed and smooth with surface ornamentation in the form of granules in their early part. The proloculus is circular and large (210μm), followed by a semi-circular, reniform deuteroconch that is almost twice as wide. The embryonic apparatus makes up 16 % of the megalospheric test and is surrounded by a thick wall (53μm). Chambers are long, narrow and numerous, increasing very slowly in size so that they are all almost equidimensional. The rate of spire opening is K=40 to 49 in the megalospheric form, where the test is formed by two to three whorls, while K=55 in the microspheric forms, where the test is formed by three to four whorls in total, with the last one extending more than three quarters of the equatorial test. The early operculine stage is made of 4 chambers that are separated by septa which are strongly curved near the periphery. The early chambers in the planostegine stage are divided by incomplete regular septula, while the later chambers are divided into almost regular rectangular chamberlets by complete septula.

*Remarks***:** The shape of the embryonic apparatus and the irregular division of the chamberlets distinguish this species from other species of *Planostegina.*

*Distribution***:** This species occurs in the Late Burdigalian to Langhian (N7-N11), in Kudu boreholes offshore Namibia, near Dombe Grande (Benguela Basin) in, Angola and in the Childs Bank Hole X-A1, offshore South Africa. It is also found in the Burdigalian of South Africa, off St. Helena Bay, OMO-4 Megadrill sample ± 4m below sea-floor, 32° 27' 45.79'' South 17° 49' 38.985'' East and in Site DN 4557 to the west of Robben Island (see Fig 5)**.**

Planostegina langhiana BouDagher-Fadel and Price, **new species.**
Plate 3, Figs u-aa, Plate 4, Fig. o

Name: This species is named *langhiana* to illustrate its biostratigraphic age.
Type locality: Offshore margin of Orange Banks (off mouth of Orange River, southernmost Namibia), offshore sample 1, Vibrocore DN 350/19300, Depth below sea-floor 3.88m, present day water depth ±200m, approximately 29° South, 14° 30$^'$ East.
Holotype: UCL MF332, Plate 3, Fig. v.
Paratypes: UCL MF331, MF333-337, Plate 3, Figs u, w-aa.
Dimensions: MMLD up to 12mm.

Description: Tests are flat, lenticuline in shape, compressed and smooth. The proloculus is circular, followed by a semi-circular, smaller reniform deuteroconch, which makes up 40% of the embryonic apparatus. Chambers are very high, narrow and numerous, increasing very slowly in width, but rapidly in height in the microspheric forms, occurring in up to three whorls. The operculine stage includes 3 chambers in the megalospheric forms, but there are 8 operculine chambers in the microspheric forms. Chambers are separated by septa that are strongly curved near the periphery. The septa of the planostegine part of the test are curved

only near the periphery, and the chambers are divided regularly by incomplete septula that vary in length but are longer near the periphery. In megalospheric forms irregular complete, septula form rectangular chamberlets in the later parts of the chambers.

Remarks: The shape of the embryonic apparatus and the irregular shape of the septula distinguish this species from other species of *Planostegina*. The lack of granulations and irregular shape of the chamberlets separate *Pl. langhiana* from those already described from the Langhian of Tethys, such as *Pl. costata* and *Pl. granulatatesta*.

Distribution: This species occur in the Langhian (N8b-N11), from Namibia and South Africa offshore of Orange Banks, together with rare planktonic foraminifera such as, *Orbulina universa, O. bilobata, Globoquadrina dehiscens, Globorotalia miozea, Globigerina praebulloides.*

ACKNOWLEDGEMENTS

REFERENCES

ADAMS, C.G. 1988. Septa, septal traces and septal filaments in the foraminiferal genus *Nummulites* Lamarck. *Journal of Micropalaeontology*, 7: 89-102.

AMARD, B., and BLONDEAU, A. 1979. Le Paléocène supérieur à *Ranikothalia bermudezi* et l'Éocène inférieur (Ilerdien basal) à *Nummulites fraasi* et *N. deserti* du Tademait-E. et Tinhert-W. *Geobios*, 12: 635–651.

ARNI, P. 1965. Contribution à la systematique des *Nummulites* s.l. *Mémoires du Bureau de recherches géologiques et minières*, 32: 21–28.

BAIN, J.H.C., and BINNEKAMP, J.G. 1973. The foraminifera and Stratigraphy of the Chimbu Limestone, New Guinea. *Bureau of Mineral Resources and Mines Geological Papers Bulletin,* 139: 1-12.

BANNER, F.T., and HODGKINSON, R.L. 1991. A revision of the foraminiferal subfamily Heterostegininae. *Revista Española de Micropaleontologia,* 23: 101–140.

BARNETT, R. S. 1974. An application of numerical taxonomy to the Classification of the Nummulitidae (Foraminiferida). *Journal of Paleontology*, 6: 1249-1263

BARTHOLDY, J. 2002. *The Architecture of Nummulites (Foraminifera) reexamined.* PhD thesis, Freie Universität Berlin, 64: 1–22.

BEAVINGTON-PENNEY, S.J., and RACEY, A. 2004. Ecology of extant nummulitids and other large benthic foraminifera, applications in palaeoenvironmental analysis. *Earth-Science Reviews*, 67: 219–265.

BERGGREN, W.A. 1973. The Pliocene time scale: calibration of planktonic foraminiferal and calcareous nannoplankton zones. *Nature*, 243: 391–397.

BLONDEAU, A. 1972. *Les Nummulites*. Vuibert, Paris. 255 pp.

BLONDEAU, A. 1982. Les nummulites de l'Afrique. *Mémoire, Quatrième colloque Africain de Micropaléontologie:* 56–57.

BLOW, W.H. 1979. *The Cainozoic Globigerinida: A Study of the Morphology, Taxonomy, Evolutionary Relationships and the Stratigraphical Distribution of Some Globigerinida,* 3. Brill, Leiden.

BOLIVAR, M.A. 1998. *Larger foraminifera and microfacies of the Eocene Masparrito Member, Barinas Sub-Basin, Western Venezuela*, MSc thesis, University College London: 70pp.

BOUDAGHER-FADEL, M.K. 2002. The stratigraphical relationship between planktonic and larger benthic foraminifera in Middle Miocene to Lower Pliocene carbonate facies of Sulawesi, Indonesia. *Micropaleontology* 48: 153–176.

BOUDAGHER-FADEL, M.K. 2008. *Evolution and Geological Significance of Larger Benthic Foraminifera*. Developments in Palaeontology and Stratigraphy, 21, Elsevier : 540pp.

BOUDAGHER-FADEL, M.K. 2013. *Biostratigraphic and Geological Significance of Planktonic Foraminifera,* 2nd edition. OVPR UCL, London, http://dx.doi.org/10.14324/99.1 : 307pp. .

BOUDAGHER-FADEL, M.K. and BANNER, F.T. 1999. Revision of the stratigraphic significance of the Oligocene–Miocene 'letter-Stages'. *Revue de Micropaléontologie*, 42: 93–97.

BOUDAGHER-FADEL, M.K. and LOKIER, S. 2005. Significant Miocene larger foraminifera from south central Java. *Revue de Micropaléontologie,* 24: 291–309.

BOUDAGHER-FADEL, M.K., NOAD, J.J. and LORD, A.R. 2000. Larger Foraminifera from Late Oligocene–Earliest Miocene reefal limestones of North East Borneo. *Revista Española de Micropaleontología,* 32: 341–362.

BOUDAGHER-FADEL, M.K. and PRICE, G.D. 2010a. American Miogypsinidae: an analysis of their phylogeny and biostratigraphy. *Micropaleontology*, 56: 567–586.

BOUDAGHER-FADEL, M.K. and PRICE, G.D. 2010b. Evolution and paleogeographic distribution of the lepidocyclinids. *J Foramin Res*, 40: 79-108.

BOUDAGHER-FADEL, M.K, PRICE, G.D. and KOUTSOUKOS, E.A.M. 2010. Foraminiferal biostratigraphy and paleoenvironments of the Oligocene–Miocene carbonate succession in Campos Basin, Southeastern Brazil. *Stratigraphy*, 7: 283–299.

BOUKHARY, M. and SCHEIBNER, C. 2009. On the origin of Nummulites: *Urnummulites schaubi* n.gen. n. sp., from the late Paleocene of Egypt. *Micropaleontology*, 55: 413–420.

BOUSSAC, J. 1906. Sur la formation du réseau des *Nummulites* réticulées. *Bulletin de la Sociéte´ géologique de France (série 4)*, 6: 98–100.

BUTTERLIN, J. 1987, Origine et évolution des Lépidocyclines de la région des Caraibes. comparisons et relations avec les Lepidocyclines des autres régions du monde: *Revue de Micropaléontologie*, 29: 203–219.

BUTTERLIN, J. and MONOD, O. 1969. Biostratigraphie (Paléocène d'Éocène moyen) d'une coupe dans le Tamus de Beysehir (Turquie). Étude des '*Nummulites* cordelées' et révision de ce groupe. *Eclogae Geologicae Helvetiae*, 62: 583–604.

CAHUZAC, B., POIGNANT, A., 1991. Morphologie des espèces de *Pararotalia* et de *Miogypsinoides* (Foraminiferida) dans l'Oligocène d'Aquitaine méridionale. *Geobios*, Mem. Sp. 13: 69–78.

CARPENTER, W.B. 1850. On the microscopic structure of Nummulina, Orbitolites and Orbitoides. *The Quarterly journal of the Geological Society of London*, 6: 181–236.

CHAPMAN, F. 1930. On a foraminiferal limestone of Upper Eocene age from the Alexandria formation, South Africa. *Annals of the South African Museum* 28|: 291-296.

COLE, C.W. 1952 Eocene and Oligocene larger foraminifera from the Panama Canal Zone and vicinity. *USGS Professional Paper*, 244: 41pp.

COLE, W.S. 1964. Orbitoididae; Discocyclinidae; Lepidocyclinidae. In: Loeblich, A.R., Jr. and Tappan, H. (Eds), *Sarcodina, Chiefly ''Thecamoebians'' and Foraminiferida, Treatise on Invertebrate Paleontology* (R.C. Moore, Ed.), Geological Society of America and University of Kansas Press, Part: C. Protista 2: C710–C724.

COSICO, R., GRAMANN, F. and PORTH, H. 1989. Larger Foraminifera from the Visayan Basin and adjacent areas of the Philippines (Eocene through Miocene). *Geologisches Jahrbuch,* B70: 147-205.

COURTILLOT, V.E., and RENNE, P.R., 2003. On the ages of flood basalt events. *Comptes Rendus Geoscience*, 335: 113–140.

COWEN, R. 1983. Algal symbiosis and its recognition in the fossil record. In: Teveszm, J.S. and McCallp, L. (Eds), *Biotic Interactions in Recent and Fossil Benthic Communities.* Plenum Press, New York: 431–478.

CRAMER, B.S., and KENT, D.V., 2005. Bolide summer: The Paleocene/Eocene thermal maximum as a response to an extraterrestrial trigger. *Palaeogeography, Palaeoclimatology, Palaeoecology.* 224, 144–166.

D'ARCHIAC, A. 1850. Histoire des progrés de la Géologie de 1834 à 1849. *Formation nummulitique de l'Éspagne* 3: 304.

DAVIES, A. M. 1935. *Tertiary faunas: A textbook for oilfield paleontologists and students of geology. The composition of Tertiary faunas.* Allen and Unwin, London, Vol. 1: 1406p.

DE LA HARPE, P. 1877. Notes sur les *Nummulites* des Alpes occidentales. *Actes de la Société Helvétique des Sciences Naturelles,* 60: 227-323.

DOORNINK, H.W. 1932. Tertiary Nummulitidae from Java. *Verhandelingen van het Geologisch en Mijnbouwkundig Genootschap voor Nederland en Koloniën,* 9: 267-315.

EAMES, F.E., BANNER, F.T., BLOW, W.H., and CLARKE, W.J., 1962. *Fundamentals of Mid-Tertiary Stratigraphical Correlation.* Cambridge University Press, Cambridge: 163p.

EAMES F.E. and CLARKE, W.J. 1967. A Palaeocene *Heterostegina. Palaeontology,* 10: 314 – 316.

FERRÀNDEZ-CAÑADELL, C., 2012. Multispiral growth in Nummulites Paleobiological implications. *Marine Micropaleontology,* 96–97: 105–122.

GALLOWAY, J.J. 1933. *A Manual of the Foraminifera.* James Furman Kemp Memorial ser. publ. 1, Principia. Press, Bloomington, Indiana: 183pp.

GATTUSO, J.-P. and BUDDEMEIER, R.W., 2000. Calcifcation and CO2. *Nature* 407: 311–312.

GLAESSNER, M.F. 1945. *Principles of Micropaleontology.* Melbourne University Press: 296p.

GRADSTEIN, F.M., OGG, J.G., SCHMITZ, M.D. and OGG, G.M. 2012 *The Geologic Time Scale 2012*, Elsevier, 2 volumes: 1144 pp.

HASHIMOTO, W. and MATSUMARU, K. 1984. Mesozoic and Cenozoic Larger Foraminifera of the Philippines and a references to those found from Borneo by the APRSA's palaeontological reconnaissance. *Geology and Palaeontology of Southeast Asia,* 25: 147-166.

HAYNES J. R., RACEY A. and. WHITTAKER, J. E. 2010. A revision of the Early Palaeogene nummulitids (Foraminifera) from northern Oman, with implications for their classification. *In* Whittaker, J. E. and Hart, M. B. (eds) *Micropalaeontology*, Sedimentary Environments and Stratigraphy: A Tribute to Dennis Curry (1912–2001). The Micropalaeontological Society, London, Special Publications, 29–89.

HAYNES, J.R. 1981. *Foraminifera.* MacMillan, London: 433p.

HOHENEGGER, J. 2011. Growth-invariant Meristic Characters Tools to Reveal Phylogenetic Relationships in Nummulitidae (Foraminifera). *Turkish Journal of Earth Sciences,* 20: 655–681.

HOLZMANN, M., HOHENEGGER and J., PAWLOWSKI, J. 2003. Molecular data reveal parallel evolution in nummulitid foraminifera. *Journal of Foraminiferal Research*, 33: 277–284.

HOTTINGER, L. 1977. Foraminifères operculiniformes. *Mémoires du Muséum National d'Histoire Naturelle,*Paris, C 40: 1–159.

HOTTINGER, L. 1978. Comparative anatomy of elementary shell structures in selected larger Foraminifera. In: Hedley, R.H., Adams, C.G. (Eds), *Foraminifera* 3. Academic Press, London, 203–266.

HOTTINGER L. 2001. Shell Cavity Systems in Elphidiid and Pellatispirine bilamellar Foraminifera. Editor's preface. *Micropaleontology,* 47, suppl.2: 1-4.

HOTTINGER, L. 2009. The Paleocene and earliest Eocene foraminiferal Family Miscellaneidae: neither nummulitids nor rotaliids. *Carnets de Géologie/Notebooks on Geology*, Brest, Article 2009/06 (CG2009_A06).

HOTTINGER, L. and DREHER, D. 1974. Differentiation of Protoplasm in Nummulitidae (Foraminifera) from Elat, Red Sea. *Marine Biology*, 25: 41–61.

HOTTINGER, L., HALICZ, E. and REISS, Z. 1991. The foraminiferal genera *Pararotalia*, Neorotalia, and Calcarina, taxonomic revision. *Journal of Paleontology*, 65: 18–33.

HOTTINGER, L. and LEUTENEGGER, S. 1980. The structure of calcarinid foraminifers. *Schweizerische Palaeontologische Abhandlungen,* Basel, 101: 115–154.

HOTTINGER, L., REISS, Z. and LANGER, M. 2001. Spiral canals of some Elphididae. *Micropaleontology,* 47, supplement 2: 5-34.

JORRY, S., HASLER, C.-A. and DAVAUD, E. 2006. Hydrodynamic behaviour of Nummulites, implications for depositional models. *Facies,* 52: 221–235.

KARAMI, M.P., LEEUW, A., DE, KRIJGSMAN, W., MEIJER, P., TH. and WORTEL M.J.R. 2011. The role of gateways in the evolution of temperature and salinity of semi-enclosed basins: An oceanic box model for the Miocene Mediterranean Sea and Paratethys. *Global and Planetary Change*, 79: 73–88.

KRIJNEN, W.F. 1931. *Het genus Spiroclypeus in het Indo-Pacifische gebied. Verhandelingen van het Geologisch Mijnbouwkundig Genootschap voor Nederland, Kolonien Geologische Serie*, IX: 77-112.

LANGER, M.R. and HOTTINGER, L., 2000. Biogeography of selected "larger" foraminifera. *Micropaleontology,* 46 (supplement 1*)*: 105-127.

LANGER, M.R. and SCHMIDT-SINNS, J. 2006. Biogeography of modern benthic foraminifera from South Africa, Namibia and Mozambique Anuário do Instituto de Geociências – UFRJ ISSN 0101-9759, 29: 686-687.

LEE, J.J. 1990. Phylum granuloreticulosa (Foraminifera). *In*: MARGULIS, L., CORLISS, J.O., MELKONIAN, M. and CHAPMAN, D.J. (eds) *Handbook of Protoctista: The Structure, Cultivation, Habitats and Life Histories of the Eukaryotic Microorganisms and Their Descendants Exclusive of Animals, Plants and Fungi*. Jones and Bartlett, Boston, MA: 524–548.

LESS, G. and ÖZCAN, E. 2008. The late Eocene evolution of nummulitid foraminifer *Spiroclypeus* in the Western Tethys. *Acta Palaeontologica Polonica,* 53: 303–316.

LESS, G. and ÖZCAN, E. 2012. Bartonian-Priabonian larger benthic foraminiferal events in the Western Tethys. *Austrian Journal of Earth Sciences*, 105: 129-140.

LESS, G., ÖZCAN, E., PAPAZZONI, C.A. and STÖCKAR, R. 2008. The middle to late Eocene evolution of nummulitid foraminifer *Heterostegina* in the Western Tethys. *Acta Palaeontologica Polonica,* 53: 317–350.

LEUTENEGGER, S. 1977. Ultrastructure de Foraminifères pérforés et imperforés ainsi que de leurs symbiotes. *Cahier de Micropaléontologie*, 3: 1–52.

LOEBLICH, A.R., JR. and TAPPAN, H. 1987. *Foraminiferal Genera and their Classification*. Van Nostrand Reinhold, New York: 2047pp.

LOEBLICH, A.R., JR., and TAPPAN, H. 1964. Protista 2, Sarcodina, chiefly ''Thecamoebians'' and Foraminiferida. *In*: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology*, University of Kansas Press, Kansas, Part C, Vols. 1 and 2.

MACGILLAVRY, H.J. 1978. Foraminifera and parallel evolution-How or why? *Geologieen Mijnbouw*, 57: 385–394.

MACLEOD, N. 2013 *The Great Extinctions: What Causes Them and How They Shape Life*. Natural History Museum, London: 208p.

MATSUMARU, K. 1996. Tertiary Larger Foraminifera (Foraminiferida) from the Ogasawara Islands, Japan. *Palaeontological Society of Japan,* Special Papers 36: 1–239.

MATSUMARU, K. and SARMA, A. 2010 Larger foraminiferal biostratigraphy of the lower Tertiary of Jaintia Hills, Meghalaya, NE India. *Micropaleontology,* 56: 539-565.

MELLO E SOUSA, S. H., FAIRCHILD, T. R., and TIBANA, P., 2003. Cenozoic biostratigraphy of larger foraminifera from the Foz Do Amazonas basin, Brazil: *Micropaleontology*, 49: 253–266.

MILLER, K.G., MOUNTAIN, G.S., WRIGHT, J.D. and BROWNING, J.V. 2011. A 180-million-year record of sea-level and ice volume variations from continental margin and deep-sea isotopic records. *Oceanography*: 24, 40–53.

MURRAY, J.W. 2006. *Ecology and Applications of Benthic Foraminifera*. Cambridge University Press, Cambridge: 426p.

NAGAPPA, Y. 1959. Foraminiferal biostratigraphy of the Cretaceous-Eocene succession in the India-Pakistan- Burma region. *Micropaleontology,* 5: 145-192.

NEMKOV, G.I. 1962. Remarques sur la paléoécologie des *Nummulites*. *Voprosy Mikropaleontologii*, 6: 64–72.

ÖZCAN, E. and LESS, G.Y. 2009. First record of the co-occurrence of Western Tethyan and Indo-Pacific larger Foraminifera in the Burdigalian of the Mediterranean province. *Journal of Foraminiferal Research*, 39: 23-39.

PIGNATTI, J.S. 1998. The philosophy of larger foraminiferal biozonation – a discussion. *In*: Hottinger, L., Drobne, K. (Eds), *Paleogene Shallow Benthos of the Tethys*, Slovenian Academy of Sciences and Arts, Ljubljana, 2: 15–20.

PILLER, W.E. and HARZHAUSER, M. 2005. The myth of the brackish Sarmatian Sea. *Terra Nova*, 17: 450-455.

PURTON, L. and BRASIER, M. 1999. Giant protist *Nummulites* and its Eocene environment: Life span and habitat insights from delta [18]O and delta ^{13}C data from *Nummulites* and *Venericadia*, Hampshire Basin UK. *Geology,* 27: 711–714.

RACEY, A. 1995 Lithostratigraphy and Larger Foraminiferal (Nummulitid) Biostratigraphy of the Tertiary of Northern Oman. *Micropaleontology Supplement,* 41: 1-123.

RENEMA, W. 2002. Larger foraminifera and their distribution patterns on the Spermonde shelf, South Sulawesi. *Scripta Geologica*, 124: 1–263.

RÖGL, F. 1999. Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (Short Overview). *Geologica Carpathica*, 50(4): 339– 349.

ROMERO, J., HOTTINGER, L. and CAUS, E. 1999. Early appearance of larger foraminifera supposedly characteristic for Late Eocene in the Igualada Basin NE Spain. *Revista Española de Paleontología,* 14: 79-92.

RÖTTGER, R. 1984. Ökologie der Grobforaminiferen. Film C 1497 des IWF, Göttingen 1983. Publikation von R. Röttger, *wissenschaftliche Publikation Film*, Sekt. Biol., Ser. 16, Nr. 20/C: 20p.

SACHS, J., Jr. and ADEGOKE, O.S. 1975. Paleocene *Nummulites* from Nigeria. *Journal of Foraminiferal Research*, 5: 71-75.

SARASWATI P.K., PATRA, P.K. and BANERJI, R.K. 2000. Biometric study of some Eocene *Nummulites* and *Assilina* from Kutch and Jaisalmer, India. *Journal of the Palaeontological Society of India*, 45: 91-122.

SCHAUB, H. 1981. *Nummulites* et *Assilines* de la Tethys paleogène. Taxonomie, phylogenèse et biostratigraphie. *Schweizerische Palaeontologische Abhandlungen,* 104: 1-238.

SERRA-KIEL, J., HOTTINGER, L., CAUS, E., DROBNE, K., FERNANDEZ, C., JAUHRI, A.K., LESS, G., PAVLOVEC, R., PIGNATTI, J., SAMSO, J.M., SCHAUB, H., SIREL, E., STROUGO, A., TAMBAREAU, Y., TOSQUELLA, Y. and ZAKREVSKAYA, E. 1998. Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. *Bulletin de la Société Géologique de France,* 169: 281-299.

TAN SIN HOK, 1932. The genus *Cycloclypeus* Carpenter. *Wetenschappelijke Mededeelingen Dienst van den Mijnbouw in Nederlands-Indië,* 19: 3-194.

TAN SIN HOK, 1937. Weitere Untersuchungen ueber die Miogypsiniden, I–II. De Ingenieur in Nederlandsch-Indië. *Geologie en Mijnbouw*, 4: 35–45.

UMBGROVE, J.H.F. 1928. Het genus *Pellatispira* in het Indo-pacifische gebeid. WetenschappelijkeMededeelingen van de Dienst van de Mijnbouw in Nederlandsch-Oost-Indië, 10: 43–71.

VAUGHAN, T.W. 1933. The Biogeographic Relations of the Orbitoid Foraminifera. *Proc Natl Acad Sci*, 19: 922–938.

WADE, B.S., PEARSON, P.N., BERGGREN, W.A. and PÄLIKE, H. 2011. Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale. *Earth Science Reviews*, 104: 111–142.

ZACHOS, J.C., PAGANI, M., SLOAN, L., THOMAS, E., and BILLUPS, K. 2001. Trends, rhythms, and aberrations in global climate: 65Ma to present. *Science,* 292: 686–693.

Fig. 1. a, *Nummulites deserti* De La Harpe, Egypt, P5, UCL coll., 4mm longest diameter (LD); **b**, *Nummulites irregularis* Deshayes, France, P8, UCL coll., 4mm LD; **c**, *Nummulites* sp., axial section Barton Bed, Chewton Bunny, Highcliffe, P8, UCL coll., 1.5mm LD; **d-e**, *Nummulites fichteli* Michelotti: **d**, France, P11, axial section, NHM P49522 (recently figured by BouDagher-Fadel, 2008), 3mm LD: **e**, solid specimen, Tang-i-Puhal area, P11, UCL coll., 5mm LD; **f**, enlargement of *Nummulites* sp. showing protoconch (P), deuteroconch (D), UCL coll., scale bar on figure; **g, j**, *Nummulites* sp.: **g**, Egypt, Eocene, UCL coll., 10mm LD : **j**, Gernona, Spain, Eocene, 8mm, UCL coll. (recently figured by BouDagher-Fadel, 2008); **h**, *Nummulites intermedius* (d'Archiac), India, Eocene, NHM P30148, (recently figured by BouDagher-Fadel, 2008),12mm LD; **i**, *Nummulites gizehensis* (Forskal), Spain, Late Lutetian, UCL coll., (recently figured by BouDagher-Fadel, 2008),17mm LD; **k**, *Nummulites fichteli-intermedius* (d'Archiac), Lower Nari Formation, Pakistan, Oligocene, UCL coll. (recently figured by BouDagher-Fadel, 2008), 2.5mm LD; **l**, enlargement of chambers of *Nummulites* sp., France, Middle Eocene, width of field view 1.5mm; **m,n**, *Operculina aegyptiaca* Hamam: **m**, solid specimen, Egypt, Early Eocene, UCL coll., 2mm LD: **n**, axial section, megalospheric form, latest Early Eocene, Gebel Gurnah, Luxor, Egypt, paratype, NHM P49827 (recently figured by BouDagher-Fadel, 2008), 2.2mm LD; **o,p**, *Assilina daviesi* de Cizancourt, Lower Bhadrar Beds (Salt Range), Pakistan, Early Eocene, NHM coll. (recently figured by BouDagher-Fadel, 2008): **o**, equatorial setion, NHM P41529, 2.4mm LD: **p**, axial section, NHM P41524, 3.4mm LD; **q**, *Heterostegina (Heterostegina)* sp., Brazil, Eocene, UCL coll., 2mm LD; **r,** *Heterostegina (Vlerkina) borneensis* van der Vlerk, axial section, Borneo, Late Oligocene, UCL coll., 6mm LD; **s**, *Cycloclypeus eidae* Tan Sin Hok, Kinabatangan River, Sabah, North Borneo, Early Miocene, NHM coll., N.B. NB9067, enlargement of early part of test, width of field view 1mm; **t**, *Cycloclypeus carpenteri* Brady, off Jutanga, Holocene, UCL coll., 6mm LD.

Fig. 2. The evolution of nummulitoids from a ?*Pararotalia* ancestor.

Fig. 3. The generic ranges and suggested evolution of the nummulitoids in the four identified provinces. (1) Suggested migration from the American province. (2) Suggested migration from the Western Tethyan province.

Fig. 4. Range chart of some key *Nummulites* species in the Western Tethyan and Indo-Pacific provinces.

Fig. 5. A southern Africa locality map modified from notes provided by Prof. Ian McMillan (*pers. comm.*). **a**. *Planostegina* spp. at Cacuaco Cliff, just north of Luanda (Kwanza Basin) and near Dombe Grande (Benguela Basin) in Angola, Burdigalian; **b**. South of Luderitz in Namibia, Burdigalian and Middle Eocene volcanics; **c.** Kudu boreholes, Namibia, *Planostegina* spp. in Burdigalian, *Nummulites* in Early Oligocene; **d.** offshore margin of Orange Banks (off mouth of Orange River, southernmost Namibia), offshore sample 1, Vibrocore DN 350/19300, 1929, Depth below sea-floor 3.88m, present day water depth ±200m, approximately 29° South, 14° 30' East; **e.** Childs Bank, Borehole K-A1, South Africa,

abundant *Miogypsina* spp. (see BouDagher-Fadel and Price, 2013) and a few *Planostegina* spp., Burdigalian; **f.** Shelly and glauconitic sandstone with axial sections of *P. southernia.* South Africa, off St. Helena Bay, OMO-4 Megadrill sample ± 4m below sea-floor, 32° 27' 45.79'' South 17° 49' 38.985'' East; **g.** Early Miocene, Trial Vibrocore, West of Robben Island, most southerly larger benthic foraminifera, abundant *Planostegina,* Burdigalian; **h.** Plettenberg bay, South Africa, *Nummulites spp.* reworked into latest Pleistocene sands; **i.** *Discocyclina* spp. at Birbury and E'Kalikeni (BouDagher-Fadel and Price, in preparation), Eocene; **j.** Burman Drive, South Africa, *Nummulites* reworked in Pleistocene sands.

Fig. 6. The major Cenozoic tectonic, oceanic and climatic events likely to have affected larger benthic foraminifera migration, evolution and extinction.

Fig. 7. Variation in sea-level and temperature during the Paleogene based on Zachos *et al.* (2001) and Miller *et al.* (2011).

Fig. 8. The inferred migration routes of nummulitoids during the Paleogene, shown by black arrows, from the Americas (1), to the Mediterranean (2), and on to the Indo-Pacific (3), and SW Africa (4).

Fig. 9. Morphometric measurements in the equatorial section of megalospheric *Planostegina africana* new species. P, proloculus, and D, deuteroconch; the number of pre-planosteginid chambers (X) is 8; l, the maximum diameter of the shell in the first whorl; L, the maximum diameter of the first one and subsequent half whorl.

Fig. 10. Range chart of *Planostegina* spp. in South West Africa.

Plate 1.

(a) *Chordoperculinoides bermudezi* (Palmer, 1934), 1-BAS 122 well, offshore Brazil, Middle Paleocene, UCL MF318, x20; **(b-c)** *Chordoperculinoides sahnii* (Davies), India, Palaeocene, x9, NHM P40350; **(d-e)** *Operculinella ocalanus* (Cushman), Brazil, Oligocene, **(d)** UCL MF319, x30, **(e)** UCL MF320, x27; **(f)** *Operculinella kugleri* (Vaughan and Cole), Masparito Member, Barinas Sub-Basin, Western Venezuela, Eocene (P12-P14), UCL coll., figured previously by Bolivar (1998), x15; **(g)** *Operculinella cumingi* (Carpenter), Port Moresby, Papua, Holocene, NHM P1960, illustrated by Eames *et al.*, (1961), x18; **(h)** *Operculinella trinitatensis* (Nuttall), Masparito Member, Barinas Sub-Basin, Western Venezuela, Eocene (P12-P14), UCL coll., figured previously by Bolivar (1998), x18; **(i)** *Operculinella* sp., Cyprus, Oligocene, UCL MF321, x30; **(j)** *Palaeonummulites* sp., Cyprus, Early Miocene, UCL MF, x22; **(k)** *Palaeonummulites panamensis* (Cushman), Miocene Brazil, (Aquitanian), UCL MF322, x13; **(l)** *Palaeonummulites willcoxi* (Heilprin, 1883), Masparito Member, Barinas Sub-Basin, Western Venezuela, Eocene (P12-P14), UCL coll., figured previously by Bolivar (1998), x13; **(m-n)** *Palaeonummulites kugleri* (Vaughan and Cole), Falling Waters *State Park,* Chipley, Florida, Suwannee Limestone, USA, Oligocene, UCL MF323, x15; **(p-q)** *Palaeonummulites antiguensis* (Vaughan and Cole), La Rambla, Puerto Rico, Juana Diaz Formation, Early Miocene, NHM P47351-2, x15; **(r, s)** *Palaeonummulites pristinus* Brady, mistakingly considered by Brady as coming from the Carboniferous Formation, Calcaire de Namur, Belgium, Eocene, Syntypes NHM P35504, figured previously by Eames *et al.* (1961), x36; **(t-u)** *Heterostegina israelsky* Gravell and Hanna, offshore Brazil, (Siri Member) of Campos Basin, Oligocene, Rupelian, P20, UCL MF324, x60.

Plate 2.

(a-b) ?*Lenticulina* sp. BouDagher-Fadel and Price new species. Unlike typical *Lenticulina* sp. the final aperture is lacking in these forms and the sutural canals ramify into many canals near the periphery. Namibia, Kudu borehole, line -940, sample 80-01, 940/8000, 6.6-6.7m, Early Burdigalian (N5b), **(a)** thin section, UCL MF281, x30, **(b)** solid specimen, UCL MF282, x30; **(c-l)** *Planostegina africana* BouDagher-Fadel and Price new species. Namibia, Kudu borehole, line -940, sample 80-01, 940/8000, 6.6-6.7m, Early Burdigalian (N5b), **(c)** holotype, UCL MF283, megalospheric form, x10, **(d-l)** paratypes, UCL MF284-92, **(d)** solid specimen showing smooth features, x42, **(e-i)** microspheric forms, **(e)** x7, **(f)** solid specimen, x6, **(g)** thin section, x6, **(h)** solid specimen x6, **(i-k)** thin section showing division of chamberlets in the last whorls, **(i)** x7, **(j)** x14, **(k)** x12, **(l)** a megalospheric test with chamber extending to an almost circular test, x16; **(m-af)** *Planostegina mcmillania* BouDagher-Fadel and Price new species, **(m-o, q-af)** Namibia, Kudu borehole, 1130/14500, at sample 1, base of core DN 1624, Late Burdigalian (N6-N7), **(p)** offshore side of Orange Banks 1929, sample 1 DN 350/19300, 3.88m below sea-floor, present day water depth +/- 200m, approximately 29^0 south, 14^0 30^0 east, **(n)** UCL MF294 holotype, x8, **(m-w)** paratypes, UCL MF2293-310, **(m),** x15, **(p)** UCL MF 311, **(o)** x8, **(p)** x7, **(q)** x5, **(r)** x25, **(s-t)** x6, **(u)** x15, **(v)** x15, **(w)** x15, **(x-af)** solid specimens, **(x)** solid specimen of a sectioned form showing internal structures, **(y-ac, ae)** x6, **(ad, af)** megalospheric and microspheric specimens x5.

Plate 3.

(**a-t**) *Planostegina southernia* BouDagher-Fadel and Price new species, (**a-j, l-n**) Namibia, Kudu borehole, 1130/14500, at sample 1, base of core DN 1624, Late Burdigalian (N6-N7), (**a**) holotype, UCL MF310, x8, (**b-n**) paratypes, UCL MF311-24, (**b**) x8, (**c**) x15, (**d**) x6, (**e**) x15, (**f**) x5, (**g**) x8, (**h**) x7, (**i**) x5, (**j**) x6, (**k**) offshore side of Orange Banks 1929, sample 1 DN 350/19300, 3.88m below sea-floor, present day water depth +/- 200m, approximately 29^0 south, 14^0 30^0 east, Late Langhian (N9-N11), x8, (**l-n**) axial sections, (**l**) x6, (**m**) x7, (**n**) x5; (**o-p**) Shelly and glauconitic sandstone with axial sections of *P. southernia.* South Africa, off St. Helena Bay, OMO-4 Megadrill sample ± 4m below sea-floor, 32° 27' 45.79'' South 17° 49' 38.985'' East, UCL MF325-326, (**o**) x8, (**p**) x7, (**q-t**) Site DN 4557 to the west of Robben Island, UCL MF327-30, (**q**) x10, (**r**) x8, (**s**) x10, (**t**) x5; (**u-aa**) *Planostegina langhiana* BouDagher-Fadel and Price new species offshore side of Orange Banks 1929, sample 1 DN 350/19300, 3.88m below sea-floor, present day water depth +/- 200m, approximately 29^0 south, 14^0 30^0 east, Late Langhian (N9-N11), (**v**) holotype, UCL MF332, x15, (**u, w-aa**) paratypes, UCL MF331, 333-337, (**u**) x5, (**w**) x3, (**x**) x4, (**y**) x4 (**z**) x9, (**aa**) x4.

Plate 4.

(**a-i**) *Planostegina langhiana* BouDagher-Fadel and Price new species offshore side of Orange Banks 1929, sample 1 DN 350/19300, 3.88m below sea-floor, present day water depth +/- 200m, approximately 29° south, 14° 30° east, Late Langhian (N9-N11), UCL MF338-45, (**a**) x9, (**b**) x10, (**c**) x9, (**d**) x7, (**e**) x15, (**f**) x9, (**f-i**) x5; (**j-k**) Assemblages of *Planostegina africana from* Namibia, Kudu borehole, line -940, sample 80-01, 940/8000, 6.6-6.7m, Early Burdigalian (N5b), MF346-7, x3; (**l**) Assemblages of *Planostegina mcmilliana* and *Pl. southernia* from Namibia, Kudu borehole, 1130/14500, at sample 1, base of core DN 1624, Late Burdigalian (N6-N7), MF348, x3; (**m**) Solid axial sections of *Planostegina southernia* in shelly and glauconitic sandstone, South Africa, off St. Helena Bay, OMO-4 Megadrill sample ± 4m below sea-floor, 32^0 27' 45.79'' South 17^0 49' 38.985'' East, MF349, x10. (**n**) Assemblages of *Planostegina southernia* from site to the west of Robben Island, DN 4557, MF350, x5; (**o**) Assemblages of *Planostegina langhiana* from offshore side of Orange Banks 1929, sample 1 DN 350/19300, Depth below sea-floor 3.88m, present day water depth +/- 200m, approximately 29^0 south, 14^0 30^0 east, Late Langhian (N9-N11), MF351, x3.