

RRH: EVOLUTION OF THE ORTHOPHRAGMINIDS

LRH: BOUDAGHER-FADEL AND PRICE

THE PALEOGEOGRAPHIC EVOLUTION OF THE ORTHOPHRAGMINIDS OF THE
PALEOGENE

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ABSTRACT

Orthophragminids are larger benthic foraminifera (LBF) and, together with the nummulitids, were the major rock-forming foraminifera from the middle Paleocene to the late Eocene. Today, porous, LBF-bearing, Paleogene limestones, which occur globally from the Pacific and Atlantic margins of the Americas to the Indo-Pacific, form potentially valuable oil reservoirs, and their biota have formed the basis of the definition of three paleobiogeographic provinces, namely those of the Americas, Tethys, and the Indo-Pacific. The orthophragminids of the western part of the Tethyan Province have been studied extensively, however, the other provinces are less well characterized, and until now the origin and paleogeographic development of this group have not been fully articulated. New material described here allows the clear definition of a fourth, South African paleobiogeographic province, and, when combined with refined biostratigraphic dating based on new material from the Americas, Europe, South Asia and SE Asia, enables their paleogeographic and biostratigraphic evolution to be determined. Critically, the occurrence of cosmopolitan planktonic foraminifera (PF) within LBF assemblages enables the first occurrences of various LBF forms within each province to be dated relative to well-calibrated planktonic zones (PZ). From this, we infer that, like the previously studied lepidocyclinids and nummulitids, the orthophragminids originated in the Americas during the Paleocene, probably between the late Danian (PZ P1c, 63.5 Ma) and the early Selandian (PZ P3a, 61.6 Ma). By the middle Paleocene, the orthophragminids had migrated across the Atlantic to the previously isolated West African coast at the extreme of Tethys, probably during global sea-level low stands at 60.3 Ma and again at 56.4 Ma. Subsequently, the American Province again became isolated. In the Tethys, the orthophragminid migrations followed two paths: northeastward through the Tethyan corridor in the late Paleocene (Thanetian), and south in the earliest Eocene (Ypresian) to South Africa. The Tethyan forms evolved during the Eocene into many

lineages, which in turn migrated, after a few million years of their first appearances into the Indo-Pacific, where they again became isolated and diversified further. Meanwhile the South African forms remained similar to their American ancestors in both small size and external ornamentation, while their internal evolution closely followed that of Tethys forms, as exhibited by three species of *Nemkovella* and *Discocyclusina* described here from South Africa (*Nemkovella mcmilliana* n. sp., *Discocyclusina davyi* n. sp. and *D. africana* n. sp.).

INTRODUCTION

The larger benthic foraminifera (LBF) were major contributors to shallow-marine carbonate sediments in the tropics and subtropics during the Paleogene (BouDagher-Fadel, 2008). In addition to stratigraphically important groups such as the rotaliids (Hottinger, 2009) and the nummulitids (BouDagher-Fadel & Price, 2014), the orthophragminids are important components of carbonate platform deposits formed during this period (Less, 1998). Traditionally, researchers have defined three distinct paleobiogeographic provinces for LBF during this period, namely those of the Americas, the Tethys, and the Indo-Pacific (Hottinger, 1960; Caudri, 1972, 1975a, 1996; Drobne, 1977; Schaub, 1981; Racey, 2001; Özcan, 2002; Drobne & Ćosović, 2009; BouDagher-Fadel, 2008). In recent studies of the nummulitids, BouDagher-Fadel & Price (2014) recognized a fourth, South African Province. Here, we confirm the existence of this distinct Paleogene South African Province with the discovery of three new provincial orthophragminid species, namely *Nemkovella mcmilliana* n. sp., *Discocyclina davyi* n. sp. and *D. africana* n. sp.

The orthophragminids described here usually co-occur with planktonic foraminifera (PF), which had a more cosmopolitan distribution than the provincial LBF. These occurrences allow the first and final occurrences of various LBF forms within each province to be dated relative to well-calibrated planktonic zones (PZ). In our definitions of these stratigraphic ranges, we primarily use the PZ scheme of BouDagher-Fadel (2013, 2015), which is tied to the time scale of Gradstein et al. (2012). In this paper, the PZ scheme of BouDagher-Fadel (2015) is also correlated with the larger benthic foraminiferal ‘letter stages’ of the Far East, as defined by BouDagher-Fadel & Banner (1999) and later revised by BouDagher-Fadel (2008), and with the biogeographic zonation of benthic larger foraminifera (ZBZ) as defined by Serra-Kiel et al. (1998).

In the following sections, we describe briefly the morphological characteristics of the orthophragminids and provide a review of earlier work done on their global and stratigraphic distributions. Then, using new material from the Americas, Europe, South Asia and SE Asia, we define the provincial dating of the first and last occurrences of key orthophragminid forms. Building on our previous studies of the lepidocyclinids (BouDagher-Fadel & Price, 2010b), and the nummulitids (BouDagher-Fadel & Price, 2014), we infer that the orthophragminids originated in the Americas during the Paleocene, probably between the late Danian (PZ P1c, 63.5 Ma) and the early Selandian (PZ P3a, 61.6 Ma). By the middle Paleocene (no later than Selandian, PZ P4a, 60.0 Ma) the first orthophragminids had migrated across the Atlantic to the previously isolated West African coast during global sea-level low stands at around 60.3 Ma. A second wave may have arrived during the late Thanetian sea-level low of 56.4 Ma (Miller et al., 2011). From there, their migration routes followed two paths: northeastward through the Tethyan corridor by the late Paleocene (Thanetian), and south by the earliest Eocene (Ypresian) to South Africa. The orthophragminids from the again isolated American and Tethyan Provinces subsequently developed parallel but independent lines of evolution, with the Tethyan forms evolving many well documented lineages during the Eocene (e.g., Özcan et al., 2007), which in turn migrated, a few million years after their first appearances, into the Indo-Pacific, where they became isolated and diversified further. Meanwhile the South African forms remained similar to their American ancestors with their small size and external ornamentation, while their internal evolution closely followed that of Tethys forms.

MORPHOLOGICAL CHARACTERISTICS OF THE ORTHOPHRAGMINIDS

The orthophragminids, the term used to describe members of the Family Orthophragminidae, are of Paleocene to Eocene age. Morphologically, they are bilamellar, perforate, orbitoidal LBF, and are characterized by a discoidal, lenticular test with a fine equatorial layer and small lateral

chamberlets (Fig. 1). The growth of orthophragminids was both cyclical and involute. Each chamber had a bilamellar structure with an inner lining and an outer lamella, with the subdivision of the equatorial chamberlets provided by different inner linings (Ferràndez-Canàdell & Serra-Kiel, 1992) (Fig. 2). No canal system is evident (cf. the nummulitids), and connections between chambers are provided by a tridimensional stolon system (see Ferràndez-Canàdell & Serra-Kiel, 1992).

Orthophragminids are classified based on the general shape of their tests, the pillar-lateral chamberlet network, the different kinds of stolons, and the size of their pillars. Moreover, their most important evolutionary parameters are associated with the shape of the embryos in the megalospheric generations and the characters of nepionic stages in the microspheric orthophragminid juvenaria, and features of the equatorial chambers (Less, 1987; Brönnimann, 1951; Ferràndez-Cañadell & Serra-Kiel, 1992; BouDagher-Fadel, 2008). The Orthophragminidae are divided into two subfamilies, the Discocyclinae Galloway, 1928, which includes the genera: *Asterophragmina*, *Athecocyclina*, *Discocyclina*, *Hexagonocyclina*, *Nemkovella*, *Proporocyclina*, *Pseudophragmina*, and the subfamily Orbitoclypeinae Brönnimann, 1946, which includes *Asterocyclina*, *Orbitoclypeus*, *Neodiscocyclina*, and *Stenocyclina*.

Loeblich and Tappan (1987) considered *Proporocyclina* and *Athecocyclina* as synonyms of *Pseudophragmina* (see BouDagher-Fadel, 2008). However, in this study, we consider them to be different genera, as they exhibit stratigraphically-characteristic, distinguishing morphological features: *Athecocyclina* has no incipient septula; *Pseudophragmina* has irregular septula; while *Proporocyclina* has well-developed, radial septula with distal annular connections.

Dimorphism in the orthophragminids is common and is reflected in the size of the test, which is larger in sexually produced microspheric specimens than in the asexually produced megalospheric forms. The diameter of megalospheric specimens is ~3 mm or less, while microspheric specimens may exceed 10 mm in diameter. As in occurrences of most LBF, the megalospheric

orthophragminids are more common than the microspheric ones (Ćosović & Drobne, 1995; Hottinger, 2001).

The megalospheric forms of the discocyclinines have a subspherical protoconch enclosed by a larger reniform deuteroconch (Figs. 1.1–1.6). Their microspheric forms have a *Cycloclypeus*-like microspheric juvenile (see Figs. 1.3–1.9) with an initial spiral of small chambers; later stages exhibit cyclical chambers (annuli) subdivided by septula into small rectangular chamberlets connected by annular and radial stolons. Externally, the test surface is either smooth, with scattered pillars, or has radially developed ribs (see Fig. 3). An inflated central part or umbo (Figs. 3.3–3.4) is occasionally present. Members of orbitoclypeines have an early planispiral microspheric coil, while megalospheric tests have a globular protoconch, enclosed by a larger reniform deuteroconch. Tests may occur with or without ribs. These taxa have a single equatorial layer of chamberlets and several layers of small lateral chamberlets, ranging from arcuate, spatulate to hexagonal in shape, and cyclical chambers that are not subdivided into chamberlets.

Biometric data are frequently used in specific definitions and were first developed for *Discocyclina* by Neumann (1958) and subsequently expanded by Broolsma (1973), Fermont (1982), and Setiawa (1983). The degree of embryonic enclosure, the dimensions of the embryonic chambers, and the number of the periembryonic chambers have all been used as characteristic orthophragminid morphometrics (Broolsma, 1973; Fermont, 1982; Setiawan, 1983). More recently the morphological features of the whole group have been revised by authors such as Less (1987, 1998) and Özcan et al. (2006). These authors focused on internal features found in equatorial sections; they emphasized the description of the embryo, and highlighted the significance of a number of parameters, thus:

- P1 and P2 (diameter of protoconch perpendicular and parallel to P–D axis);
- D1 and D2 (diameter of deuteroconch perpendicular and parallel to P–D axis);
- A, the number of auxiliary chamberlets directly arising from the deuteroconch;
- the number of adauxiliary chamberlets (see Fig. 1) or, according to Hottinger

(2006), corona, in which the first cycle of chamberlets envelops the embryonal apparatus completely, at least in one plane of sectioning, as in *Discocyclina*;

- the number of annuli within a 0.5 mm wide stripe measured from the rim of the deuteroconch along P–D axis;
- H and W (height and width) of the equatorial chamberlets in the first annulus; and
- h and w (height and width) of the equatorial chamberlets around the periphery of the equatorial layer.

The development of annular stolons in the orthophragminids is deemed to be of generic significance (Samanta, 1967). Annular stolons occur at the proximal end of the radial walls and connect adjacent chamberlets in *Discocyclina* and *Asterocyclina* (BouDagher-Fadel, 2008), and at the distal end in *Pseudophragmina* and *Asterophragmina* (Haynes, 1981).

The study of the evolutionary lineages and stratigraphic distribution of the Tethyan orthophragminids, alveolinids and nummulitids led Serra-Kiel et al. (1998) to propose 20 shallow benthic zones (SBZ) for the Paleocene–Eocene epochs. Less & Kovács (1995) and Less (1998) documented the stratigraphic ranges of Tethyan orthophragminids with reference to these standard zones. Less et al. (2007) separated 18 orthophragminids zones, from OZ 1a to 16, ranging from the early Thanetian to the late Priabonian.

The orthophragminids reached their widest latitudinal distribution within the early Eocene (Ypresian), especially *Asterocyclina*, which reached a paleolatitude of 45°N (in the North Atlantic, Porcupine Bank). This coincides with the acme of Eocene marine transgression and associated climatic optimum. Orthophragminid foraminifera disappeared completely at the end of the Eocene (33.9 Ma).

Today LBF-bearing limestones, which occur globally from the Pacific and Atlantic margins of the Americas, through West Africa, the Mediterranean and the Arabian/Persian Gulf to the Indo-Pacific, form valuable aquifers and oil reservoirs. The study of orthophragminid species and the

definition of their stratigraphic ranges are therefore of considerable economic importance. As such, they have been the subject of many regional investigations. The orthophragminids of the Western Tethys have been intensively studied (e.g., Neumann, 1958; Van der Weijden, 1940; Brönnimann, 1940, 1945; Pokorny, 1958; Caudri, 1972, Less, 1987; Drooger, 1993; Less et al., 2007; Özcan et al., 2007, 2010, 2014; BouDagher-Fadel, 2008). The current orthophragminid zonation (OZ), defined relative to forms to be found in these Western Tethyan platforms (Ćosović & Drobne, 1995; Less, 1998; Meulenkamp & Sissingh, 2003; Özcan et al., 2001, 2007, 2014; Less et al., 2007; Ben Ismail-Latrache et al., 2014), has been used to date the Paleogene of the region (Serra-Kiel et al., 1998). However, until now, it has not been possible to develop an effective global view of orthophragminid evolution, since 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 among these geographically dispersed assemblages.

Descriptions of forms from the American Province rely on papers such as Vaughan (1929, 1936), Cole (1952) and Caudri (1972). Likewise, relatively few discocyclinine species have been described from Tibet, Taiwan and the Indo-Pacific (e.g., Huang et al., 2013; BouDagher-Fadel et al., 2015), and there have been few attempts to define a taxonomy for forms from the Indo-Pacific and to biostratigraphically correlate them with forms from the Western Tethys (e.g., Renema, 2002).

Orthophragminids have been rarely reported from South Africa (Newton, 1896, 1924), and the forms described previously have been ascribed as being Tethyan or American. In this study, we describe material from two outcrops, at Birbury and Pato's Kop (e'Kalikeni) in the Eastern Cape, which contain examples of the first provincial record of novel orthophragminids, namely *Nemkovella mcmilliana* n. sp., *Discocyclina davyi* n. sp. and *D. africana* n. sp., which are unique to the region (see Fig. 4).

Haughton (1925) referred to the Birbury LBFs as *Orbitolites*, a larger benthic milioline genus. Chapman (1930) described these foraminifera as *Orthophragmina*, a junior synonym of

Discocyclina, and he associated them with Tethyan discocyclinines. He named his forms “*Discocyclina*” *prattii* and “*D.*” *varians*. He also reported his Slide 4459 as containing *Nummulites* sp., but on close inspection these are found to be large *Lenticulina* sp. Most of the smaller benthic species names used by Chapman (1930) are Holocene/Quaternary names, and are incorrect. Mountain (1962) described additional smaller benthic foraminiferal species from the same locality. Bourdon & Magnier (1969) regarded the LBF at Birbury as *Discocyclina* aff. *sheppardi* Barker, a middle to late Eocene American species. Siesser & Miles (1979) made no further comments on the LBF, except to review Chapman’s names, but they identified the planktonic foraminiferal species *Morozovella subbotinae* (Morozova) wrongly in their specimens. They are in fact *Morozovella aequa* (Cushman & Renz) and *M. edgari* (Premoli Silva & Bolli). Both species define the age as being earliest early Eocene (see BouDagher-Fadel, 2013). The LBF have not been previously described from Pato's Kop. Maud et al. (1987) identified calcareous nannofossils from this outcrop, but their dating of the Birbury and Pato's Kop outcrops was confused over the differences and similarities between these outcrops and their respective assemblages.

In this paper, we present examples of orthophragminids from newly described LBF-bearing carbonates. They included specimens from Spain (the Hecho Group deposits of the Ainsa Basin, south central Pyrenees; Fig. 1.6, see also Scotchman et al., 2015), France (west-southwest of Fontcouverte, Aude; Figs 5.1–5.4), South Tibet (from the Zongpubei, the Shenkeza, the Cuojiangding and the Dajin sections in the Gamba and Tingri areas; Fig. 5.7, see also BouDagher-Fadel et al., 2015), India (Goojerat, Western India, at Baboa Hill, Wagé-ké-pudda, Baboa Hill, Cutch; Figs. 5.8–5.9), Pakistan (Upper Ranikot Beds, Patala Formation in the Samana Range; Fig. 6.1), Bangladesh (Kopili Formation overlying the Sylhet Limestone, the Surma Basin; Fig. 6.2, see also Najman et al., 2008), the Sarawak Basin, Borneo (from onshore in the Tinjar Province, offshore Sarawak, Sarawak Basin; Figs. 6.3–6.6, Ali et al., in press), Barbados (from blocks contained in the Joes River mudflows, Scotland District; Figs. 7.5, 7.8–7.9), and South Africa (from Birbury and

Pato's Kop; Figs. 8, 9). These observations from new material have been augmented by studies of topotypes from Turkey (the Akveren Formation; Figs. 5.5–5.6), Cuba (North Cuba Basin; Fig. 7.1), Peru (*Terebratula* Bed; Figs. 7.2–7.3), Mexico (El Cristo Well, Vera Cruz; Fig. 7.4), Trinidad (Soldado Rock; Figs. 7.6–7.7), and California (Vaqueros Formation; Figs. 7.10–7.12). By combining our observations with those in the literature, we are able to propose a novel, comprehensive analysis of the paleogeographic evolution of the orthophragminids. We are also able to calibrate their occurrences with the planktonic foraminifera in many thin sections [e.g., *Turborotalia centralis* (Cushman and Bermudez) (Fig. 6.3B), *Globigerinatheka barri* Brönnimann (Fig. 6.5C)], thus refining their biostratigraphy.

PROVINCIAL BIOSTRATIGRAPHIC SYNTHESIS OF THE ORTHOPHRAGMINIDS

THE AMERICAN PROVINCE

Globally, the end Maastrichtian mass extinction was followed by a recovery period in the early Paleocene. The earliest American Paleocene orthophragminid reported is the discocyclinine *Athecocyclina*. This form, with poorly developed radial septula (Vaughan, 1945), was initially described from the Paleocene of the Soldado formation of Trinidad, where we also found in situ the PF *Subbotina triloculinoides* (Plummer), which defines the base of the Danian PZ P1c, 63.5 Ma. Vaughan (1945) also reported *Athecocyclina* limestones on the southeast side of Soldado Rock, Trinidad, containing the nummulitid “*Ranikothalia*”. This American form was renamed by Haynes et al. (2010) as *Chordoperculinooides*, and ranged from middle to late Paleocene (P3a–P5a, 61.6–56.5 Ma) (see BouDagher-Fadel, 2008; BouDagher-Fadel & Price, 2015). We infer therefore that the American discocyclinine *Athecocyclina* evolved no earlier than PZ P1c (63.5 Ma) and no later than P3a (61.6 Ma).

The earliest American orbitoclypeine, *Neodiscocyclina* [e.g., *N. anconensis* (Barker), Figs. 7.5, 7.8–7.9] had also appeared by the middle Paleocene (P3a, 61.6 Ma) (Blanco-Bustamente et al., 1999). This form has irregular equatorial chambers, which enlarge from the proloculus to the periphery (Caudri, 1972, 1975b). *Neodiscocyclina* gave rise in the early Eocene (P5b, 56.0 Ma) to the stellate-ribbed orbitoclypeine *Asterocyclina* (Rutten, 1935; Iturralde et al., 2008).

By the early Eocene (Ypresian, 56.0 Ma), the American discocyclinines had developed a six-stolon system, as seen in *Hexagonocyclina* (Drooger, 1993). They have predominantly hexagonal chambers, which differentiates them from the Tethyan *Discocyclina* (discussed below), and they are also totally different from any of the Tethyan forms in their ontogenetic development: they start out with two symmetric auxiliary chambers on either side of the nucleoconch and four symmetric nepionic spirals, a pattern never observed in any of the Tethyan forms. *Hexagonocyclina* (Fig. 7.4) has not been recorded from the Eastern Hemisphere.

More evolved forms of American discocyclinines, *Discocyclina* similar to those in Tethys but having evolved separately, have a spherical embryonic protoconch embraced partly by a reniform deuteroconch. The periembryonic chambers consist of two long, narrow, principal auxiliary chambers and five shorter chambers. Equatorial chambers are arcuate, mainly rectangular to square, but occasionally are hexagonal, and early ones are somewhat arcuate (e.g., *Discocyclina sheppardi*, Figs. 1.7, 7.6–7.7). Some other more advanced forms have their protoconch completely surrounded by the deuteroconch, and in equatorial section, have square equatorial chambers in the early parts, becoming rectangular in the later part [e.g., *D. californica* (Schenck), Figs. 7.10–7.12].

Both the orbitoclypeines and the discocyclinines became extinct in the Americas in the late Eocene.

THE TETHYAN PROVINCE

In the Tethys, forms similar to the American *Neodiscocyclina barkeri* Vaughan & Cole, *N. weaver* Vaughan, *Athecocyclina soldadensis* Vaughan & Cole, and *A. stephensoni* Vaughan are found in Senegal, West Africa (Castelain, 1965; Monciardini, 1966; Cariou, 1968). The oldest of these West African forms dates from the late Paleocene (Thanetian, P4b–P5a, 59.2–56.0 Ma; Ly & Butterlin, 1996). These early West African orthophragminids evolved in the Eocene into distinctive Tethyan forms (e.g., the Lutetian *Discocyclina senegalensis* Abrard, 1956; see also Özcan et al., 2007), which have close affinities to those found more widely in the modern Mediterranean region, but which are distinct from the contemporaneous American orthophragminids.

Apparently contemporaneous with their appearance in West Africa, orthophragminids such as *Discocyclina* (Less et al., 2007) are also found in the region of the modern day Mediterranean dating from the early Thanetian (P4b, 59.2Ma). *Discocyclina* was followed directly in the early Eocene (Ypresian, P5b, 56.0Ma) by the appearance of the characteristically Tethyan form *Nemkovella* (Less, 1987). The latter differs from *Discocyclina* in lacking annular stolons. It only survived until the early Bartonian (P13, 39.2 Ma) (İsmail-Latrache et al., 2014), while *Discocyclina* continued to the late Eocene (Priabonian, P17, 33.9 Ma).

The discocyclinines developed many evolutionary lineages in the Paleogene of the Western Tethys (Less, 1987; Özcan et al., 2007) and, together with the nummulitids, they became a common constituent of Upper Paleocene-Eocene carbonate platforms. Less et al. (2007) recorded many different morphotypical lineages [e.g., *Discocyclina prattii* (Michelin), Figs. 1.2, 5.2; *D. tenuis* Douvillé, Fig. 5.1]. Western Tethyan forms migrated eastward over time, so, for example, in a study of samples from Tibet (BouDagher-Fadel et al., 2015), the first appearance of *Discocyclina sella* (d'Archiac) was recorded in the late Thanetian, P5a (56.4 Ma), while in Western Tethys it dates from the middle Thanetian (P4c, 57.0 Ma).

The Tethyan orbitoclypeines developed in parallel with their discocyclinine relatives. The first Tethyan orbitoclypeines, found in the late Paleocene (Thanetian, P4b, 59.2 Ma, see Özcan et al.,

2001), was the non-ribbed *Orbitoclypeus*, which was followed by the stellate *Asterocyclina* in the early Eocene (Ypresian, P5b, 56.0 Ma). Both survived the Paleocene–Eocene boundary and became extinct, with all other orthophragminids, at the end of the Eocene (end Priabonian, P17, 33.9 Ma, see BouDagher-Fadel, 2008).

THE INDO-PACIFIC PROVINCE

In the Indo-Pacific, most orthophragminid genera were similar to those of the Tethyan Province and they were represented mainly by *Discocyclina* and *Asterocyclina*. The establishment of these taxa in the Indo-Pacific occurred in the Lutetian (P10, 47.8 Ma), compared with their first appearance in the late Thanetian (P4b, 59.2 Ma) and Ypresian (P5b, 56.0 Ma) respectively in the Western Tethys (see Renema, 2002; BouDagher-Fadel, 2008). They are both locally placed at the lower Ta3 Letter Stage. Thus, the forms seen in the Indo-Pacific likely migrated eastward along the coastal regions a few million years after their first appearance in the Western Tethys. However, some typical Tethyan forms, such as the early Eocene *Nemkovella*, are never found in the Indo-Pacific province.

As soon as orthophragminids were established in the Indo-Pacific, 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 Tethys, some of them particularly thrived in the Indo-Pacific and reached maximum sizes of up to 150 mm (Renema, 2002), but appeared in geographically isolated areas [e.g., *Discocyclina javana* Samanta, 1964 (Fig. 2.5A) is only found in Indonesia and Western India]. Many of the Indo-Pacific orthophragminids evolved similar but distinct features to Tethyan forms (e.g., *Discocyclina ranikotensis* Davies (Figs. 2.1, 2.3, 6.1–6.2), *Discocyclina ramaraoi* Samanta (Figs. 6.3A, 6.4A, 6.6A), *D. omphalus* (Fritsch) (Fig. 6.4C).

As in Tethys, the Indo-Pacific orthophragminids did not survive the Eocene-Oligocene boundary (33.9 Ma).

THE SOUTH AFRICAN PROVINCE

In the South African Province, newly described Paleogene orthophragminids found in this study are closer in shape to those from the Tethyan Province, although they also show some affinities with forms from the American Province. No orthophragminids had been correctly described from South Africa prior to this study. The earliest forms we found are of early Eocene (Ypresian, P5b–P6, 56.0–52.3 Ma) age, *Discocyclina davyi* n. sp. (Figs. 3.7, 4.1–4.2, 8.10–8.14), and *Nemkovella mcmilliana* n. sp. (Figs. 3.10–3.12, 8.1–8.9, 10.1–10.5), which are described in detail in the following section. This discovery marks the first occurrence of a *Nemkovella* species from outside the Tethys. However, although it is similar to the Tethyan forms, *N. mcmilliana* lacks the ribbed characters of the Tethyan forms, while it possesses special morphological characters, such as the presence of protruding pillars all over the surface of the test and the irregular shape of the equatorial chamberlets. The pillars are considered to be ecologically induced features that serve to concentrate the light necessary for the insolation of the algal symbionts (Ferràndez-Cañadell & Serra-Kiel, 1992). However, in many three-layered LBF (e.g., *Lepidocyclina*), they are considered specific characteristics (BouDagher-Fadel & Lord, 2000). The shape of the early equatorial chamberlets of *Discocyclina davyi* is rectangular, as in typical Tethyan *Discocyclina*, but chamberlets in later whorls are predominantly hexagonal as in the American *Hexagonocyclina*. On the other hand, Tethyan *Orbitoclypeus* is spatulate in the inner cycles and distinctly hexagonal in the external ones (Özcan et al., 2014).

Discocyclina africana n. sp. (Figs. 3.8–3.9, 4.3–4.6, 9.1–9.11) is of middle Eocene age (Bartonian, P12, 42.3–40.2 Ma) and also shares morphological features with both American and

Tethyan discocyclinines. The shape of the adauxiliary chamberlets are similar to the Tethyan and Indo-Pacific forms [e.g., *Discocyclina dispansa* (Sowerby), Figs. 1.3, 1.9, 2.4, 5.7–5.9, 3.4B, 3.5A], while the surface ornaments and the equatorial chamberlets are similar to those of the American form *Neodiscocyclina* (Fig. 7.5, 7.8–7.9).

In contrast to forms of a similar age from the Tethys, these early Eocene South African forms of *Nemkovella* and *Discocyclina* have pillars between the lateral chamberlets, which protrude to the surface instead of having a smooth surface or small subspherical pustules (Ferràndez-Cañadell & Serra-Kiel, 1992). In relatively robust tests, such features may indicate adaptation to high energy environments (BouDagher-Fadel et al., 2000). Alternatively, as noted by Ferràndez-Cañadell & Serra-Kiel (1992) in middle Eocene forms with flatter tests and thinner test walls, the pillars grew on the lateral walls and might have acted as lenses that focused light into the test to provide insolation for algal symbionts. The lateral chamberlets of these younger *Discocyclina* were particularly flat in shape and they likely lived at the lower limit of the photic zone (see Hottinger, 1997; BouDagher-Fadel, 2008). The limited diversity, with only one species of LBF found in the outcrop studied, and the complete absence of large nummulitids at these two sites of South Africa (see BouDagher-Fadel & Price, 2014), might reflect a cooler climate and different tolerance limits of the various members of these two important Paleogene LBF families to oceanic water temperatures.

TAXONOMY OF NEW ORTHOPHRAGMINIDS FROM SOUTH AFRICA

Below we describe new material from South Africa. All the newly discovered orthophragminid species have lenticular tests, some are slender, while others are somewhat inflated. We were only able to separate them on a specific level through study in oriented thin sections. The distinctive and specific characteristic is the presence or absence of pillars on the test surface. The small size of the tests, pillars embedded in the lateral chamberlets, the irregular ornamentation, and

chamber shapes distinguish the South African species from the Tethyan forms. Microspheric specimens were not encountered in the material studied.

The specific features of the megalospheric embryos are described quantitatively using the morphometric system introduced by Less (1987, 1998) and Özcan et al. (2006). We have established the biometric characteristics of these forms from measurements of several specimens. All materials relating to the new species described below are deposited in the UCL Geology Collection (<http://www.ucl.ac.uk/museums/geology>).

SYSTEMATICS

Order FORAMINIFERIDA Eichwald, 1830

Family ORTHOPHRAGMINIDAE Vedekind, 1937

Subfamily DISCOCYCLININAE Galloway, 1928

Genus *Nemkovella* Less, 1987

Type species: *Orbitoides strophiolata* Gümbel, 1870

Nemkovella mcmilliana n. sp,

Figs. 3.10–3.12, 8.1–8.9, 10.1–10.5

Name derivation: This species is named in honor of Professor Ian McMillan, who collected and donated the material described.

Type locality: Outcrop at Birbury (33°28'45"S 26°55'55"E, Eastern Cape, South Africa).

Holotype: UCL MF491, Fig. 8.6.

Paratypes: UCL MF492–9, Fig. 8.7–8.9.

Measurements: Maximum diameter 2.7 mm.

Material: 86 specimens.

Description: *Nemkovella mcmilliana* n. sp. is a small, inflated, and unribbed form with pillars scattered over the test surface. The megalospheric embryo is relatively large, having a length of ~0.2 mm (~10% of the largest diameter of the test), with a protoconch of ~0.11 mm, slightly larger than the deuterococonch which is ~0.09 mm (with an almost isolepidine-type configuration), forming 55% of the embryonic apparatus (see Fig. 10). The wall, common to the protoconch and deuterococonch, is slightly curved. The 11 auxiliary chamberlets are small, unequal in size (largest 26 μm), and irregular in shape. There is one small principal auxiliary chamberlet. The surrounding chamberlets are quadriserial, irregular in size, and asymmetric. The equatorial chamberlets are circular, with the first ten annuli formed of irregularly shaped chamberlets, which are either arcuate or spatulate in the inner cycles, followed by two annuli of rectangular chamberlets, and then distinctly hexagonal chamberlets in the six outer cycles of the equatorial section. The axial section is broad in the center with a width of 0.67 mm, tapering gradually to the sides where they reach a width of ~0.23 mm in megalospheric forms (Fig. 8.7) to ~0.1 mm in microspheric forms (Figs. 7.7; 7.9). Centrum chamberlets are up to 16 μm high and to 30 μm broad, with thin floors and walls. Maximum thickness of pillars is ~50 μm .

Remarks: *Nemkovella mcmilliana* is distinguished from other species of *Nemkovella* by the shape of the test and the equatorial chamberlets. The presence of pillars all over the outside surface of the test and the irregular shape of the chamberlets, separate *N. mcmilliana* from those already described from the middle Eocene of Tethys, such as those of the *N. strophiolata* (Gümbel) lineage. The test of *N. mcmilliana* is more lenticuline than those of *Discocyclina davyi* and *D. africana*.

Distribution: This species is of earliest Eocene age and occurs in association with planktonic foraminifera including *Morozovella aequa* and *Morozovella edgari* (Premoli Silva & Bolli). The occurrence of these two species indicate an early Ypresian age, P5b–P6a, 56–54 Ma (see BouDagher-Fadel, 2015). *Acarinina soldadoensis* (Brönnimann), a latest Paleocene–early Eocene species (see BouDagher-Fadel, 2015), is seen embedded in the test of the holotype (Fig. 10.6).

Genus *Discocyclina* Gümbel, 1870

Type species: *Orbitolites prattii* Michelin, 1846

Discocyclina davyi n. sp.

Fig. 8.10–8.14

Name derivation: This species is named in honor of James Davy, Dept. Earth Sciences, UCL.

Type locality: Outcrop at Birbury (33°28'45"S 26°55'55"E, Eastern Cape, South Africa).

Holotype: UCL MF500, Fig. 8.10.

Paratypes: UCL MF504, Fig. 8.11–8.14.

Measurements: Maximum diameter 3.5 mm.

Material: 110 specimens.

Description: *Discocyclina davyi* n. sp. is lenticular in shape, with evenly slopping sides, slender, and moderately flattened with a smooth test surface, but is ornamented by numerous pillars with a distinct pillared umbo. In the equatorial section, the megalospheric embryo, ~0.4 mm, is round and eulepidine-like in shape, and makes up 11% of the test. The protoconch is relatively large, 0.24 mm, makes up 60% of the embryonic apparatus, and is surrounded by a small reniform deuteroconch, up to 0.16 mm. The auxiliary chamberlets are small, square in shape, of the “*archiaci*” type, and moderately narrow and low. The adauxiliary chamberlets are not observed. The equatorial chamberlets are narrow, and predominantly hexagonal. The early chamberlets of 6–7 annuli are almost square (2 µm x 2 µm). The dimensions of the chamberlets in the successive annuli are more irregular and much thinner later (2 µm x 1 µm). All chamberlets are separated with walls of ~1 µm in thickness. The annuli are circular, and the growth pattern is of the “*archiaci*” type, uniformly spread over the test. The axial section shows the presence of pillars all over the test starting only from the

sixth or seventh rows of lateral layers, the thickest ones being on the inflated center of the test, reaching 130 µm thickness near the periphery. The median layer increases gradually in thickness from 14 µm near the embryo to 28–30 µm near the periphery.

Remarks: *Discocyclina davyi* is differentiated from Tethyan discocyclinines in having a large eulepidine-type embryont, surrounded by small auxiliary chamberlets similar in size to those in adjacent annuli that are uniform in size all over the test. It differs from the other species of *Discocyclina* with similar embryonic apparatus in which the embryo is entirely surrounded by deuterocoench [e.g., *D. archiaci* (Schlumberger), *D. marthae* (Schlumberger) and *D. californica* Schenck)] in having a larger protoconch, different shapes of auxiliary c and equatorial chamberlets. *Discocyclina davyi* differs from *D. sheppardi* (see Figs. 2.7, 7.6–7.7) in the shape of the equatorial chambers and surface ornaments. The number of adauxiliary chamberlets cannot be counted as they were not observed, or were tiny or broken in the prepared sections. Unlike all Tethyan species, the surface ornamentations are irregular and do not seem to be of any of the “rosette” types described from the Tethys (see İsmail-Lattrache et al., 2014). The equatorial chamberlets are small and predominantly hexagonal, similar to those of *Hexagonocyclina*.

Distribution: This species occurs in the earliest Eocene in association with planktonic foraminifera including *Morozovella aequa* (Cushman & Renz) and *Morozovella edgari* (Premoli Silva & Bolli). The occurrence of these two species indicate an early Ypresian age, P5b–P6a, 56–54 Ma (see BouDagher-Fadel, 2015).

Discocyclina africana n. sp.

Figs 9.1–9.11

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

Type locality: Outcrop at Pato's Kop (also known as e'Kalikeni, 33°14'09.4"S 27°17'13.3"E, Eastern Cape, South Africa).

Holotype: Fig. 9.1, UCL MF505.

Paratypes: Figs. 9.2–9.11, UCL MF506–515.

Dimensions: Maximum diameter up to 5 mm.

Material: 71 specimens.

Description: *Discocyclusina africana* n. sp. is an un-ribbed species with a diameter ranging from 3.5–5 mm. The test is lenticular in cross section with the edges sloping rapidly. The embryonic apparatus is large, 0.36 mm, trybliolepidine-type, and circular in horizontal section, with the protoconch entirely surrounded by a circular deutoconch. The internal diameter of the deutoconch is 0.24 mm, while that of the protoconch is 0.12 mm. There are numerous moderately wide and high, “*prattii*”-type auxiliary chamberlets (34 µm x 51 µm), followed by rectangular, narrow but high equatorial chamberlets, increasing gradually in size and reaching 50 µm x 16 µm, with walls 8–10 µm thick. The external surface is ornamented by numerous shallow pillars. However, a vertical section shows the presence of very few pillars embedded within the lateral chamberlets, which are particularly low in shape. The median layer increases gradually in thickness from 24 µm near the embryo to 48 µm near the periphery.

Remarks: *Discocyclusina africana* is differentiated from Tethyan discocyclusinines in having a large embryo, and by surface ornamentation that is irregular and does exhibit the “rosette” forms described from the Tethys (see İsmail-Latrache et al., 2014). The un-ribbed test and the irregularity of the chamberlets distinguish this species from *D. prattii* (Michelin) (Figs. 1.2, 5.2). In axial section, the pillars are seen growing on the walls and are not embedded in the lateral walls, as seen in *D. davyi*. The shape of the auxiliary chambers and equatorial chambers differentiate *D. africana* species from *D. varians* (Kaufman). This new species differs from the American *Neodiscocyclusina anconensis* (Figs. 7.5, 7.8–7.9) by the size of the embryo, and the gradual enlargement of the

chamberlets in the annuli towards the periphery. It differs from *D. archiaci* (Schlumberger) by the surface ornamentation and the enlargement of the chambers towards the periphery, and the presence of pillars, and from *D. marthae* (Schlumberger) by the thinner lenticular test, the shape of the equatorial chambers and the larger embryo.

Distribution: This species coexists with planktonic foraminifera including *Pseudohastigerina micra* (Cole), *Acarinina matthewsae* Blow, and *Truncorotaloides rohri* (Brönnimann & Bermudez) which are of middle Eocene age, (late Lutetian–early Bartonian, P12, 42.3–40.2 Ma).

ORIGIN AND PALEOGEOGRAPHIC DISTRIBUTION OF THE ORTHOPHRAGMINIDS

The phylogenetic origins of the various orthophragminid lineages have been discussed by many authors (Brönnimann, 1945; MacGillavry, 1963; Caudri, 1972; Haynes, 1981; Fermont, 1982; Sirotti, 1987; Less, 1987; Drooger, 1993; Less et al., 2007). Earlier researchers stated that they might have evolved from an earlier nummulitid (Vaughan, 1945). More recent authors, however, have disputed the presence of true canals in orthophragminids (Brönnimann, 1951; Samanta, 1967), and so have suggested that it is more probable that they evolved from the Rotalioidea. Ferràndez-Canàdell (1999), by comparing the stellar structure of the initial spire of microspheric *Orbitoclypeus* (Fig. 5.3–5.4) and *Asterocyclina* (Fig. 5.5–5.6), proposed an asterigerinid ancestor to the orbitoclypeines. Other authors suggest a connection with the Cretaceous *Lepidorbitoides* (MacGillavry, 1963), which also has a bilocular embryo and very thin layers, however, the earliest megalospheric forms, from the early Thanetian, are well developed and do not yield pre-orbitoidal stages (Ferràndez-Canàdell & Serra-Kiel, 1992; Less et al., 2007), and the presence of a *Cycloclypeus*-like initial part in microspheric forms of *Discocyclina* seems to rule out this idea (Brönnimann, 1945; Caudri, 1972; BouDagher-Fadel, 2008).

Most recently, Drooger (1993) suggested that the orthophragminids might have descended from a Cretaceous pseudorbitoid ancestor, such as the American *Vaughanina* (Fig. 5.1). This appears to be the most plausible proposal for both the discocyclinines and the orbitoclypeines, considering that we have shown above that the earliest orthophragminids are indeed found in the American Province. In the most advanced *Vaughanina* form, the annular chambers are developed in the outer part of the equatorial layer, and if *Vaughanina* should lose its radial plates, it would look very similar to the American discocyclinine genus *Athecocyclina*, with its poorly developed radial septula. The latter is the most primitive genus of the discocyclinines (Less, 1987), and has been described only from the American Paleocene (Vaughan, 1945). In addition, MacGillavry (1963) described rectangular equatorial chamberlets between the earlier spiral and the latter annular ones. These intermediate chambers are connected through radial stolons (Drooger, 1993). This is also shown in microspheric discocyclinines where the intermediate *Cycloclypeus*-like chambers seem to be the result of a lateral alignment after fusion of not so regular chamberlets (Sirotti, 1987).

From the existing observations, we therefore infer that the first American orthophragminids, the discocyclinine *Athecocyclina* and the orbitoclypeine *Neodiscocyclina*, appear to have evolved approximately contemporaneously in the middle Paleocene (no earlier than in the early Selandian, P3a, 61.6 Ma), most probably from rotaliid survivors of the end Cretaceous extinction event. They subsequently gave rise to a series of provincial American lineages (see Fig. 11).

We also infer from the subsequent first appearance of orthophragminid forms in West Africa in the Thanetian (P4b, 59.2 Ma), that the American forms migrated across the Atlantic to colonize the Tethyan Province just before that time. From the largely distinct natures of the American and Tethyan Provinces, we suggest that migration was a rare event, and for the entire Eocene, the two Provinces appear to have been isolated, and had forms that evolved independently. We suggest that migration may have been enabled for a limited period by the global sea-level low stands (Fig. 12), of the Selandian (P3b, 60.3 Ma).

During the middle Paleocene in the Americas, *Neodiscocyclina* gave rise to stellate-ribbed forms of *Asterocyclina*. Similar forms are not reported in the Tethys before the beginning of the Eocene (Ypresian, P5b, 56 Ma). The appearance of *Asterocyclina* in the Tethys might be an example of parallel evolution from the Tethyan form *Orbitoclypeus* by developing the stellate ribs or, perhaps more likely, its appearance might be as a result of the migration of the American *Asterocyclina* after the last major Paleocene sea-level drop (Fig. 12) in the late Thanetian (P5a, 56.4 Ma).

Subsequent sea level rise then presumably re-isolated the two Provinces, so by the latest Paleocene, several Tethyan orthophragminids lineages had developed and become distinct from their American counterparts. For examples, Western Tethyan species of orthophragminids developed various types of adauxiliary chamberlets, growth patterns and embryo types (see Ben Ismail-Latrache et al., 2014) and became more diverse than their American counterparts. They evolved different discocyclinine lineages than those of the Americas (e.g., the American *Pseudophragmina* and *Proporocyclina* never appeared in Tethys). Similarly, *Discocyclina s.s.*, *Nemkovella* and the *Orbitoclypeus* developed exclusively in the Tethyan Province.

In the Eocene successive forms of Tethyan orthophragminids continued their migration eastward through the open seaway from the Western Tethys into the Indo-Pacific, where they arrived up to 10 million years after their first appearance in the Western Tethys (see Fig. 11). Once in the tropical setting of the Indo-Pacific, with its diverse paleogeography, the migrants gave rise to similar, but local species, which evolved into isolated lineages parallel to, yet distinct from, those seen in the Western Tethys (see Fig. 11).

Although the South African Province may have been isolated or un-colonized in the late Paleocene, we conclude that there was a migration of primitive West African Tethyan or American orthophragminids to South Africa at the beginning of the Eocene (early Ypresian age, P5b, 56 Ma). This sudden colonization and creation of the South African Province might also be linked to the late Thanetian (P5a, 56.4Ma) sea-level drop (Fig. 12). The presence of Tethyan discocyclinines such as

Nemkovella in the early Ypresian (P5b–P6a, 56–54 Ma) of South Africa differentiates the assemblages of this province from those of the Americas. However, *Discocyclina davyi* n. sp. still shares some characters of the early American orbitoclypeine, and indeed it could be a relic, transitional between the American to the Tethyan forms. Subsequently during the Eocene, the Tethyan and South African Provinces were completely isolated from the American Province, yet the presence of combined Tethyan and American characteristics in the South African orthophragminids seem to emphasize their common American origin.

Finally, in the middle Eocene (late Lutetian–early Bartonian, P12, 42.3–40.2 Ma), the Tethyan discocyclinine, *Discocyclina africana* n. sp. became established for a short time in South Africa, before disappearing completely by the end of the Bartonian. This species might have evolved directly from the earlier South African discocyclinines or, as it appears 11 Ma later than those found in Birbury, it may have been introduced by a migration from Tethys, possibly enabled at that time by the major Late Lutetian (42.3 Ma) sea-level fall (Fig. 12).

CONCLUSIONS

By correlating first occurrences of orthophragminid lineages with defined PZ, we have established that they originated in the Americas in the early Selandian. They are not found in West Africa until the Thanetian and we suggest that these Tethyan forms are derived from American ancestors. We further hypothesize trans-Atlantic migrations of the orthophragminids coinciding with the major middle Selandian regression, and also possibly also after the last major Paleocene sea-level drop in the late Thanetian (Fig. 12).

We infer that major eustatic regressions would have reduced the effective width of the early Atlantic Ocean sufficiently to facilitate trans-oceanic migration, probably by embryonic stages, of

the first orthophragminids from the American Province to West Africa (see also for example BouDagher-Fadel & Price, 2014).

As the morphologies of American and Western Tethyan orthophragminids were crucially different between provinces, their evolutionary development was clearly independent, albeit parallel). We therefore conclude that after the initial trans-Atlantic migrations, the provinces again became isolated in the early Eocene (Ypresian), as sea-levels rose to a record high. During this time, the Tethyan orthophragminids continued their migration eastward through the open seaway from the Western Tethys into the Indo-Pacific, where they arrived sometimes up to 10 million years or so after their first appearance in the Western Tethys.

We have described three new South African orthophragminid species, and defined a new paleobiogeographic province. These forms remained small and never developed the large sizes and diversity of the Tethyan orthophragminids. The early Eocene South African forms were replaced by a Tethyan form in the middle Eocene, when again global sea-levels fell.

The origination of LBF stock in the Americas and their subsequent migration to Tethys and South Africa (Fig. 13) was not unique to the orthophragminids. The appearance of American stock in the Tethys after low sea-level stands has also been inferred for the nummulitids and, in more recent geological epochs, for the lepidocyclinids and the miogypsinids (see BouDagher-Fadel & Price 2010a; 2010b, 2013, 2014). The development of high resolution PZ dating, tied to accurate time scales, now opens up the possibility of correlating evolutionary events with paleoclimate and tectonic processes, and so is beginning to provide unprecedented insights into the phylogenetic and paleogeographic evolution of LBF and potentially other marine forms.

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FIGURE CAPTIONS

FIGURE 1. The morphological features of **1–6** megalospheric forms: **1–3** highlighting the embryonic apparatus of the equatorial section, **1** schematic figure of the embryonic apparatus, **2** *Discocyclina prattii* (Michelin), France, **3** *Discocyclina dispansa* Sowerby, Tibet. **4–6** axial sections: **4** Schematic figure showing the three layers of the test, **5** *Discocyclina sheppardi* Barker, Soldado Rock, Trinidad, **6** *Discocyclina* sp., the Hecho Group deposits of the Ainsa Basin, south central Pyrenees, Spain. **7–9** Microspheric forms: **7** schematic figure of the microspheric apparatus, **8** *Discocyclina* sp. France, **9** Oblique axial section of *Discocyclina dispansa* Sowerby, Tibet. Scale bars = 1mm, except for 1, scale bar = 0.25mm.

FIGURE 2. The morphological structures of different chambers of *Discocyclina*: **1, 3** *Discocyclina ranikotensis* Davies, Upper Ranikot Beds, Patala Formation in the Samana Range, Pakistan. **2** enlargement of the equatorial chambers of a solid specimen of *Discocyclina* sp., France. **4** *Discocyclina dispansa* Sowerby, Western India, Goojerat, at Baboa Hill, Wagé-ké-pudda, Cutch. **5** Sarawak in the Island of Borneo, **5A** *Discocyclina javana* (Verbeek), **5B** *Discocyclina* sp. **6** *Discocyclina* sp., Barbados, Joes River mudflows, Scotland District. **7** *Discocyclina sheppardi* Barker, Soldado Rock, Trinidad. In 1, 6, scale bars = 0.25mm, 2, scale bar = 0.02mm, 3, 5, scale bars = 1mm, 4, scale bar = 0.5mm.

FIGURE 3. External surface of tests of *Discocyclina*: **1–6** solid specimens of *Discocyclina*, GS/50, UCL Grimsdale Coll., France; **2** enlargement showing fine granules; **4** enlargement showing an inflated central umbo; **6** test surface showing a network of granules of the “marthae”-type rosette on the test surface, surface Bangladesh, Kopili Formation. **7** Solid specimen of *Discocyclina davyi* n. sp. showing surface test with strong pillars, largest concentrated in the centre, Birbury outcrop, South Africa. **8–9** solid specimens of *Discocyclina africana* n. sp. showing fine pillars scattered all over the

test, outcrop at, South Africa. **10–12** solid specimens of *Nemkovella mcmilliana* n. sp. showing strong pillars found mainly in the centre of the test. In 1, 2–3, 7, 11, scale bars = 1mm, 4, 5, 8, 12, scale bars = 0.5mm, 5, scale bar = 0.25mm, 6, 9, 10 = 0.12mm.

FIGURE 4. **1–3** Enlargements of *Discocyclusina davyi* n. sp. showing irregular, almost hexagonal chambers. **4–6** enlargement of the chambers of *Discocyclusina africana* n. sp. showing rectangular chamberlets with curved edges.

FIGURE 5. **1** *Discocyclusina tenuis* Douvillé, Eocene, Ypresian, Fontcouverte, France, UCL MF488. **2** *Discocyclusina prattii* (Michelin), Eocene, Lutetian, west-southwest of Fontcouverte, Aude France, UCL MF489, **A** oblique axial section, **B** equatorial section; **3–4** *Orbitoclypeus varians* (Kaufmann), Eocene, Bartonian, west-southwest of Fontcouverte, Aude, France, UCL MF490. **5–6** *Asterocyclusina stella* (Gümbel), late Eocene, the Akveren formation, Turkey, NHM P37910. **7–9** *Discocyclusina dispansa* Sowerby, **7** Eocene, Ypresian, Tibet, Zhepure Shan Formation, **8–9** Goojerat, Western India, at Baboa Hill, Wagé-ké-pudda, baboa hill, Cutch, NHM P539. Scale bars = 1mm.

FIGURE 6. **1–2** *Discocyclusina ranikotensis* Davies, microspheric form, late Palaeocene, Upper Ranikot Beds, **1** Pakistan, NHM coll., **2** North of Kotkai, Afghanistan, NHM coll. **3** **A.** *Discocyclusina ramaraoi* Samanta, **B.** *Turborotalia centralis* (Cushman & Bermudez), **C.** *Victoriella* sp., Batu Gading Limestone, Middle Baram, Sarawak, Borneo, late Eocene, Priabonian, YA S3–70. **4** **A.** *Discocyclusina ramaraoi* Samanta, **B.** *Discocyclusina dispansa* (Sowerby), **C.** *Discocyclusina omphalus* (Fritsch), Gading Limestone, Middle Baram, Sarawak in the Island of Borneo, late Eocene, Priabonian, YA S370. **5** **A.** *Discocyclusina dispansa* (Sowerby), **B.** *Subbotina* sp., **C.** *Globigerinatheka barri* (Brönnimann), Gading Limestone, Middle Baram, Sarawak, Borneo, late Eocene, P15b–P16, Priabonian, YA S370. **6** **A.** *Discocyclusina ramaraoi* Samanta, **B.** *Pellatispira* sp., Batu Gading Limestone, Middle Baram, Sarawak, Borneo, late Eocene, Priabonian, YA BG. Scale bars = 1mm.

FIGURE 7. **1** *Vaughanina* sp., Maastrichtian, Madruga, North Cuba Basin, UCL MF480. **2–3** *Discocyclusina peruviana* (Cushman), topotypes, Lobitos Formation, *Terebratula* Bed, Lagunitas,

Peru, (2) equatorial section, (3) axial section. UCL MF481–2. **4** *Hexagonocyclina cristensis* (Vaughan), early Eocene, Mexico, El Cristo well, Vera Cruz, topotype, NHM P32633,4. **5, 8–9** *Neodiscocyclina anconensis* (Barker), Eocene, Joes River mudflows, Scotland District, Barbados, **5** figured by Vaughan (1945), Eocene, UCL MF483; **8–9** UCL MF484. **6–7** *Discocyclina sheppardi* Barker, Paleocene, Soldado Rock, Trinidad, NHM P33350. **10–12** *Discocyclina californica* (Schenck), topotype, Vaquelos Formation, California, UCL MK486–7. Scale bars = 1mm.

FIGURE 8. **1–9** *Nemkovella mcmilliana* n. sp. Outcrop at Birbury (33°28'45"S 26°55'55"E, Eastern Cape, South Africa), early Ypresian, P5b–P6a, 56–54Ma, **6** holotype, UCL MF491, **1–5, 7–9**, paratypes UCL MF492–9. **10–14** *Discocyclina davyi* n. sp. Outcrop at Birbury (33°28'45"S 26°55'55"E, Eastern Cape, South Africa). **10**, Holotype UCL MF500. **11–14** oblique axial sections showing almost triangular and protruding pillars, distributed uniformly in the outer part of the test, UCL MF504. Scale bars = 1mm.

FIGURE 9. **1–11** *Discocyclina africana* n. sp. Outcrop at at Pato's Kop (also known as e'Kalikeni, 33°14'09.4"S 27°17'13.3"E, Eastern Cape, South Africa), **1** Holotype, UCL MF505, **2–11** UCLMF515. Scale bars = 1mm.

FIGURE 10. Enlargement of: **1** *Nemkovella mcmilliana* n. sp., **2** the almost isolepidine-type embryonic apparatus, and **3–5** the irregularly shaped equatorial chambers of *Nemkovella mcmilliana*, **6**, *Acarinina soldadoensis* (Brönnimann) is embedded in the test.

FIGURE 11. Range of major genera of orthophragminids in the four provinces.

FIGURE 12. Variation in sea level and temperature during the Paleogene, based on Miller et al. (2011).

FIGURE 13. The inferred migration routes of orthophragminids during the Paleogene, shown by black arrows, from the Americas (1), to the Western Tethys (2), and on to the Indo-Pacific (3), and to South Africa (4).