

Acarinina multicamerata n. sp. (Foraminifera): a new marker for the Paleocene–Eocene thermal maximum

ELISA GUASTI¹ & ROBERT P. SPEIJER²

¹ Department of Geoscience, Bremen University, PO Box 330 440, Bremen, Germany (Current address: Geobiology team – TNO, Princetonlaan, 6, 3584 CB Utrecht, The Netherlands, e-mail: elisa.guasti@tno.nl)

² Department of Geography and Geology, KU Leuven, Celestijnenlaan 200E, 3001 Leuven, Belgium (e-mail: Robert.Speijer@geo.kuleuven.be)

ABSTRACT – During the Paleocene–Eocene thermal maximum (PETM), low to mid-latitude planktic foraminiferal assemblages were characterized by blooms of the surface-dwelling *Acarinina*. Among this group a new ‘excursion taxon’ is identified, *Acarinina multicamerata* n. sp. Previously, this taxon was lumped together with *Acarinina sibaiaensis* El-Naggar. Considering that *A. sibaiaensis* already occurred prior to the hyperthermal event, both in open ocean and ocean margin deposits, it is proposed that these taxa are differentiated in order to avoid taxonomic and biostratigraphic ambiguities. *Acarinina multicamerata* n. sp. occurred exclusively during the PETM, hence this taxon represents an excellent biostratigraphic marker of the PETM, while its common occurrence in various marine settings makes it an excellent marker of Subzone P5b or its new equivalent zone E1. *J. Micropalaeontol.* 27(1): 5–12, May 2008.

KEYWORDS: planktic foraminifera, *Acarinina*, excursion taxa, Paleocene, PETM

INTRODUCTION

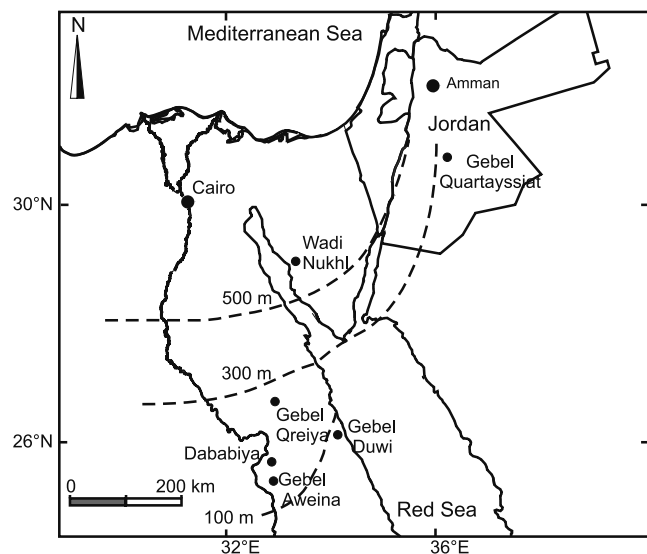
The Paleocene–Eocene thermal maximum (PETM) represents a period of extreme global warmth (Zachos *et al.*, 1993), associated with various biotic turnovers on land and in the sea. Among the latter is an evolutionary rejuvenation in planktic foraminifera, leading to short-lived species of *Acarinina* and *Morozovella* (Kelly *et al.*, 1996). During the PETM, planktic foraminiferal assemblages in open-marine environments worldwide are dominated strongly by *Acarinina*. Both in open ocean ODP sites and in the marginal Tethys, a number of authors have described the occurrence of new planktic foraminifera taxa, called ‘excursion’ taxa, at the PETM; these include *Acarinina sibaiaensis*, *A. africana* and *Morozovella allisonensis*. These are generally thought to have evolved during the early part of the PETM (Kelly *et al.*, 1996, 1998; Bolle *et al.*, 2000; Berggren & Ouda, 2003; Ouda *et al.*, 2003). Observations on Egyptian successions, however, show that *A. sibaiaensis* and *A. africana* (= *M. africana*) indeed bloom during the PETM, but had already evolved prior to this event (Speijer *et al.*, 2000; Guasti & Speijer, 2007), confirming the early observations of El-Naggar (1966), the author who erected these taxa.

This study examined material from upper Paleocene–lower Eocene successions in Egypt (Dababiya, Gebel Duwi, Gebel Aweina, Gebel Qreiya and Wadi Nukhl) and Jordan (Gebel Qurtassyat) (Figs 1, 2) in order to investigate the occurrence and taxonomy of excursion taxa. It was found that there are some ambiguities in the taxonomy of the PETM excursion taxa. In this paper, the longer-ranging species *A. sibaiaensis* is differentiated from a multi-chambered *Acarinina* species, which only occurred during the PETM. The latter is defined as *A. multicamerata* n. sp. In addition, environmental scanning electron microscope (ESEM) images of the holotypes of *A. sibaiaensis* and *A. africana* are provided. Images of these holotypes, as well as the holotype and paratype of *A. multicamerata* n. sp., were taken at the Natural History Museum of London (UK), using an ESEM with variable pressure (LEO 1455 VP), which allowed photography of specimens in a mounting slide without coating.

ACARININA SIBAIYAENSIS

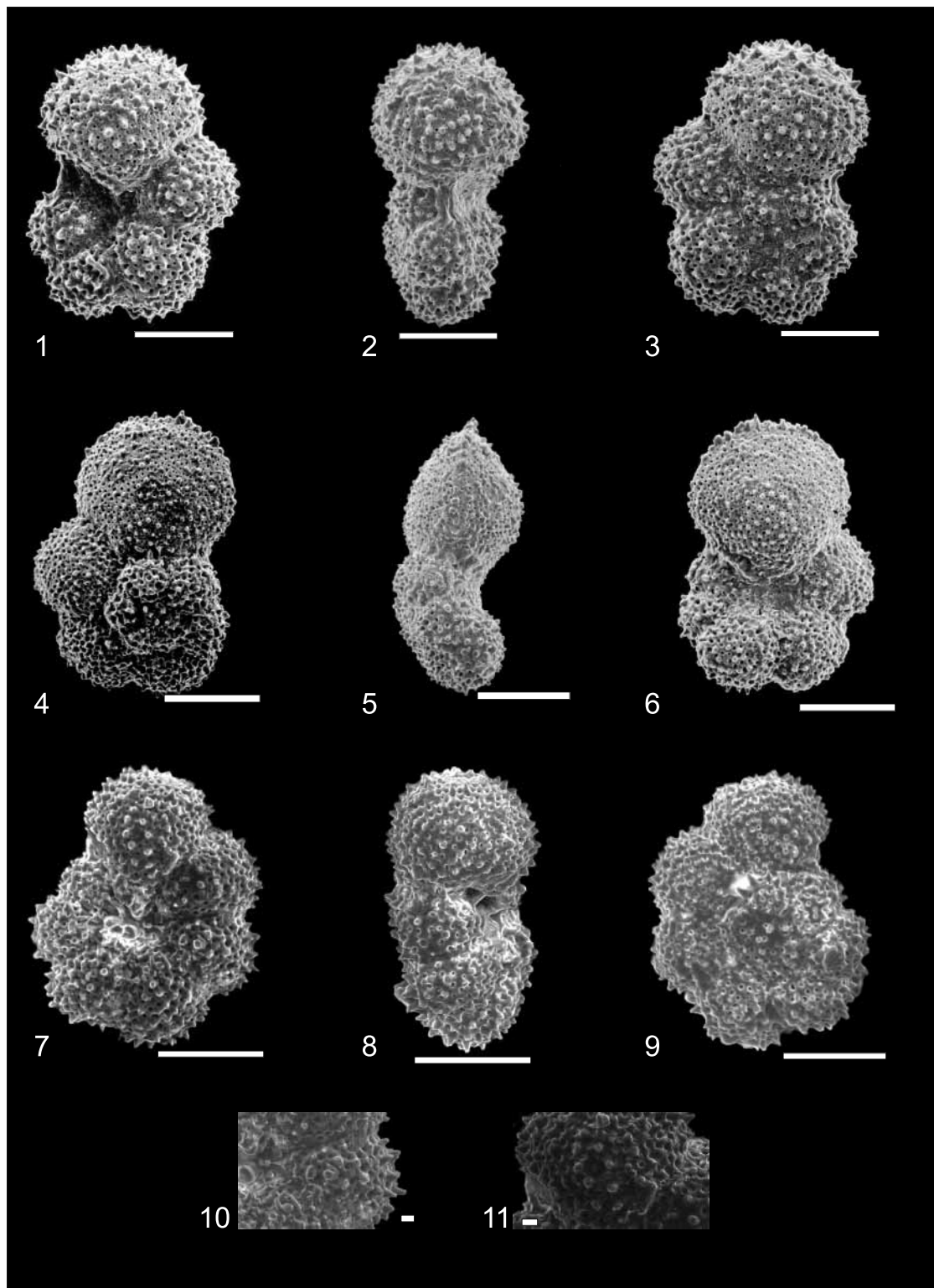
The holotypes of *Acarinina sibaiaensis* and *A. africana* were described originally by El-Naggar (1966) as *Globorotalia sibaiaensis* and *Globorotalia africana*, respectively (Pl. 1). He observed these species in the upper Paleocene, at Gebel Aweina in the Nile Valley, Egypt. In the original description, *Globorotalia sibaiaensis* was described as a compressed small, globular species, in which the last whorl is composed of 5.5 chambers, having a long narrow aperture. El-Naggar (1966) suggested that this taxon may have evolved from *G. perclara* Loeblich & Tappan (1957).

Our observations uncovered a number of problems on the evolution, morphology and range of *A. sibaiaensis* in the literature. For instance, Kelly *et al.* (1998) provided a very



Source: GEBCO.

Fig. 1. Location map of the studied profiles (black dots). The normal dashed lines indicate the estimated palaeobathymetry based on Speijer & Van der Zwaan (1994).



Explanation of Plate 1.

figs 1–3. *Acarinina sibaiyaensis* (El-Naggar) 1966, holotype: **1**, umbilical view; **2**, side view; **3**, spiral view. Collection number P.45628, the Natural History Museum, London (NHM). **figs 4–6.** *Acarinina africana* (El-Naggar) 1966, holotype: **4**, umbilical view; **5**, side view; **6**, spiral view. Collection number P.45593, the NHM. (figs 1–6 all from sample S. 50, 8 m above the base of the Esna Formation ('upper Owaina Shale') at Gebel Aweina ('Owaina'), Nile Valley, Egypt.) **figs 7–11.** *Acarinina multicamerata* n. sp., holotype: **7**, umbilical view; **8**, side view; **9**, spiral view; **10, 11**, details of the wall texture (scale bar 10 μ m). From sample B13+8–12, 15 m above the base of the Esna Formation at Gebel Duwi, Red Sea Coast, Egypt. Collection number PF 67590, the NHM. Scale bar represents 100 μ m, unless otherwise specified.

Berggren *et al.* (2006) re-described *A. sibaiyaensis* based on material from a couple of ODP cores, most notably from Bass River, New Jersey. In their description these authors considerably widened the concept of *A. sibaiyaensis* by including specimens with much more numerous chambers to a whorl. In contrast, El-Naggar's holotype is comprised of 5.5 chambers in the last whorl, whereas one of his paratypes (depicted here in Pl. 2) has only 4 chambers in the last whorl. Apparently the specimens of El-Naggar came from an upper Paleocene population with relatively few chambers to a whorl. This is the kind of variation that was also observed for *A. sibaiyaensis* in upper Paleocene deposits in Egypt. Berggren *et al.* (2006) studied lowermost Eocene populations of flat-spined *Acarinina* and proposed intergradations between typical specimens of *A. sibaiyaensis* conformable with El-Naggar's concept and a variety with more numerous chambers in the last whorl. The latter variety has been observed associated with the PETM also by various other authors (i.e. Kelly *et al.*, 1996, 1998; Pardo *et al.*, 1999; Arenillas *et al.*, 2004) and was also identified as *A. sibaiyaensis*.

In the current authors' view the variety with 6–9 chambers in the last whorl qualifies as a new species, *Acarinina multicamerata* n. sp., described below. The concept of this taxon includes specimens 7, and 9–14 of plate 9.21 of Berggren *et al.* (2006). Besides the larger number of chambers in the last whorl, these specimens have a more rounded outline and a wider umbilicus compared with *A. sibaiyaensis*. All other specimens depicted by Berggren *et al.* (2006) seem to represent transitional forms between *A. sibaiyaensis* and *A. multicamerata* in having features typical of both these specimens. This reinforces the idea that during the PETM diversification of muricate taxa (*Acarinina*, *Morozovella*) occurred (Kelly *et al.*, 1998) and that a variety of flat-spined *Acarinina* bloomed. Before the PETM, morphological variability was subdued and only the typical *A. sibaiyaensis* occurred sporadically. During the PETM *A. multicamerata* diverged from *A. sibaiyaensis*.

Lumping these two morphologically distinct taxa into one species would also lead to a loss of stratigraphic resolution. *Acarinina multicamerata* has been observed exclusively within PETM beds. *A. sibaiyaensis* and *A. africana* (by some considered as *Morozovella* because of the slightly keeled last chamber(s)) already appeared during the late Paleocene as indicated by the data of El-Naggar (1966). He recorded these taxa from the topmost metres of the upper Paleocene 'Middle Owaina Chalk' (=Tarawan Formation) and the lowermost 14 m of the overlying 'Upper Owaina Shale' (=Esna Formation) in the Aweina section (El-Naggar, 1966, fig. 18). This corresponds to a range from Zone P4 to the lower part of Zone P5 (Subzone P5a and possibly slightly higher) of Berggren *et al.* (1995), when compared to more recent studies on this section (Speijer *et al.*, 1995, 2000; Ouda *et al.*, 2003). Observations have confirmed the occurrence of *A. africana* and *A. sibaiyaensis* in Aweina at least 40 cm below the P/E boundary (Pl. 2, Table 1). El-Naggar's observations lower in the Aweina section cannot be confirmed, because planktic taxa in samples from below the PETM (upper Tarawan Fm. and lower Esna Fm) are poor in number and preservation (Speijer & Schmitz, 1998). Ouda *et al.* (2003) also observed these taxa below the unconformity at the basis of the 'calcarenitic bed', which, according to earlier studies (Speijer *et al.*, 1995,

2000; Schmitz *et al.*, 1997), marks the P/E boundary. In contrast to the opinion of Ouda *et al.* (2003), who considered this interval an early part of the PETM, the beds below the 'calcarenitic bed' belong to the uppermost Paleocene as indicated by the position of the carbon isotopic excursion coinciding with the unconformity (Speijer *et al.*, 1995; Guasti & Speijer, 2007).

This view is corroborated further by recent preliminary observations of pre-PETM occurrences of these taxa in ODP Hole 1220, equatorial Pacific (Norris & Nunes, 2004). In conclusion, the widely adopted reference to *A. africana* and *A. sibaiyaensis* as 'excursion taxa' is erroneous. *Morozovella allisonensis* and *Acarinina multicamerata* n. sp. are thus far the only planktic 'excursion taxa' exclusively observed in PETM beds.

SYSTEMATIC DESCRIPTIONS

Suborder **Globigerinida** Blow, 1979

Superfamily **Globigerinacea** Carpenter, Parker & Jones, 1862

Family **Truncorotaloididae** Loeblich & Tappan, 1961

Subfamily **Truncorotaloidinae** Loeblich & Tappan, 1961

Genus *Acarinina* Subbotina, 1953

Acarinina multicamerata n. sp.

(Pl. 1, figs 7–11; Pl. 2, figs 4–15)

1996 *A. sibaiyaensis* (El-Naggar); Kelly *et al.*: 424, figs 2–1a to 2-1b.

1998 *A. sibaiyaensis* (El-Naggar); Kelly *et al.*: 145, fig. 5c; 150 fig. 9D–E (hypotype).

1999 *A. sibaiyaensis* (El-Naggar); Pardo *et al.*: 44, figs 19–20.

2006 *A. sibaiyaensis* (El-Naggar); Berggren *et al.*: chapter 9, pl. 9.21, figs 7, 9–14.

Non *Globorotalia sibaiyaensis* El Naggar (1966): 235, pl. 23, figs 6a–c (holotype).

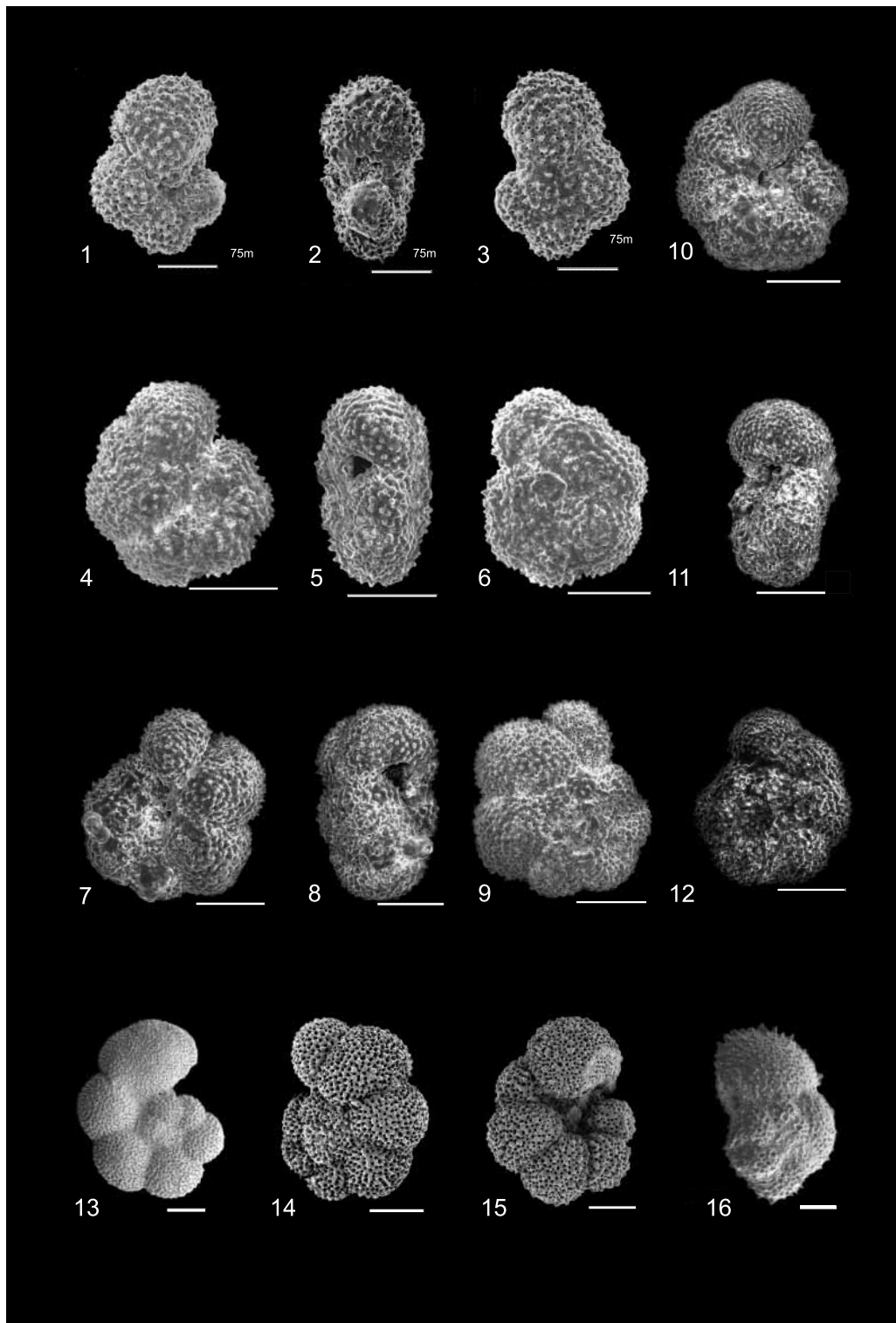
Type species. *Acarinina multicamerata* n. sp.

Derivation of name. The species name *multicamerata* derives from the numerous chambers in the final whorl, which characterize this taxon.

Diagnosis. Test coiled in a low trochospire, containing 6–9 chambers in the final whorl. The chambers are globular and gradually increase in size. Dorsally flattened tests with rounded and lobate peripheral margin. The umbilicus is generally deep. The sutures are radial on both sides and strongly depressed, particularly on the ventral side. The aperture is an interior-marginal, extraumbilical–umbilical low elongate arch extending from the umbilicus to the periphery. Wall texture: non spinose, muricate.

Locality and horizon. Gebel Duwi, 26°05' N and 34°07' E, 12 km east of the town of Quseir (Red Sea Coast, Egypt). Sample BI3+8–12, collected from the 30 cm thick pink coprolite-rich marl bed, 15 m above the base of the Esna Formation. This bed appears to be an equivalent to Dababiya Quarry bed 3 in the GSSP section of Dababiya (Dupuis *et al.*, 2003).

Age. Base Ypresian.



Explanation of Plate 2.

figs 1–3. *Acarinina sibaiaensis* (El Naggar) 1966, paratype: **1**, umbilical view; **2**, side view; **3**, spiral view. Collection number P.45629, the NHM (scale bar 75 μ m). **figs 4–6.** *Acarinina multicamerata* n. sp., paratype 1: **4**, umbilical view; **5**, side view; **6**, spiral view. Collection number PF 67591, the NHM. **figs 7–9.** *Acarinina multicamerata* n. sp., paratype 2: **7**, umbilical view; **8**, side view; **9**, spiral view. Collection number PF 67592, the NHM. **figs 10–12.** *Acarinina multicamerata* n. sp., paratype 3: **10**, umbilical view; **11**, side view; **12**, spiral view. Collection number PF 67593, the NHM. **figs 13–15.** *Acarinina multicamerata* n. sp.: **13**, from sample B13+12–14 in the Esna Formation at Gebel Duwi, Red Sea Coast, Egypt; **14, 15** and figs 4–12 all from sample B13+8–12, 15 m above the base of the Esna Formation at Gebel Duwi, Red Sea Coast, Egypt. **fig. 16.** *Acarinina africana*: from sample O95-30-40 in the Esna Formation at Gebel Aweina, Egypt (scale bar 50 μ m). Scale bar represents 100 μ m unless otherwise specified.

Samples	Depth (m)	$\delta^{13}\text{C}$ (whole rock)	<i>A. multicamerata</i>	<i>A. sibaiyaensis</i>	P/E boundary
Gebel Qurtassyat					
JQ 66	62.5	-0.27			
JQ 65	61.9	-1.92	X		
JQ 64	61.1	-2.19	X		60.8 m
hiatus					
JQ 63	60.5	-0.18			
Gebel Dababyia					
DBH 4.5	4.5	-25.05			
DBH 4	4	-25.59	X	X	
DBH 3.75	3.75	-25.44	X	X	
DBH 3.25	3.25	-26.39	X	X	
DBH 3.12	3.12		X		
DBH 3	3	-27.18 dissolution			
DBH 2.72	2.72	-27.33	X	X	
DBH 2.52	2.52	dissolution			
DBH 2.3	2.3	-27.14	X		
DBH 2.25	2	-26.98 dissolution			
DBH 2.17	2.25				
DBH 1.8	1.8	-26.68			
DBH 2	2	-25.82			
DBH 1.65	1.65	-26.06			
DBH 1.6	1.6	-25.38			
DBH 1.57	1.57	-25.61			1.57 m
DBH 1.56	1.56	-24.39			
Wadi Nukhl					
S 1374	6.8	-0.1			
S 1373	6.55	-0.696	X		
S 1372	6.3	-1.389	X	X	6.2 m
S 1371	6.05	1.756			
S 1370	5.8	0.776			
Gebel Aweina					
32-35	133.5	-0.21			
21-25	123				
17-21	119	-0.34			
15-18	116.5				
9-12	110.5				
7-9	108	-0.45			7 cm (omission surface)
6-7	106.5				
2-6	104				
0-2 (bur)	101				
0-2	101				
-0-2	99	1.15			
-2-6	96				
-6-10	92	1.05			
-10-13	88.5				
-13-15	86				
-15-20	82.5				
-20-25	77.5	1.1		X	
-25-30	72.5				
-30-40	65	1.05		X	
Gebel Qreiya					
271185/22	16.4	0.25			
271185/23	13.8	-0.23			
271185/24	11.8	0.81			
271185/25	9.4	-1.49		X	
271185/26	8.4	-2.46	X	X	8 m
271185/28	5.4	-1.12			
Gebel Duwi					
1030	60	-2.28			
14-16	15	-2.59	X	X	
8-12	10	-2.81	X	X	
1029	10	-2.73	X	X	
0-3	1.5	-3.56	X	X	0 cm
1028	-40	-1.33			
1027	-90	-0.12			
1026	-140	-0.3			
1025	-190	-0.23		X	

The data were published previously in Guasti & Speijer (2007), Dupui *et al.* (2003), Speijer *et al.* (1997, 2000) and Schmitz *et al.* (1996).

Table 1. Samples list and depths across the Paleocene/Eocene boundary for each locality, together with the $\delta^{13}\text{C}$, the occurrences of *A. sibaiyaensis* and *A. multicamerata* and the position of the Paleocene/Eocene boundary.

Distribution. Tropical-subtropical latitudes.

Dimensions. Maximum diameter: 253 µm; minimum diameter: 218 µm; thickness: 118 µm.

Stratigraphic range. Restricted to the Paleocene–Eocene thermal maximum (DQB2–DQB4 in the GSSP section of Dababiya), in the middle part of Zone P5 sensu Berggren *et al.* (1995) or Zone E1 of Berggren & Pearson (2005). The range of *Acarinina multicamerata* replaces *M. allisonensis* as the marker species of Subzone P5b. The common occurrence of this species makes it a more suitable subzonal marker than the occasionally rare *M. allisonensis*, as proposed by Speijer *et al.* (2000). It would also be a better replacement for *A. sibaiaensis* as the zonal marker of Zone E1 in the scheme of Berggren & Pearson (2005). As pointed out above, *A. sibaiaensis* is not restricted to the lowermost Eocene and, consequently, E1 as defined now would span the uppermost Paleocene to lowermost Eocene, at least at Aweina and Duwi and, according to the data of Norris & Nunes (2004), also at ODP Site 1220 in the central Pacific

Remarks. *Acarinina multicamerata* differs from *A. sibaiaensis* in several features. *A. multicamerata* has a larger number of chambers per whorl and the outline is overall more rounded. The chambers increase more gradually in size compared to *A. sibaiaensis*. In some specimens, the wall texture of *A. multicamerata* is dominated by the large pores, instead of being covered with spiky pustules. The umbilicus is generally narrower in *A. sibaiaensis*, resulting in a more tightly coiled test compared to *A. multicamerata*. The number of chambers (6), a rounded outline and a wider umbilicus are also evident in the specimens of Berggren *et al.* (2006, pl. 9.21, figs 9–14), suggesting the attribution of these specimens to *A. multicamerata*. All the other specimens seem to represent a transitional form between *A. sibaiaensis* and *A. multicamerata*.

Origin of the species. El-Naggar suggested that *A. sibaiaensis* evolved from *G. perclara* Loeblich & Tappan (1957), which already occurred in the Danian, but it has been reinterpreted as benthic foraminifera by Liu *et al.* (1998). Instead, Kelly *et al.* (1998) suggested that *A. sibaiaensis* (= *A. multicamerata*) evolved from *A. soldadoensis*. Berggren *et al.* (2006) proposed *Acarinina esnehensis* as the ancestor of *A. sibaiaensis*. The possibility that *A. sibaiaensis* could derive from *A. esnehensis* is not excluded, although the morphology is distinctively different.

It is suggested that *A. multicamerata* is derived from *A. sibaiaensis*, as evidenced in the similar wall-textures and in the occurrence of transitional specimens. *A. multicamerata* diverged from the parent species to adapt to different environmental conditions.

Repository. The holotype (PF 67590) and three paratypes (PF 67591, PF 67592, PF 67593) are deposited at the Natural History Museum of London (UK).

CONCLUSION

The studied material indicates that *Acarinina multicamerata* is the only known *Acarinina* species occurring exclusively within the PETM beds. It can be distinguished easily from its precursor

species *A. sibaiaensis*, with which it has been confused previously. Hence, it is proposed that *A. multicamerata* n. sp. and *M. allisonensis* are presently the only true PETM excursion taxa among planktic foraminifera. Because of the exclusive and common occurrence within the PETM, *A. multicamerata* acts as an excellent marker of Subzone P5b or E1, replacing the less common *M. allisonensis* or the longer-ranging *A. sibaiaensis*.

ACKNOWLEDGEMENTS

The authors warmly thank Drs John Whittaker, Andy Henderson and Ben Williamson (all of the Natural Museum, London) for providing photographic material of the holotypes and paratypes of *Acarinina multicamerata*, *A. sibaiaensis* and *A. africana*. Thoughtful suggestions from Clay Kelly, an anonymous reviewer and the editor John Gregory (PetroStrat Ltd) improved the manuscript greatly.

Manuscript received 6 October 2005

Manuscript accepted 29 May 2007

REFERENCES

- Arenillas, I., Alegret, L., Molina, E. & Ortiz, S. 2004. Planktic and small benthic foraminiferal correlation of the Paleocene/Eocene boundary across the Tethys area (Spain, Italy, Israel, Egypt). Poster presented at IGC32, Florence.
- Berggren, W.A. & Ouda, K. 2003. Upper Paleocene–lower Eocene planktic foraminiferal biostratigraphy of the Dababiya section, Upper Nile Valley (Egypt). In: Ouda, K. & Aubry, M.-P. (Eds), The upper Paleocene–lower Eocene of the upper Nile Valley: part 1, stratigraphy. *Micropaleontology*, **49**: 61–92.
- Berggren, W.A. & Pearson, P.N. 2005. A revised tropical to subtropical Paleogene planktic foraminiferal zonation. *Journal of Foraminiferal Research*, **35** (4): 279–298.
- Berggren, W.A., Kent, D.V., Swisher, C.C. III & Aubry, M.-P. 1995. A revised Cenozoic geochronology and chronostratigraphy. In: Berggren, W.A., *et al.* (Eds), *Geochronology, time scales and global stratigraphic correlation*. SEPM (Society for Sedimentary Geology) Special Publication, **54**: 129–212.
- Berggren, W.A., Pearson, P.N., Huber, B.T. & Wade, B.S. 2006. Taxonomy, Biostratigraphy and Phylogeny of Eocene *Acarinina*. In: Pearson, P.N., Olsson, R.K., Huber, B.T., Hemleben, C. & Berggren, W.A. (Eds), *Atlas of Eocene Planktic Foraminifera*. Cushman Foundation Special Publication, **41**: 257–326.
- Blow, W.H. 1979. *The Cainozoic Globigerinida*. E.J. Brill, Leiden, The Netherlands, 1413pp.
- Bolle, M.-P., Pardo, A., Hinrichs, K.-U., *et al.* 2000. The Paleocene–Eocene transition in the marginal north-eastern Tethys (Kazakhstan and Uzbekistan). *International Journal of Earth Science*, **89**: 390–414.
- Brönniman, P. 1952. Trinidad Paleocene and Lower Eocene Globigerinidae. *Bulletins of American Paleontology*, **34**: 1–34.
- Carpenter, W.B., Parker, W.K. & Jones, T.R. 1862. *Introduction to the Study of the Foraminifera*. Ray Society Publications, London, 139pp.
- Dupuis, C., Aubry, M.-P., Steurbaut, E., *et al.* 2003. The Dababiya Quarry section: lithostratigraphy, clay mineralogy, geochemistry and paleontology. In: Ouda, K. & Aubry, M.-P. (Eds), The upper Paleocene–lower Eocene of the upper Nile Valley: part 1 stratigraphy. *Micropaleontology*, **49**: 41–59.
- El-Naggar, Z.R. 1966. Stratigraphy and planktic foraminifera of the upper Cretaceous–lower Tertiary succession in the Esna–Idfu region, Nile Valley, Egypt, U. A. R. *British Museum (Natural History), Bulletin*, **2**: 1–235.
- Guastrini, E. & Speijer, R.P. 2007. The Paleocene–Eocene thermal maximum in Egypt and Jordan: an overview of the planktic foraminiferal record. In: Monechi, S., Coccioni, R. & Rampino, M. (Eds), *Large ecosystem perturbations: causes and consequences*. GSA Special Publication, **424**: 53–67.

- Kelly, C.D., Bralower, T.J., Zachos, J.C., Premoli Silva, I. & Thomas, E. 1996. Rapid diversification of planktonic foraminifera in the tropical Pacific (ODP Site 865) during the late Paleocene thermal maximum. *Geology*, **24** (5): 423–426.
- Kelly, C.D., Bralower, T.J. & Zachos, J.C. 1998. Evolutionary consequences of the latest Paleocene thermal maximum for tropical planktonic foraminifera. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **141**: 139–161.
- LeRoy, L.W. 1953. Biostratigraphy of the Maqfi section, Egypt. *Geological Society of America Memoirs*, **54**: 31.
- Liu, C., Olsson, R.K. & Huber, B.T. 1998. A benthic paleohabitat for *Praepararotalia* gen. nov. and *Antarcticella* Loeblich and Tappan. *Journal of Foraminiferal Research*, **28** (1): 3–18.
- Loeblich, A.R. Jr & Tappan, H. 1957. *Planktonic foraminifera of Paleocene and early Eocene age from the Gulf and Atlantic Coastal Plains. Studies in foraminifera: Part 1 – Planktonic foraminifera*. United States National Museum Bulletin, **251**: 191pp.
- Loeblich, A.R. Jr & Tappan, H. 1961. Suprageneric classification of the Rhizopodea. *Journal of Paleontology*, **35**: 245–330.
- Lu, G., Keller, G. & Pardo, A. 1998. Stability and change in Tethyan planktic foraminifera across the Paleocene–Eocene transition. *Marine Micropaleontology*, **35**: 203–233.
- Norris, R.D. & Nunes, F. 2004. Productivity maximum across the Paleocene–Eocene boundary supported by faunal evidence. Abstract presented at the ICP 8, Biarritz, France, p.48.
- Olsson, R.K., Hemleben, C., Berggren, W.A. & Huber, B.T. 1999. Atlas of Paleocene planktonic foraminifera. *Smithsonian Contributions to Paleobiology*, **85**: 254pp.
- Ouda, K., Berggren, W.A. & Saad, K. 2003. The Gebel Oweina and Kilabiya sections in the Idfu–Esna area, Upper Nile Valley (Egypt). In: Ouda, K. & Aubry, M.-P. (Eds), *The upper Paleocene–lower Eocene of the Upper Nile Valley: part 1, stratigraphy*. *Micropaleontology*, **49**: 147–166.
- Pardo, A., Keller, G. & Oberhänsli, H. 1999. Paleocologic and paleoceanographic evolution of the Tethyan realm during the Paleocene–Eocene transition. *Journal of Foraminiferal Research*, **29** (1): 37–57.
- Schmitz, B., Speijer, R.P. & Aubry, M.-P. 1996. Latest Paleocene benthonic extinction event on the southern Tethyan shelf (Egypt): foraminiferal stable isotope ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) records. *Geology*, **24**: 347–350.
- Schmitz, B., Charisi, S.D., Thompson, E.I. & Speijer, R.P. 1997. Barium, SiO_2 (excess), and P_2O_5 as proxies for biological productivity in the Middle East during the Paleocene and the latest Paleocene benthic extinction event. *Terra Nova*, **9**: 95–99.
- Speijer, R.P. & Van der Zwaan, G.J. 1994. The differential effect on the Paleocene/Eocene boundary event: extinction and survivorship in shallow and deep water Egyptian benthic foraminiferal assemblages. In: *Extinction and recovery patterns in benthic foraminiferal paleocommunities across the Cretaceous/Paleogene and Paleocene/Eocene boundaries*. *Geologica Ultraiectina*, **124**: 121–168.
- Speijer, R.P. & Schmitz, B. 1998. A benthic record of Paleocene sea-level and trophic/redox conditions at Gebel Aweina, Egypt. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **137**: 79–101.
- Speijer, R.P., Schmitz, B., Aubry, M.-P. & Charisi, S.D. 1995. The latest Paleocene benthic extinction event: punctuated turnover in outer neritic foraminiferal faunas from Gebel Aweina, Egypt. *Israel Journal of Earth Science*, **44**: 207–222.
- Speijer, R.P., Schmitz, B. & Van der Zwaan, G. 1997. Benthic foraminiferal extinction and repopulation in response to latest Paleocene Tethyan anoxia. *Geology*, **25**: 683–686.
- Speijer, R.P., Schmitz, B. & Luger, P. 2000. Stratigraphy of late Paleocene events in the Middle East: implications for low- to middle-latitude successions and correlations. *Journal of the Geological Society, London*, **157**: 37–47.
- Subbotina, N.N. 1953. Iskopaemye foraminifery SSSR (Globigerinidy, Khantkeninidy i Globalotaliidy). *Trudy Vsesoyznogo Neftyanogo Nauchno-Issledovatel'skogo Geologo-Razvedochnogo Instituta (VNIGRI)*, **76**: 1–296.
- Zachos, J.C., Lohmann, K.C., Walker, J.C.G. & Wise, S.W. 1993. Abrupt climate change and transient climates during the Paleocene: a marine perspective. *The Journal of Geology*, **101**: 191–213.