On the stratigraphical and palaeobiogeographical significance of Borelis melo melo (Fichtel & Moll, 1798) and B. melo curdica (Reichel, 1937) (Foraminifera, Miliolida, Alveolinidae)

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ABSTRACT – The stratigraphical and palaeobiogeographical significance of Borelis melo melo (Fichtel & Moll, 1798) and B. melo curdica (Reichel, 1937) is re-assessed in the light of a taxonomic review. Borelis melo melo ranges at least throughout the Miocene, whereas B. melo curdica is restricted to the late Early to Middle Miocene. Both sub-species occur only in the Indo-Pacific Province in the late Early Miocene (‘early’ Burdigalian), but in both the Indo-Pacific and Mediterranean provinces in the latest Early–early Middle Miocene (‘middle’ Burdigalian–Langhian), implying a marine (re-)connection between the two regions at this time. J. Micropalaeontol. 25(2): 175–185, November 2006.

KEYWORDS: Borelis, biostratigraphy, palaeobiogeography

INTRODUCTION
The genus Borelis is a stratigraphically important constituent of the larger benthic foraminiferal (LBF) faunas of the Eocene–Holocene (see, for instance, Adams, 1970). It is represented in all of the low-latitude shallow-water palaeobiogeographical provinces of the period, namely the Mediterranean, Indo-Pacific and Caribbean provinces (Adams, 1967; Jones, 1999, and additional references cited therein), which latter two, incidentally, were contiguous prior to the formation of the Isthmus of Panama in the Pliocene. Modern LBF species live in areas with minimum sea-surface temperatures greater than 18°C, and are essentially restricted to the tropics (Langer & Hottinger, 2000). They also host photosynthetic algal symbionts, and are restricted to sea-surface temperatures greater than 18°C. They are also restricted to the tropics (Langer & Hottinger, 2000). They also host photosynthetic algal symbionts, and are restricted to sea-surface temperatures greater than 18°C. They are also restricted to the tropics (Langer & Hottinger, 2000). They also host photosynthetic algal symbionts, and are restricted to sea-surface temperatures greater than 18°C. They are also restricted to the tropics (Langer & Hottinger, 2000). They also host photosynthetic algal symbionts, and are restricted to sea-surface temperatures greater than 18°C. They are also restricted to the tropics (Langer & Hottinger, 2000). They also host photosynthetic algal symbionts, and are restricted to sea-surface temperatures greater than 18°C. They are also restricted to the tropics (Langer & Hottinger, 2000). They also host photosynthetic algal symbionts, and are restricted to sea-surface temperatures greater than 18°C. They are also restricted to the tropics (Langer & Hottinger, 2000). They also host photosynthetic algal symbionts, and are restricted to sea-surface temperatures greater than 18°C. They are also restricted to the tropics (Langer & Hottinger, 2000).

At least sixteen nominal species and sub-species were considered by Samanta et al. (1990) or are considered by the present authors to be attributable to Borelis (note that, following Samanta et al. (1990) and other authors cited therein, a number of additional nominal species from the Upper Cretaceous and Lower Tertiary of the Caribbean Province have been excluded). Unfortunately, the precise nature of the type species, Nautilus melo melo Fichtel & Moll, 1798, which was first described and illustrated, inadequately by modern standards, as long ago as the late eighteenth century, remained poorly known until comparatively recently, with the result that many nominal species described in the interim are candidate junior synonyms.

The purpose of this paper is to review the taxonomy of the sub-species Borelis melo melo and B. melo curdica, and, in the light of this review, to re-assess their stratigraphical and palaeobiogeographical significance.

SYSTEMATIC MICROPALAEONTOLOGY
Order Miliolida Calkins, 1909
Family Alveolinidae Ehrenberg, 1839

Diagnosis. Wall porcellaneous, imperforate. Test free, typically large (macroscopically visible), spherical to ellipsoidal depending upon degree of elongation along axis of coiling. Proloculus followed by spiral tube or flexostyle; later chambers initially irregularly coiled, at least in microspheric generation, later becoming planispiral. Chambers numerous, may be divided into one or more rows of chamberlets by means of secondary partitions or septula parallelising direction of coiling; those of upper (attic) row(s) smaller than those of lower row; septula of adjacent chambers either continuous or alternating. Basal layer thickening (‘flosculinization’) may be developed. External apertures generally arranged in one or more rows; apertural teeth present or absent.

Genus Borelis de Montfort, 1808

Type species. Borelis melonoides de Montfort, 1808≡Nautilus melo Fichtel & Moll, 1798; original designation.

Synonym. Neoalveolina Silvestri, 1928 [Alveolina bradyi Silvestri, 1927≡Nautilus melo Fichtel & Moll, 1798; subsequent designation (Bakx, 1932)].

Diagnosis. Chamberlets generally arranged in single row, but incipient attic chamberlets separated by Y-shaped septula developed in some forms; septula of adjacent chambers continuous. External apertures generally arranged in single row, but a second row of intercalar apertures developed in one form. Basal layer thickening (‘flosculinization’) not developed.

Stratigraphical distribution. Eocene to Holocene.

Palaeobiogeographical distribution. Mediterranean, Indo-Pacific and Caribbean provinces.

Remarks. As Alveolina bradyi Silvestri, 1927 is the type species by the subsequent designation of Borelis de Montfort, 1808, as bradyi is a junior synonym of melo, Neoalveolina is consequently a junior synonym of Borelis.
Borelis melo melo (Fichtel & Moll, 1798) (Pl. 1, fig. 1)

1798 Nautilus melo var. alpha Fichtel & Moll: 118; pl. 24, figs a–f (non var. beta).
1846 Alveolina melo d’Orbigny: 147, pl. 7, figs 15–16.
1928 Alveolina melo d’Orbigny (sic); Silvestri: pl. 1, figs 11–12.
1928 Alveolina melo Brady (sic); Silvestri: pl. 1, figs 13–16.
1937 Neoalveolina melo (Fichtel & Moll); Reichel: 105–108, pl. 10, figs 8–9; text-fig. 22 (pl. 10, fig. 8=neotype designated by Smout, 1963).
1957 Borelis melo (Fichtel & Moll); Cole: 766; pl. 240, fig. 2.
1962 Borelis melo (Fichtel & Moll); Eames et al.: pl. 7, fig. f.
1963 Neoalveolina melo (Fichtel & Moll); Souaya: 445–446, pl. 58, fig. 20.
1966 Borelis melo melo (Fichtel & Moll); Reiss & Gvirtzman: pl. 1, figs 1–7, pl. 2, fig. 2.
1966 Neoalveolina Saavedra: figs. 19A–B, 20.1.
1968 Borelis melo (Fichtel & Moll); Azema et al.: 447, pl. 27, figs 1–8.
1968 Borelis melo (Fichtel & Moll); Korecz-Laky: 96, pl. 6, fig. 6, pl. 7, fig. 4.
1975 Borelis melo melo (Fichtel & Moll); Ctyroky et al.: 40, text-figs 1–2, 5–6.
1978 Borelis melo melo (Fichtel & Moll); Karim: pl. 2, figs 2–4.
1982 Borelis melo (Fichtel & Moll); Grasso et al.: pl. 2, fig. D (left centre).
1983 Borelis melo (Fichtel & Moll); Dullo et al.: pl. 1, fig. 5.
1983 Borelis melo (Fichtel & Moll); Gagic: figs 2–4.
1984 Borelis melo (Fichtel & Moll); Rögl & Hansen: 71–72, pl. 29, figs 5–6; pl. 30, figs 1–4 (pl. 30, figs 1–2=unnecessary neotype).
1985 Borelis melo melo (Fichtel & Moll); Al-Hashimi & Amer: pls 145, 148.
1985 Alveolina melo d’Orbigny (sic); Papp & Schmid (pars): 55–56, pl. 7, figs 1–2; pl. 47, figs 1, 22, 3, 6.
1987 Borelis melo (Fichtel & Moll); Loeblich & Tappan (pars): pl. 374, figs 1–6 (not pl. 375, fig. 2).
1988 Borelis melo (Fichtel & Moll); Sartorio & Venturini: unnumbered plates (on p. 169).
1990 'Miliolid foraminifera'; Jenkyns et al.: fig. 69.
1993 Borelis melo melo (Fichtel & Moll); Buchbinder et al.: fig. 2E.
1997 Borelis melo (Fichtel & Moll); Betzler & Schmitz: 211–212, figs 3e–g.
1998 Borelis melo melo (Fichtel & Moll); Cicha et al.: 86, pl. 19, figs 10, 13, 15; pl. 20, figs 1–2.
1999 Borelis melo (Fichtel & Moll); Hughes et al.: fig. 22(a).
2000 Borelis melo (Fichtel & Moll); Hughes et al.: fig. 22.

Plate 1.

Explanation of Plate 1. fig. 1. Borelis melo melo (Fichtel & Moll, 1798). Axial section, approximately ×22. Neotype designated by Smout (1963). Leithakalk (‘Tortonien’, in context probably early Middle Miocene, Badenian), Bujtur, Transylvania. Collection Schlumberger, La Sorbonne, Paris, No. 2405(3). After Reichel (1937). figs 2, 3. Borelis melo haueri sensu Cicha et al., 1998 – external view of matrix-free specimen, approximately ×22 (after Cicha et al., 1998); 2, with outer whorls partially removed, showing internal structure, Early Badenian, Staropatica, Bulgaria (Naturhistorisches Museum, Wien); 3, showing apertural face, Upper Lagenidae Zone, Badenian, Vienna Basin, Austria (d’Orbigny Collection, No. 102, Geologische Bundesanstalt, Wien). figs 4, 5. Borelis melo (Fichtel & Moll) curtica (Reichel, 1937), axial section, approximately ×22; 4, syntype herein designated lectotype. Miocene, Garzan, Turkey (Institut de Géologie de l’Université de Bâle, Basel), after Reichel (1937); 5, Badenian, Nussdorf/Steinfeld, Vienna Basin, Austria (D’Orbigny Collection, No. 101, Geologische Bundesanstalt, Wien), after Cicha et al. (1998).
### Table 1. Stratigraphical distribution of *Borelis melo melo* in the Indo-Pacific Province.

| Location                  | Period                      | Authors’ observations                                                                 | Remarks                                                                 |
|--------------------------|-----------------------------|---------------------------------------------------------------------------------------|------------------------------------------------------------------------|
| Turkey                    | ‘Middle Miocene’, Alexandretta | Authors’ observations on material in the Iraq Petroleum Company (IPC) collection in the Natural History Museum (NHM), London, Slides PF54331, PF54332, PF54333 and PF54335. | [No more refined stratigraphic interpretation possible].               |
|                          | ‘Miocene’                   | Authors’ observations on material in Caesar collection in the NHM.                      | [No more refined stratigraphic interpretation possible].               |
| Syria                    | ‘Middle Miocene’, J. Terbol   | Authors’ observations on material in the IPC collection in the NHM, Slide PF54341.     | [No more refined stratigraphic interpretation possible].               |
| Iran and Iraq            | ‘Oligocene’                 | Authors’ observations on material in the IPC collection in the NHM, Slide PF54341.     | [No more refined stratigraphic interpretation possible].               |
|                          | (at least in part Miocene)  | Authors’ observations on material in the IPC collection in the NHM, Slide PF54341.     | [No more refined stratigraphic interpretation possible].               |
|                          | to Miocene                  | Authors’ observations on material in the IPC collection in the NHM, Slide PF54341.     | [No more refined stratigraphic interpretation possible].               |
| Euphrates Formation      | Tell Hamad, Al-Medlij, Western Desert | Authors’ observations on material in the IPC collection in the NHM, Slide PF54341.    | [No more refined stratigraphic interpretation possible].               |
| Govanda Formation        | Hillwa Nassara village, north of Amadiya, N. Iraq | Authors’ observations on material in the IPC collection in the NHM, Slide PF54341.    | [No more refined stratigraphic interpretation possible].               |
| Jeribe Formation         | Hatamia Village, near Al-Baghdadi, W. Iraq | Authors’ observations on material in the IPC collection in the NHM, Slide PF54341.    | [No more refined stratigraphic interpretation possible].               |
| Wadi Hauran              | Authors’ observations on material in the IPC collection in the NHM, Slide PF54342. | [No more refined stratigraphic interpretation possible].               |
| Red Sea Coast, Saudi Arabia | Al Bad Formation            | Authors’ observations on material in the IPC collection in the NHM, Slide PF54342.     | [No more refined stratigraphic interpretation possible].               |
|                          | Midyan area, Red Sea coast, NW Saudi Arabia | Authors’ observations on material in the IPC collection in the NHM, Slide PF54342.    | [Probably equivalent to Maqna Group of Hughes & Filatoff (1995) and Hughes et al. (1999)=early Middle Miocene, Langhian (see below)]. |
| Wadi Waqib Member, Jabal Kibrit Formation, Maqna Group | Red Sea coast, Saudi Arabia (Hughes et al., 1999, 2000). | Authors’ observations on material in the IPC collection in the NHM, Slide PF54342.     | [Early Middle Miocene, Langhian, planktonic foraminiferal Zones N8–N9 on basis of occurrence of *Prazak* (1978), presumably on presence of *Praeorbulina* and absence of *Orbulina*. ] |
| Gulf Coast, Qatar        | Dam Formation               | Authors’ observations on material in the IPC collection in the NHM, Slide PF54342.     | [No more refined stratigraphic interpretation possible].               |
| East Africa              | ‘Burdigalian’ (T1f) limestone | Authors’ observations on material in the IPC collection in the NHM, Slide PF54342.     | [No more refined stratigraphic interpretation possible].               |
|                          | ‘Miocene’ reef limestone    | Authors’ observations on material in the IPC collection in the NHM, Slide PF54342.     | [No more refined stratigraphic interpretation possible].               |
| West Pacific             | Tertiary e                 | Authors’ observations on material in the IPC collection in the NHM, Slide PF54342.     | [No more refined stratigraphic interpretation possible].               |

In fact *Upper Te* on basis of associated microfauna (*Gypsina marianensis* and *Miogypsinoides dehaarti*), i.e. Early Miocene, Aquitanian–Burdigalian, planktonic foraminiferal Zones N4–N6 (Boudagher-Fadel & Banner, 1999).
| Region                  | Epoch          | Localities                                                                 |
|-------------------------|----------------|-----------------------------------------------------------------------------|
| Paratethys              | Badenian to 'early' Sarmatian | Styrian Basin, Baden, Brunn am Steinfeld (Brunn an der Schneebergbahn), Grinzling, Kalksburg (Leithakalk), Nussdorf, Theresienbad, 'limestone of the building of the Magdalena Chapel', Vienna (Leithakalk) and Voslau, Vienna Basin, Austria; Bulgaria; Moravia, former Czechoslovakia; Grusbach or Kroisbach (=Fertorakos, near Sopron) and other localities, Hungary; Duino, northwest of Trieste, Italy; Lapugia or Lapugiu de Sus or Lapugy, Bega Basin, Romania, Leithakalk, Bujtur, also Globukrajawa, Hunyad, Krasso-Szorensz and Pest, Peschtisch or Pesestu and Siebenburgen, Transylvanian Basin, Romania; Croatia, Serbia and Slovenia, former Yugoslavia (Fichtel & Moll, 1798; d’Orbigny, 1846; Reichel, 1937; Smout, 1963; Korecz-Laky, 1968; Ctyroky et al., 1975; Gagic, 1983; Rögl & Hansen, 1984; Papp & Schmid, 1985; Cicha et al., 1998; authors’ observations on material in the F. Rögl Collection in the NHM). |
| Konkian (late Badenian equivalent) | Northern Caucasus and Crimea, former Soviet Union (Zhizhchenko, 1959, as Borelis haueri). [Middle Miocene, Langhian–Serravallian, calcareous nannoplankton Zones NN4A–NN6 (Papp & Schmid, 1985; Jones & Simmons, 1996; Cicha et al., 1998)]. |
| Southern Europe         | ‘Tortoniense’   | Cabo de Gata, Almeria Province, SE Spain (Saavedra, 1966). eastern Betic Cordillera, SE Spain (Azema et al., 1968). [No more refined stratigraphic interpretation possible]. |
|                         | Middle Miocene, ‘Helvetian’ (Serravallian)-Tortonian | Siracusa Limestone Member, Monte Climiti Formation and Car lentini Formation, Sortino Group. |
|                         |                  | Monte Carrubba, SE Sicily (Grasso et al., 1982) – questionable in view of poor quality of photograph. [By correlation with dated section at Licodica Eubea, Car lentini Formation Late Miocene, Tortonian (Globorotalia acostaensis Zone). Monti C limiti Formation undated]. |
|                         | ‘Middle Miocene’ | S. Cesarea Termine, Apulia (Sartorio & Venturini, 1988). [No more refined stratigraphic interpretation possible]. |
|                         | Middle Miocene or Late Miocene, Messinian | Porto Cristo, Mallorca (Jen kyns et al., 1990; authors’ observations on material presented by Miss A. Taylor in the NHM). [No more refined stratigraphic interpretation possible]. |
|                         | Late Miocene, Cantera Member | Cabo de Gata, Almeria Province, SE Spain (Betzler & Schmitz, 1997). [Late Miocene, Tortonian–Messinian, planktonic foraminiferal Zones N16–N17 on basis of occurrence of sinistral Neogloboquadrina acostaensis (Betzler & Schmitz, 1997). Underlying volcanic rocks radiometrically dated to 8 Ma (Betzler & Schmitz, 1997)]. |
|                         | ‘Miocene’        | Ras Kala, Malta (authors’ observations on material in the IPC Collection in the NHM, Slide PF54338). [No more refined stratigraphic interpretation possible]. |
| North Africa            | ‘Miocene medio’ | ‘tra El-Abiar e Sidi-Mahius nella Cyrenaica’ [Libya], also ‘Escr-Scegga nella Marmarica’ [Libya] (Silvestri, 1928). [No more refined stratigraphic interpretation possible]. |
|                         | Zone of Neoalveolina melo, ‘Vindobonian’ | Gebel Gharra, Cairo–Suez Road, Egypt (Souaya, 1963). [Probably early Middle Miocene, Langhian. Overlies zonule of Miogypsina cushmani, restricted to Early Miocene, Burdigalian (planktonic foraminiferal N7) in Western Tethys (Cahuzac, 1984; Cahuzac & Poignant, 1997)]. |
|                         | ‘Middle Miocene’ | El Abyar, Libya (Sartorio & Venturini, 1988). [No more refined stratigraphic interpretation possible]. |
|                         | Units II-IV, Marmarica Formation | El-Dabaa, NW Egypt (Ibrahim & Mansour, 2002). [Middle Miocene, Langhian-Serravallian, planktonic foraminiferal Zones N8–N13 on basis of occurrence of Praeorbula sina, Orbula sina, Globorotalia fohsi lobata and G. fohsi robusta]. |
| Israel                  | ‘Unit 4’, Ziqlag Formation | Khirbet es Sura and Lakhish (Reiss & Gvirtzman, 1966). [Lower part of Ziqlag (‘Unit 4a’) Middle Miocene, Serravallian, planktonic foraminiferal Zones N12–N14 on basis of occurrence of Globorotalia menardii and G. mayeri in presumed equivalent basinal section]. |
|                         | Ziqlag and Pattish formations | Olaqim and other boreholes, coastal plain (Buchbinder et al., 1993). [Late Miocene, Tortonian–Messinian, planktonic foraminiferal Zones N15–N17 (Buchbinder et al., 1993, and additional references cited therein)]. |

**Table 2.** Stratigraphical distribution of *Borelis melo melo* in the Mediterranean Province.
Stratigraphy and palaeobiogeography of *Borelis melo*

**Turkey**
- Mioocene: 2 km east of Garzan on the road between Djarbekir and Saist, Armenian Taurus, Turkey (Reichel, 1937).
- Mioocene: Sivas Basin (Dizer, 1962) - questionable in view of poor quality of photograph. [No more refined stratigraphic interpretation possible].

**Iraq**
- Euphrates Formation: Al-Qaim area, NW Iraq (Al-Saddiqi, 1972).
- Jeribe Formation: Type locality near Jaddala, also Dermanou, Erbil, Hilwa Nassara and Mawat, North Iraq, and Wadi Fuhaimi and W. Ushak, Western Desert (Karim, 1978).
- Jeribe Formation: Hatamia Village, near Al-Baghadi, W. Iraq, also Qara Chaug Dagh, Kirkuk, N. Iraq (Al-Hashimi & Amer, 1985).
- Jeribe limestone: Palani (authors’ observations on material in the IPC collection in the NHM, Slide PF54348).
- [Euphrates in Western Desert Early Miocene, probably Burdigalian, elsewhere early Middle Miocene, Langhian, planktonic foraminiferal Zone N8 (see above). Jeribe at Dermanou no older than Middle Miocene, Langhian, planktonic foraminiferal Zone N9 on occurrence of *Orbulina* sp. (Karim, 1978)].

**Zagros Basin, Southern Iran**
- Lower or Middle Fars limestones: Kan-I-Shaitan section, Darband or Derbend-I-Bazian or Bezian, Kurdistan (authors’ observations on material in the IPC collection in the NHM, including Slides PF54340 and PF54351). [No more refined stratigraphic interpretation possible].
- (Upper) Asmari Formation: Maidan-i-Naphtun [near Kuhl-e-Asmari], Marun Field area, Tang-e-Haletuk and Tang-e-Mashemi, Khuzestan and Lurestan provinces.
- Sarvestan, Interior Fars: Fars (Nicolesco, 1928; James & Wynd, 1965; Sampò, 1969; Kalantari, 1976; Rahaghi, 1984; Seyrafi & Hamedani, 1998; Seyrafi, 2000; authors’ unpublished observations).
- [Upper Asmari in part late Early Miocene, Burdigalian, 19.3 Ma on strontium isotope stratigraphic evidence (authors’ unpublished observations), in part early Middle Miocene, Serravallian, Zones N10–N12 on uncorroborated planktonic foraminiferal evidence (Adams, 1969; Jones, 1999). Razak, early Middle Miocene, Langhian, planktonic foraminiferal Zone N8 on presence of *Praeorbulina* and absence of *Orbulina* (James & Wynd, 1965). Gachsaran (in Abu Dhabi) late Early to early Middle Miocene, Burdigalian–Langhian, 20.1–16.3 Ma on strontium isotope stratigraphic evidence (Peebles, 1999)].

**Table 3. Stratigraphical distribution of *Borelis melo curdica* in the Indo-Pacific Province.**

- 2002 *Borelis melo melo* (Fichtel & Moll); Al-Saad & Ibrahim: pl. 3b, fig. 21.
- 2002 *Borelis melo melo* (Fichtel & Moll); Ibrahim & Mansour: pl. 2, figs 8–9.

**Diagnosis.** Chamberlets of same chamber of equal or nearly equal size.

**Variability.** Degree of elongation along axis of coiling variable.

**Stratigraphical distribution.** Refer to Tables 1 and 2 (only records verifiable by reference to illustrations or material have been admitted).

**Palaeobiogeographical distribution.** Indo-Pacific Province (Early–Middle Miocene, Aquitanian–Langhian); Mediterranean Province (Middle–Late Miocene, Langhian–Messinian).

**Remarks.** The following nominal species differ from *Borelis melo melo* essentially only in their marginally greater axial elongation, and are regarded as at least possibly synonymous (as they appear to fall within the range of variation exhibited by *Borelis melo melo*):

- *Alveolina pulchra* d’Orbigny, 1839, originally described from the Recent of Cuba in the Caribbean, and also recorded in the Recent elsewhere in the equatorial Atlantic and in the Indo-Pacific, and in the Pleistocene and Miocene. Adams (1970) noted that *pulchra* ‘may grade into *B. melo*.’
- *Alveolina melo sensu* Brady, 1884 (see also Jones, 1994) from the Recent of Ascension Island and Bermuda in the Atlantic. *Alveolina bradyi* Silvestri, 1927 was evidently intended by Silvestri (1927, 1928) as a new name for *A. melo sensu* Brady, 1884, which he interpreted as distinct from *melo sensu stricto*. However, Silvestri’s species concept, as indicated by his synonymy and his plates, includes some specimens of undoubted *melo* s.s., including some from the type locality, with the result that most subsequent authorities have synonymixed *bradyi* with *melo*.
- *Borelis primitivus* Cole, 1957, originally described from the Tertiary e (?Te1–4, Late Oligocene) of Eniwetok Atoll in the West Pacific.
- The following nominal species differ in their significantly greater axial elongation, and are regarded as probably distinct:
- *Neoalveolina pygmaea schlumbergeri* Reichel, 1937, originally described from the Recent of Mayotte, NW of Madagascar in
the Indian Ocean, and also recorded in the Recent elsewhere in the Indo-Pacific and in the Red Sea, and in the Pleistocene of Eniwetok Atoll in the Pacific Pacific.

**Borelis clarionensis** McCulloch, 1977, originally described from the Recent of the Pacific Ocean. Borelis or *Neoalveolina haueri* and *B. or N. pygmaea*, under which names *B. melo* *melo* is interpreted here as having been identified by other authors (see below), are also regarded as distinct.

Unfortunately, the characters of *Alveolina haueri* d’Orbigny, 1846 *sensu stricto*, originally described from the Middle Miocene, Badenian, of Baden in the Vienna Basin, are not entirely clear from the type description (d’Orbigny, 1846, p. 148) and somewhat stylized type figures (d’Orbigny, 1846, pl. 7, figs 17–18). The specimen, again from the Badenian of Baden, described and figured by Cicha et al. (1998, p. 86, pl. 19, fig. 11) as *Borelis melo haueri*, and figured herein on Plate 1, fig. 2, exhibits an internal structure reminiscent of *B. melo curdica* (see below), with alternately large and small chamberlets, and the latter displaced towards the external periphery, resulting in the development of incipient attic chamberlets separated by Y-shaped septula. The specimen, yet again from the Badenian of Baden, described and figured by Papp & Schmid (1985, p. 56, pl. 47, figs 8, 12) as ‘*Borelis melo* (=*Alveolina haueri*’) and by Cicha et al. (1998, p. 86, pl. 19, fig. 12) as *Borelis melo haueri*, and figured herein on Plate 1, fig. 3, exhibits external apertures arranged in two, staggered, rows, rather than the one seemingly suggested by the original description of *Alveolina haueri* ‘*une rangee longitudinale d’ouvertures ovales transverses*’: d’Orbigny, 1846). In this respect, it is reminiscent of the genus *Flosculinella* Schubert in Richarz, 1910, differing essentially only in possessing one supplementary attic aperture per main aperture, rather than two.

*Borelis* (*Fasciolites*) *pygmaea* Hanzawa, 1930 *sensu stricto*, originally described from the Miocene of Indonesia, appears distinct in terms not only of its greater axial elongation, but also of its incipient polar flosculinization.

**Borelis melo** (Fichtel & Moll) *curdica* (Reichel, 1937)

(Pl. 1, figs 4–5)

1928 *Alveolina cf. melo*; Nicolesco: 1086, fig. 26.
1937 *Neoalveolina melo curdica* Reichel: 108–110, pl. 10, figs 4–7; pl. 11, fig. 6a (*N. melo* on caption); 103, text-fig. 20; 104, text-fig. 21; 122, text-fig. 26, no. 5. (pl. 10, fig. 4=syntype; herein designated lectotype).
1939 *Neoalveolina melo curdica* Reichel; Lipparini: pl. 16, figs 1–7.
1962 *Neoalveolina melo curdica* Reichel; Dizer: pl. 5, fig. 1.
1964 *Neoalveolina melo* (*sic*) *curdica* Reichel; Bornovas: pl. 16, fig. 2.
1964 Neoalveolina melo curdica Reichel; Bozorgnia: pl. 148, pl. 149, fig. 1; pl. 150, pl. 151, fig. 2; pl. 152, fgs 1–2.
1964 Borelis melo curdica (Reichel); Loeblich & Tappan:

Stratigraphical distribution. Refer to Tables 3 and 4 (again, note that only records verifiable by reference to illustrations or material have been admitted).

Palaeobiogeographical distribution. Indo-Pacific Province (late Early–Middle Miocene, Burdigalian–Langhian, ?Serravallian); Mediterranean Province (late Early–Middle Miocene, ‘middle’ Burdigalian–Langhian; ?Serravallian).

Diagnosis. Chamberlets of later chambers alternately large and small, the latter displaced towards the external periphery, resulting in the development of incipient attic chamberlets separated by Y-shaped septula; external apertures arranged in somewhat staggered row (‘alternativement larges et etroites et parfois jumelees’: Reichel, 1937).

Variability. Degree of elongation along axis of coiling variable. Ratio of lengths of polar to equatorial axes ranges from 1: 1 to up to at least 1.5: 1 (see, for instance, specimens illustrated by Reiss & Gvirtzman, 1966).

SUMMARY OF DISTRIBUTION DATA
The distributions of Borelis melo melo and B. melo curdica, as determined by records verifiable by reference to illustrations or material (see above), are listed below (see also Figures 1–2).

B. melo melo (Fichtel & Moll)
?Oligocene (primitivus, haueri auctt., non d’Orbigny, pygmaea auctt., non Hanzawa); Miocene; ?Pleistocene–Recent (melo sensu Brady, pulchra).

Indo-Pacific Province in Oligocene?, Early–Middle Miocene, Aquitanian–Langhian; Mediterranean Province in Middle–Late Miocene, Langhian–Messinian; ?Atlantic/Caribbean Province in Pleistocene–Recent.

B. melo (Fichtel & Moll) curdica (Reichel)
Late Early–Middle Miocene, Burdigalian–Langhian, ?Serravallian.
Fig. 2. Palaeobiogeographical distribution of *Borelis melo melo* and *B. melo curdica*: (a) late Early Miocene, ‘early’ Burdigalian; (b) latest Early–Early Middle Miocene, ‘middle’ Burdigalian–Langhian. Superimposed on the appropriate palinspastically restored base maps (Rögl, 1998, 1999a, b). Arrows indicate possible dispersal routes.
Stratigraphy and palaeobiogeography of *Borelis melo*

Indo-Pacific Province in late Early–Middle Miocene, Burdigalian–Langhian, 7'Serravallian; Mediterranean Province in latest Early–Middle Miocene, ‘middle’ Burdigalian–Langhian, 7'Serravallian.

DISCUSSION

Stratigraphical and evolutionary significance

These distribution data can be interpreted as indicating that *Borelis melo melo* evolved into *B. melo curdica*, with its ‘more advanced’ (certainly, more complex) structure of incipient attic chamberlets, Y-shaped septula and staggered row of external apertures, in the late Early Miocene, in the Indo-Pacific Province (Fig. 1).

*Borelis melo curdica* could conceivably have then evolved into *Flosculinella bontangensis*, with true attic chamberlets, in the Middle Miocene, in the Indo-Pacific Province. Importantly, *Flosculinella bontangensis* has been described (although unfortunately not illustrated) from the Middle Miocene of Fars Province in southeastern Iran, immediately post-dating *Borelis melo curdica* (James & Wynd, 1965).

Interestingly, *Flosculinella bontangensis* has been independently interpreted as having then in turn evolved into *Alveolinella praecuoyii*, with an additional row of attic chamberlets, also in the Middle Miocene, in the Indo-Pacific Province (Wonders & Adams, 1991).

Palaeobiogeographical significance

The interpreted absences of *Borelis melo curdica* from the Indo-Pacific, and of *Flosculinella* from the Mediterranean, in the late Early Miocene, Burdigalian, were among the observations that led the late C. G. (‘Geoff’) Adams and his co-workers to suggest that the former Tethyan Sea connection between the two provinces had become interrupted by this time, by the formation of a land bridge between the converging Arabian and Eurasian Plates (Adams et al., 1983, 1999). Indeed, there is a wealth of terrestrial vertebrate evidence to indicate that there was a land bridge between Arabia and Eurasia in the late Early Miocene (Orleanian Land Mammal Age), which facilitated the dispersal not only of the primitive elephant *Gomphotherium* – after which it is colloquially known – but also of other less well-documented groups, such as fresh-water fish (see, for instance, Otero & Gayet, 2001). Corroborative evidence is provided by the existence of an emergence surface over much of Arabia (Adams, 1969). It is likely that the emergence surface and land bridge was generated by uplift of the Western Arabian Highlands by thermal doming associated with rifting in the Red Sea (Jones & Racey, 1994).

Fred Rögl and Fritz Steininger and their co-workers speculated, but were unable to prove to Adams’ satisfaction, that there might have been a later reconnection between the Indo-Pacific and Mediterranean provinces, possibly in the early Middle Miocene, Langhian, prior to the final disconnection in the late Middle Miocene, Serravallian (see, for instance, Rögl, 1998, 1999a, b; see also Jones, 1999). Perhaps, significantly, this putative reconnection would have been coincident with a global climatic optimum and associated glacio-eustatic sea-level highstand.

The evidence outlined above of the occurrence of both *Borelis melo curdica* and *B. melo melo* only in the Indo-Pacific Province (at least in the Middle East) in the late Early Miocene, ‘early’ Burdigalian, supports Adams’ interpretation of an interruption of the earlier marine connection between the Indo-Pacific and Mediterranean provinces at this time (Fig. 2a).

It is further submitted, however, that the occurrence of both sub-species, not only in the Indo-Pacific Province (in the Middle East) but also throughout the Mediterranean in the latest Early–early Middle Miocene, ‘middle’ Burdigalian–Langhian, supports Rögl & Steininger’s interpretation of a (re-)connection, or at least a partial connection or filter, between the Indo-Pacific and Mediterranean provinces at this time (Fig. 2b).

CONCLUSIONS

1. *Borelis melo melo* and *B. melo curdica* are distinguishable from one another essentially on the basis of the level of development of their internal chamberlets and external apertures.

2. *Borelis melo melo* ranges at least throughout the Miocene. *B. melo curdica* is restricted to the late Early to Middle Miocene.

3. Both sub-species occur only in the Indo-Pacific Province in the late Early Miocene, ‘early’ Burdigalian, but in the Indo-Pacific and Mediterranean provinces in the latest Early–early Middle Miocene, ‘middle’ Burdigalian–Langhian. Their occurrence in both the Indo-Pacific and Mediterranean provinces in the latest Early–early Middle Miocene points to a marine (re-)connection between the two provinces at this time.

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