

The biostratigraphical and evolutionary significance of *Alveolinella praequoyi* sp. nov. from Papua New Guinea

A. A. H. WONDERS

B.P. Research Centre, Chertsey Road, Sunbury-on-Thames, Middx TW16 7LN, UK

C. G. ADAMS

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD, UK

SYNOPSIS. A primitive species of *Alveolinella*, intermediate between *Flosculinella bontangensis* (Rutten) and *Alveolinella quoyi* (d'Orbigny), is described as new from the Darai Limestone of Papua New Guinea. In the type section, it occurs through at least 50 m of Middle Miocene limestone referable to the upper part of Tf₁ and to Tf₂ in terms of the East Indies Letter Classification of the Tertiary. The biostratigraphical significance of this find is discussed, and mention made of the relevance of the new taxon to the evolutionary debate on punctuated equilibria versus secular change.

INTRODUCTION

Alveolinella praequoyi sp. nov. was discovered independently by the authors during examinations of the Darai Limestone between 1982 and 1987. On the basis of Australasian Petroleum Company collections studied in Melbourne, Adams (1984) referred to it as *A. fennemai* Checchia-Rispoli, and noted (1984: 59) that the specimen figured by Eames, Banner, Blow & Clarke (1962) as *A. fennemai* appeared to be intermediate between *Flosculinella* and *Alveolinella*. Wonders, working with material collected more recently by the British Petroleum Company, concluded that specimens from the Darai Limestone previously referred to *A. fennemai* should be described as new.

The material described in this paper was obtained from two samples collected from an unnamed river gorge, cut through the northeastern part of the Hides Anticline, Central Highlands, P.N.G. (Figs 1, 2). In this locality the species ranges through at least 50 m of limestone. Elsewhere, it may occur through up to 250 m of the Darai Limestone, which is c. 1,500 m thick. Additional material was obtained from other areas and localities; notably, traverses across the Darai and Ori anticlines, and samples collected during an earlier reconnaissance survey of the Tari area by the Australasian Petroleum Company (1955, unpublished report). See Fig. 1.

The present study is based mainly on randomly orientated thin sections, isolated specimens not being obtainable from the hard matrix of this limestone. However, a few orientated thin sections were prepared in the Natural History Museum from specimens seen on polished rock surfaces, using the method described by Hodgkinson & Margerum (1986).

Since recognizable planktonic foraminifera are rarely present in the shallow water facies of the Darai Limestone, the material described here is dated in terms of the East Indies Letter Classification of the Tertiary (*sensu* Adams, 1984, with minor modifications). Revised definitions of the relevant letter 'stages' are given below.

Tf₃: upper boundary defined by the extinction of *Lepidocyclina*. It should be noted that the Darai Limestone is disconformably/unconformably overlain by deep-water shales of N17 age in the Hides Anticline (Fig. 2), and that the precise age of its uppermost beds is not known. *Lepidocyclina* seems to be absent from Tf₃ in this area for facies reasons.

Tf₂: upper boundary defined by the extinction of *Katacyclo-clypeus annulatus* K. Martin. It is possible, but not certain that *Flosculinella* may also range to the top of this division. Unfortunately, the Tf₂ limestones in the Papuan fold belt are often in shallow open marine facies without alveolinids.

Tf₁: upper boundary defined by the extinction of *Austrotrillina howchini* (Schlumberger) and/or *F. bontangensis* (Rutten).

Te₅ (Upper Te of Adams, 1970): upper boundary defined by the extinction of *Lepidocyclina* (*Eulepidina*) and/or *Spiroclipeus*.

Te₁₋₄ (Lower Te of Adams, 1970): upper boundary defined by the extinction of *Vlerkina* [= *Heterostegina*, auctt.] *borneensis* (van der Vlerk) and *Miogypsinoidea complanatus* (Schlumberger). Most authors draw this boundary at the first appearance of *Miogypsina*, but this is an unsatisfactory and dangerous procedure unless the species can be identified.

It is believed that three divisions of Tf₁ can be recognized in Papua New Guinea. Upper f₁ with *Austrotrillina howchini* (Schlumberger). *Flosculinella bontangensis* (Rutten) and *Alveolinella praequoyi* sp. nov.; middle f₁, a poorly fossiliferous unit, but typically containing *A. howchini* and *Flosculinella bontangensis*; and lower f₁ with *Miogypsinoidea dehaarti* van der Vlerk and *Pseudotaberina malabarica* (Carter). These units are not, however, thought to be of regional (Indo-West Pacific) significance since their boundaries seem to be facies-controlled.

The Alveolinidae is a family of larger miliolacean foraminifera which originated in the Early Cretaceous (*Ovalveolina* and *Praealveolina*, Albian), and is represented in present-day tropical seas by *Borelis* and *Alveolinella*. Its

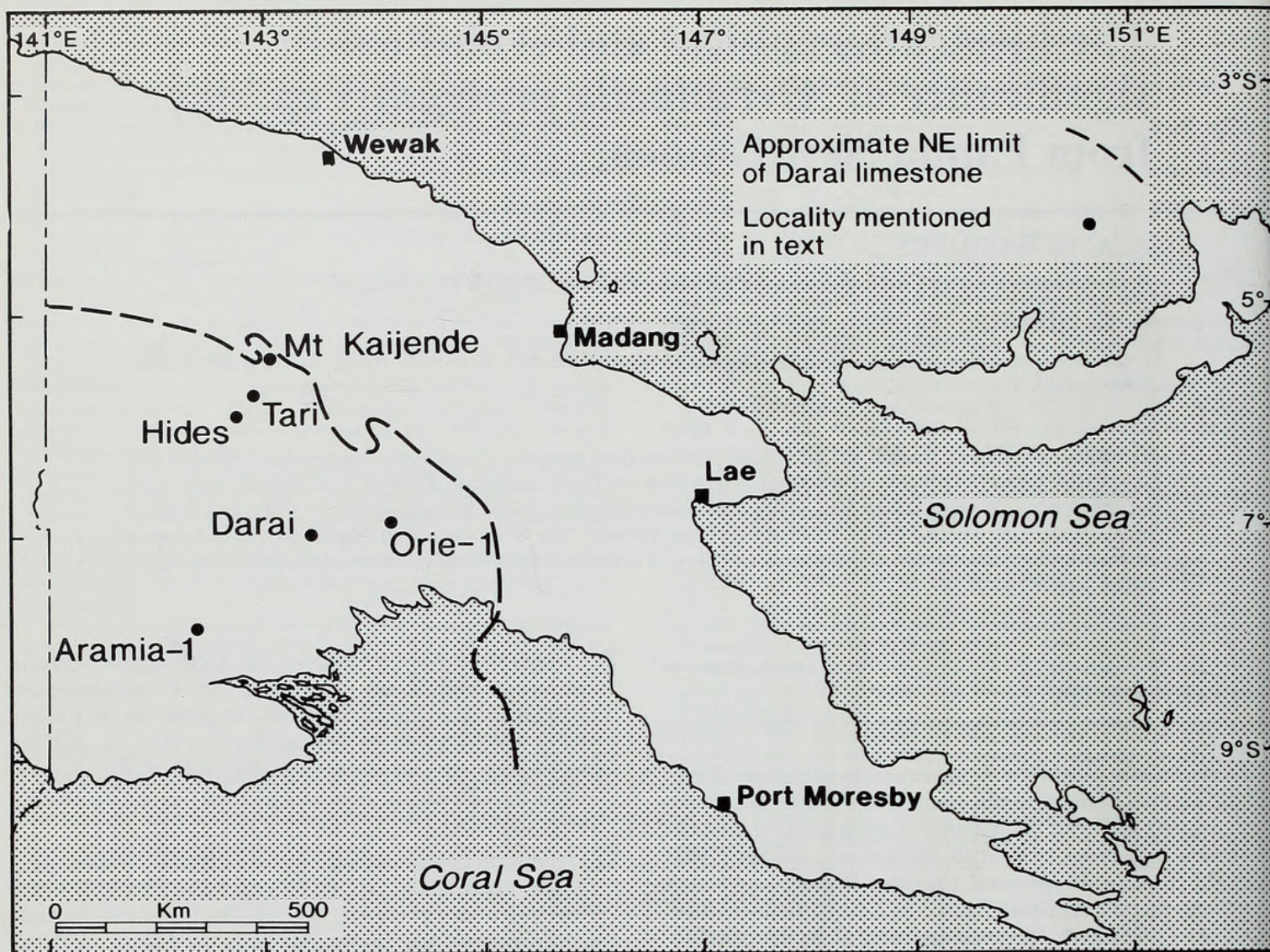


Fig. 1 Map showing the principal localities mentioned in the text.

members typically have spherical to fusiform tests. The recorded evolutionary history of the family is characterized by discontinuity, with periods of high diversity and morphological complexity alternating with poorly documented intervals of low diversity. The Cenomanian, the Senonian, and the Late Palaeocene to Mid Eocene are periods of abundance, whereas the Turonian, Maastrichtian, Early Palaeocene, and Late Eocene to Early Oligocene are characterized by low species diversity and relatively small numbers of individuals. These alternating periods of high and low diversity, and the apparent absence of morphotypes intermediate between genera in successive bloom periods, have led some authors to believe that the family could have originated several times from an obscure milioline stock and thus be polyphyletic. This was, indeed, implied by Reichel (1964), who noted that 'the Alveolinidae [is] a morphologically well-defined family but probably not a phylogenetic unit. Some of the genera that followed each other in the course of geological epochs surely did not evolve one from another.' Although Reichel (1964) did not imply that the genus *Alveolinella* contributed to the polyphyletic nature of the family as a whole, he certainly knew of no species transitional to its probable ancestral genus, *Flosculinella*.

Compared with the number of early Palaeogene species attributed to *Alveolina*, the three or four Neogene genera are

poorly diversified. This, however, may reflect the relative paucity of suitable Neogene sedimentary environments (shallow-water carbonates were less widespread than in the Eocene) as much as any innate failure of the group as a whole to radiate.

In this paper, the transition from *Flosculinella* to *Alveolinella* is documented by the description of *A. praequoyi* n. sp.

SYSTEMATIC DESCRIPTION

Order **FORAMINIFERIDA** Eichwald, 1830
 Suborder **MILIOLINA** Delage & Hérourard, 1896
 Superfamily **MILIOLACEA** Ehrenberg, 1839
 Family **ALVEOLINIDAE** Ehrenberg, 1839
 Genus **ALVEOLINELLA** Douvillé, 1906

TYPE SPECIES. *Alveolinella quoyi* (d'Orbigny, 1826).

Alveolinella praequoyi sp. nov.

Figs 4-7

?1896 *Alveolina* sp. Verbeek & Fennema (pars): 1142; pl. 11, figs 43a, b only.

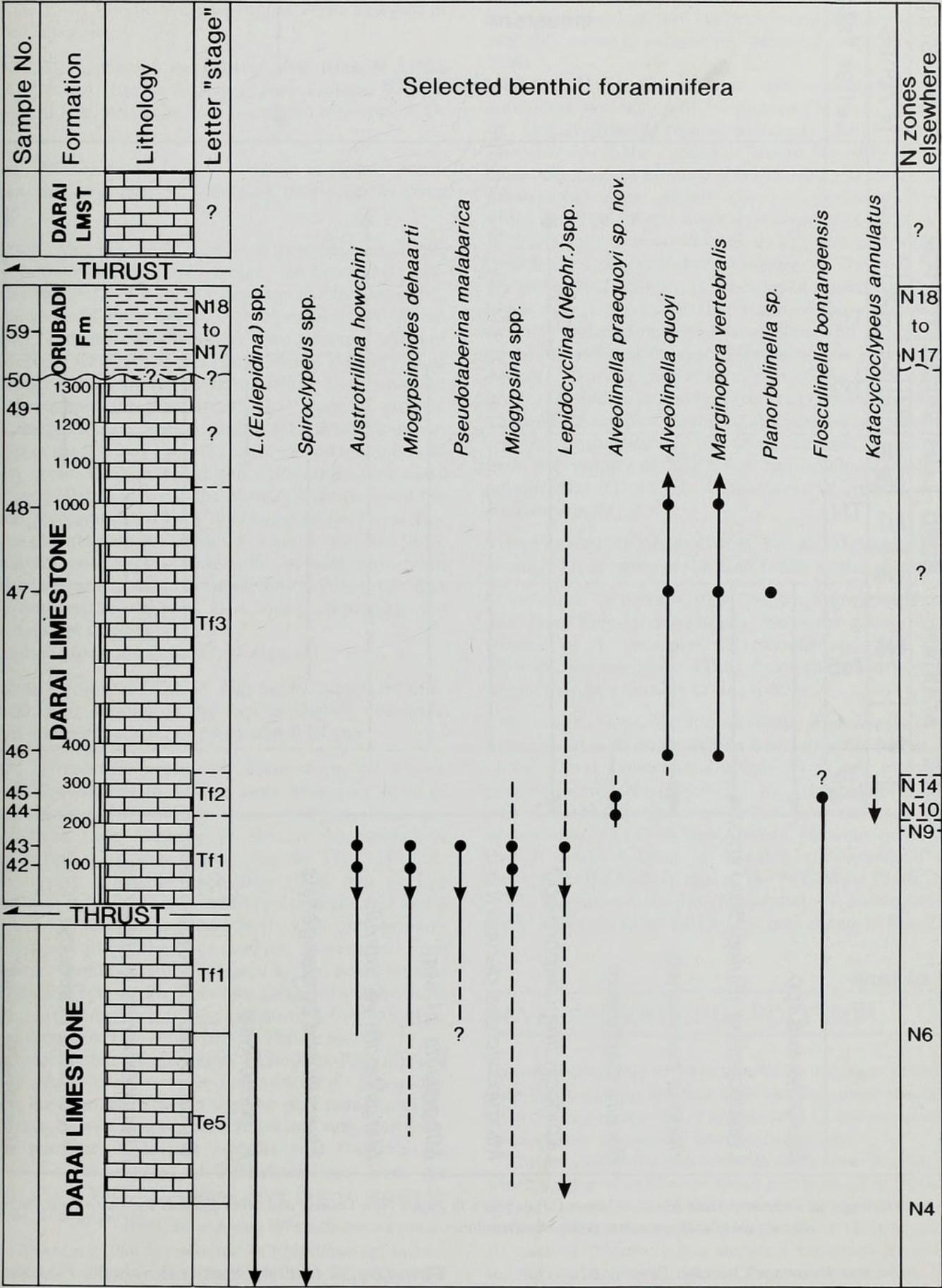


Fig. 2 Composite stratigraphical section through the Miocene part of Hides Anticline sequence, Papua New Guinea, showing the ranges of important stratigraphical markers including *A. praequoyi* sp. nov. Broken lines indicate ranges elsewhere in the Darai Limestone; black spots mark sample levels. Only the measured part of the limestone is to scale.

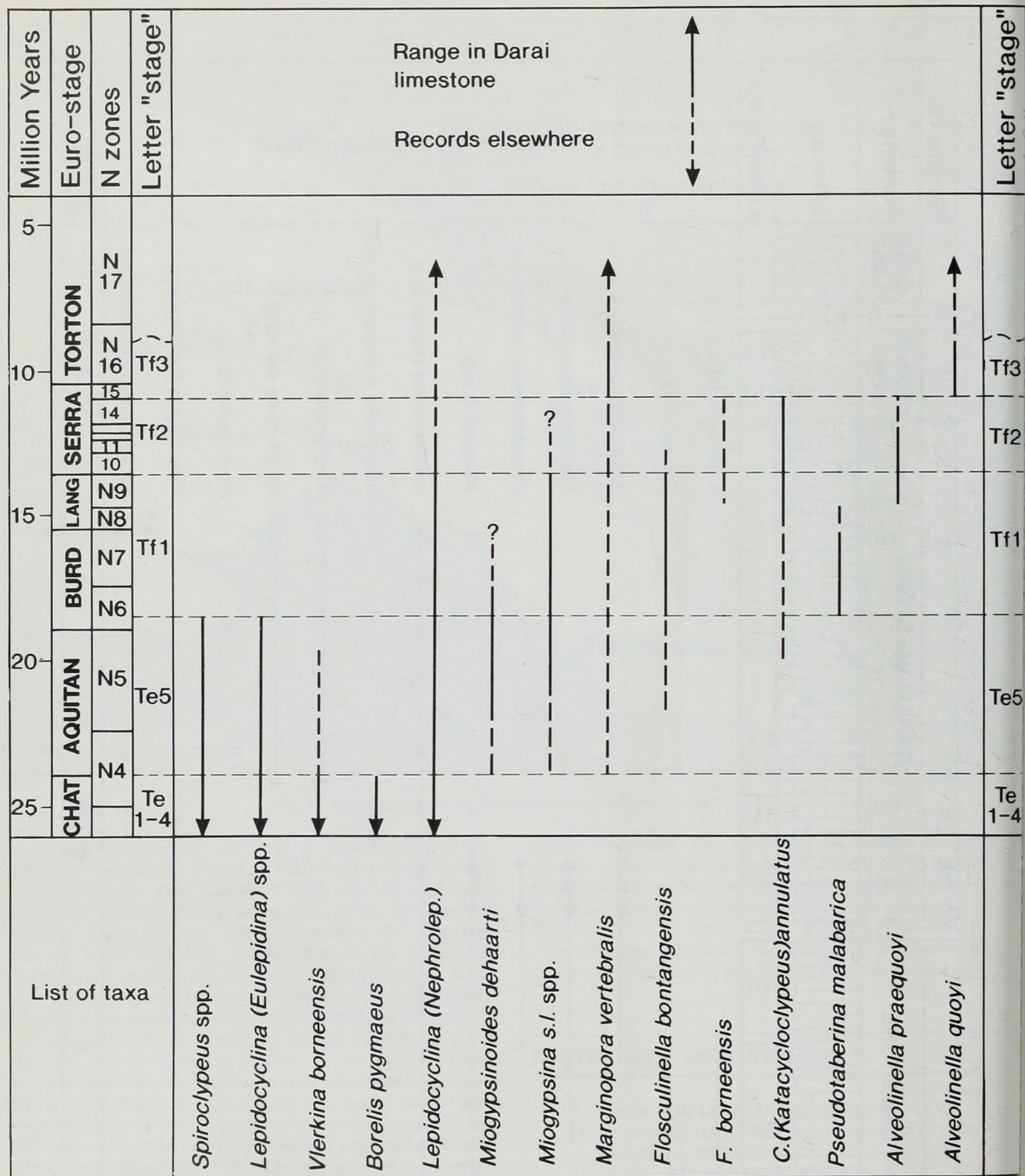


Fig. 3 Known ranges of some important Miocene larger foraminifera in Papua New Guinea and other parts of the Indo-West Pacific region. The smaller benthic marker genus, *Austrotrillina*, is not known above N9 (see Adams, 1984).

- ?1909 *Alveolina fennemai* Checchia-Rispoli: 67.
 1962 *Alveolinella* sp. Eames *et al.*: pl. 6, fig. D.
 ?1973 *Alveolinella* sp. Binnekamp: 8.
 1984 *Alveolinella fennemai* Checchia-Rispoli; Adams: 54, 59.

DIAGNOSIS. A fusiform alveolinid, initially *Flosculinella*-like (i.e., with an irregular juvenile coil and two rows of chambers per whorl in the later nepionic stage), followed by an *Alveolinella*-like adult stage comprising no more than 2-3 whorls.

NAME. To indicate that it is probably ancestral to d'Orbigny's species *A. quoyi*.

TYPE LEVEL. Early Middle Miocene (upper Tf₁ to Tf₂) part of the Darai Limestone.

TYPE LOCALITY. Unnamed river gorge. NE flank of Hides Anticline, Central Highlands, Papua New Guinea. Sample horizon 45, of B.P. Australia Ltd. Local grid reference 9119/4514.

MATERIAL. Numerous individuals seen in randomly orientated thin sections, plus 3 orientated thin sections from sample 45.

DESCRIPTION. Megalospheric form: test porcellanous, large, fusiform; initially streptospirally coiled, but becoming planispiral after the first 1–2 whorls. Chambers axially elongated, numerous; about 18 in the last whorl. Proloculus 0.06–0.08 mm in diameter (2 measured individuals). Two principal layers of chamberlets per whorl, the outer row (attics of authors) being smaller and twice as numerous as the inner. Both rows are present throughout the post-streptospiral stage of growth. Towards the poles, one or more additional stages of chamberlets appear in the last 3 or 4 whorls; these extend towards, and eventually cross, the equator in the adult stage. The extra rows are intercalated between the primary chambers and the attics, and accommodated by a thickening of the basal attic wall: these chamberlets are never more numerous than those in the primary rows. Septula continuous, at least in the adult stage. The preseptal passage is basal, and well-developed in the later ontogenetic stage, as in *A. quoyi*. Apertures not visible in random sections.

Microspheric form not definitely observed.

DIMENSIONS of holotype (P52658; Figs 5a, b): length 3.4 mm, width 1.03 mm. Whorls 7; the first is slightly eccentric. Maximum internal diameter of proloculus 0.08 mm.

REMARKS. *Alveolinella praequoyi* differs from all known species of *Flosculinella* in having more than two rows of secondary chamberlets in the later ontogenetic stage. (It differs from Late Miocene to Recent representatives (Miocene forms are poorly known, but see Fig. 12) of *A. quoyi* in having a smaller proloculus (0.08 mm or less compared with 0.10–0.22 mm), an irregular initial coil and a distinct juvenile stage of several whorls with only primary chamberlets and attics. The third (and any subsequent) rows of secondary chamberlets are confined to the polar regions except in the last few whorls. Adult megalospheric individuals of *A. quoyi* are often twice as long as mature individuals of *A. praequoyi* (compare Figs 8 and 10 with Figs 4, 5a and 7).

It is possible that *A. fennemai* (Checchia-Rispoli) will eventually prove to be a senior synonym of *A. praequoyi*. However, we think it better to use the new name until *A. fennemai* can be adequately redescribed and refigured from opotypic material. It is just possible that Binnekamp's unillustrated record (1973) of *Alveolinella* sp. from the lower part of the Yalam Limestone, New Britain, should be referred to *A. praequoyi*.

ASSOCIATED FAUNA. This is restricted to *Elphidium* sp. indet., other smaller benthic species and soritids in the Tf₁ part of the type section. Elsewhere, e.g. in the Orie and Darai anticlines (samples 364KRA, 963KRA and 1056KDA, 77KF), and in other parts of the Tari area (samples 21KT and 22KT), *A. praequoyi* has been found with one or both of *A. howchini*

and *F. bontangensis* in beds of Tf₁ age. Although it occurs within the range of *Katacycloclypeus annulatus* (Tf₂ in the Darai Limestone, but extending down into Tf₁ elsewhere), the two species have not yet been found in direct association, probably owing to palaeoenvironmental constraints. See Figs 2 and 3.

Belford (1984: 33) reported what now appears to be an anomalous association of *Miogypsina* (M.) sp., *Austrotrillina* sp., and *Alveolinella ?quoyi*, in Sample KJ10 from the Darai Limestone near the summit of Mount Kaijende (Fig. 1). We have been able to examine this material and can confirm the presence of a single, slightly off-centre, section of *Alveolinella*, which could be either a large *A. praequoyi* or a true *A. quoyi*. It occurs with *Austrotrillina* sp. indet., and an advanced, but specifically indeterminable, *Miogypsina*. The rock itself is a grainstone and contains small clasts of reworked *Globigerina* limestone. It is possible that much of the assemblage, particularly the specimens of *Austrotrillina* and *Miogypsina*, are reworked and that the age of this sample is Late Miocene or younger. If so, it cannot form part of the Darai Limestone proper. A similar assemblage has not been found in any of the hundreds of samples examined independently by us from this region. Unfortunately, no other samples were collected from the vicinity of KJ10, and the original sample is now missing (Dr G. C. H. Chaproniere, Canberra, personal communication).

STRATIGRAPHICAL DISTRIBUTION. Middle Miocene (latest Tf₁ through Tf₂ in terms of the East Indies Letter Classification).

GEOGRAPHICAL DISTRIBUTION. As yet known with certainty only from Papua New Guinea, but some poorly illustrated records of *A. fennemai*, *Alveolinella* sp., and, perhaps, *Flosculinella borneensis* (Tan) from the Indo-West Pacific region may be referable to this species.

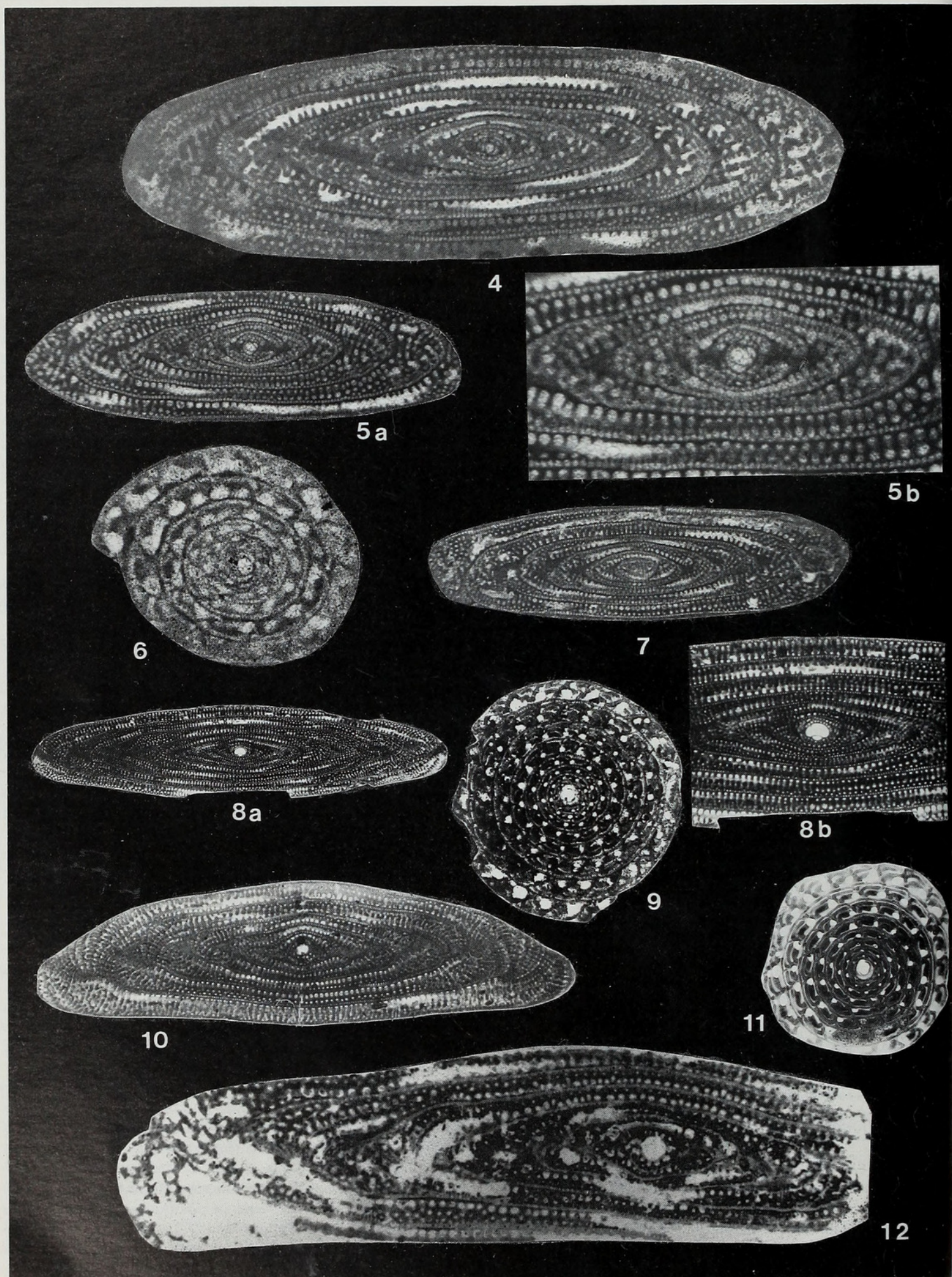
CHRONOSTRATIGRAPHIC SIGNIFICANCE. *Alveolinella praequoyi* first appears with *Austrotrillina howchini* in the upper Tf₁ part of the Darai Limestone (Sample 44 in our material) and persists locally throughout Tf₂, i.e., throughout the greater part of the Middle Miocene shallow-water carbonate sequence as developed in Papua New Guinea. Its short range suggests that it could become a valuable stratigraphical marker throughout the eastern part of the Indo-West Pacific region.

The *Alveolinella*-bearing limestones are developed in peri-reefal facies characterized by the taxa shown in Fig. 2.

DEVELOPMENT AND EVOLUTION

Since the discovery of *Flosculinella* by Schubert (1910), most authors, including Reichel who monographed the family in 1936–37, have regarded it as ancestral to *Alveolinella* despite the apparent absence of intermediate forms.

The possibility that *Alveolinella* arose from *Borelis*, a genus which appeared in Eocene times and lives on in tropical seas today, can certainly be discounted since the latter is characterized by the possession of a single row of chamberlets. Only *B. curdica* (Reichel) has shown a tendency to develop a second row, and in this species the chamberlets of the primary and secondary rows alternate in position and are therefore approximately equal in number. *Flosculinella* and *Alveolinella*, on the other hand, have two attic chamberlets for every one in the primary row.



Borelis is usually regarded as the probable ancestor of *Flosculinella*, although transitional forms have not yet been found.

The probable ancestor of *Alveolinella praequoyi* is *Flosculinella bontangensis*, a commonly occurring species in the Darai Limestone. It may well be that *F. bontangensis* grades into *F. borneensis* (from which it differs mainly in having a lower length/breadth ratio), and it would not, therefore, be surprising to find that the length/breadth ratio of *A. praequoyi* is rather variable, as seems to be suggested by the present material. For good illustrations of *F. borneensis* see Binnekamp (1973: pl. 2, figs 3–6). The only difficulty in deriving *Alveolinella* from *Flosculinella* lies in the fact that *Flosculinella* is said to possess septula which alternate in position between adjacent chambers whereas they are continuous in *Alveolinella* (Reichel 1936–37, 1964). The present material does not permit us to comment on the arrangement of septula in the juvenile stage of *A. praequoyi*.

One of us (Adams, 1983) suggested that the appearance of the attic row of chamberlets in *Flosculinella* was an example of the sudden evolutionary production of ‘novelty’ in the Foraminifera. This may well be true, but the introduction of the third row of chamberlets in *Alveolinella* is evidently a further example of gradualism.

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Figs 4–7 *Alveolinella praequoyi* sp. nov. Fig. 4, from Australasian Petroleum Co. sample 77KF, Darai Hills, associated with *Austrotrillina howchini*; age Tf₁. × 33. Figs 5a, b, **holotype** P52658, equatorial section of megalospheric form; a × 24, b (centre of test) × 48. Note irregular initial coil and gradual development of the third layer of chamberlets (see also Fig. 4). Fig. 6, P.52659, transverse section, × 48. Fig. 7, P52660, random off-centre section, × 19. Figs 5–7 all from sample 45, Hides Anticline, Central Highlands, Papua New Guinea.

Figs 8–12 *Alveolinella quoyi* (d’Orbigny). Figs 8a, b, 9, Plio-Pleistocene specimens from the Togopi Formation, North Borneo; sample NB9452 (see Whittaker & Hodgkinson 1979, for details of provenance). Note kidney shape of proloculus and planispiral coil. Figs 8a, b, P52661; a × 9.5, b × 19. Fig. 9, P52662, × 24. Figs 10, 11, sections of Recent individuals for comparison with *A. praequoyi*. Fig. 10, ZF 4911, equatorial section, × 19; New Caledonia. The subspherical appearance of the proloculus is misleading; better-orientated sections of incomplete specimens show that it is kidney-shaped. Fig. 11, ZF 4912, transverse section, × 24; Maldive Islands. Fig. 12, from Australasian Petroleum Co. well Aramia-1, 886–896 m; age early Tf₃. × 33. Figured for comparison with Fig. 4. Proloculus shape may be misleading since the centre is unclear. Note the initial planispiral coil. Few, if any, previous figures exist of *Alveolinella* from beds of Tf₃ age.



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