# On the *Heterostegina– Tansinhokella– Spiroclypeus* lineage(s) in SE Asia

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**ABSTRACT**

*The evolutionary series from Heterostegina (Vlerkina), through Tansinhokella to Spiroclypeus is reviewed. Both previously unpublished work (Muhar, 1956) and new field data is used to support the hypothesis that this evolutionary development can be observed twice in the fossil record. The first lineage became extinct at the Oligocene- Eocene boundary, and then the same morphologies re-appeared in the middle and later Oligocene. Both the negative evidence (absence) of Early Oligocene [Tc / Td Letter Stage] records, and the positive evidence of a gradual evolutionary series in Oligocene times, are discussed. At the moment there is no reliable way to distinguish the Late Eocene and later Oligocene tests, so the same generic name has to be applied to each occurrence, even though they are separated in time. This leads to the unusual situation that all three genera have to be reported as having two evolution and two extinction datums.*

*The later Oligocene transition of Tansinhokella into Spiroclypeus is observed to be more gradual than the morphological criteria used to separate these genera in 1991 (Banner and Hodgkinson), but the two names are retained for end members of a gradual series with a distinct stratigraphic record.*

*The hypothesis of iterative evolution was based on work in Java, and it was predicted that the other areas in Asia would preserve the same evolutionary pattern in the stratigraphic record. This work shows that the second evolutionary development of Tansinhokella and Spiroclypeus was at the same time in three geographically separate areas, the most reasonable explanation for which is iterative evolution, rather than ecophenotypic fluctuations or faunal migrations.*

*The importance of Tansinhokella in the biostratigraphic subdivision of Letter Stage Te is highlighted.*

## INTRODUCTION

The genus *Spiroclypeus* is an important biostratigraphic index fossil for mid-Oligocene to basal Miocene carbonates in the Indo-Pacific area. It was one of the two index taxa used to define the Letter Stage Tertiary “e” (Te) in the first proposal of the East Indies Letter Stages by van der Vlerk and Umbgrove (1927). Since the review of Krijnen in 1931 five main "species" have been recognised in the Indo-Pacific area, which have been used in the reports of the Indonesian Geological Survey and later workers. However all Krijnen’s species, with the exception of the morphologically most distinct *Spiroclypeus orbitoideus*, occur throughout almost the whole of the Te Letter Stage, and it is suspected these “species” may be ecophenotypic variants. *Spiroclypeus orbitoideus* is the type species for the genus, and is unique in being defined on the microspheric generation. It occurs only in the youngest part of the Te Letter Stage, from latest Oligocene to basal Miocene.

In 1937 Tan Sin Hok described a new species, *Spiroclypeus vermicularis*, which he considered a primitive spiroclypeid from the Late Eocene of Sungai Atan in Kalimantan (Figure 1). Since then publications have not been clear on the stratigraphic range of the group. The widely-cited works of Eames et al. (1962) and Adams (1970) noted the apparent absence of the group in Early Oligocene times (Letter Stages Tc and Td), but more recently Banner and Hodgkinson (1991) and BouDagher-Fadel (2008) gave the range of the lineage as continuous from Late Eocene to basal Miocene (Tb through Te). However, Less (2008) studied western Tethyan involute *Heterostegina* [=*Vlerkina*] and concluded that they became extinct near the end of the Eocene, apparently with no Oligocene successors.

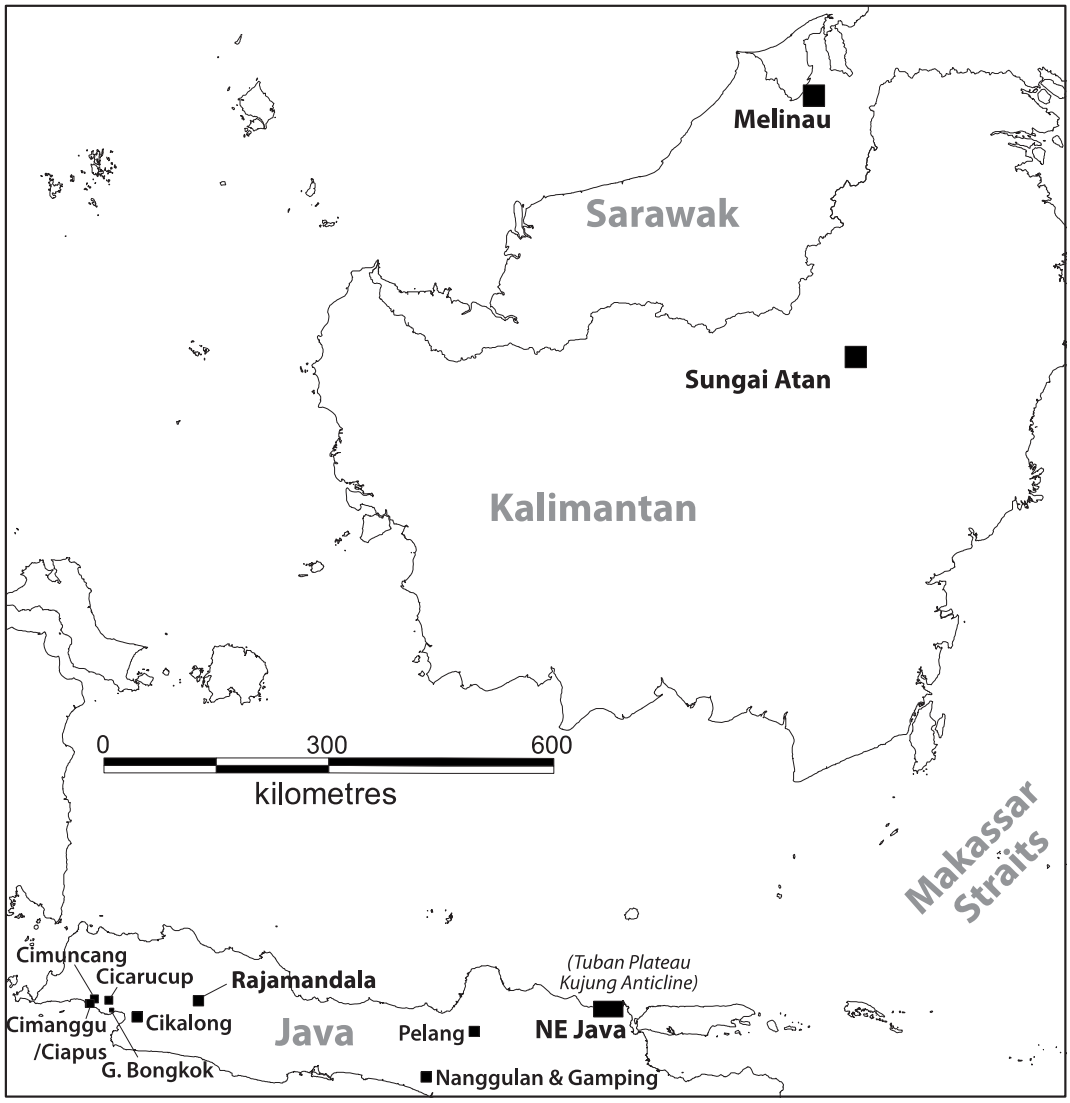



***Figure 1**. Location map of sites studied*

In 1984 Adams reviewed Neogene Indo-Pacific larger foraminifera, including *Spiroclypeus* sensu lato He noted "Until relatively recently there were no known occurrences in rocks of Early Oligocene age, but Kaever (1970) reported *Spiroclypeus* sp. from the Lower Oligocene of Afghanistan, and Rasheed and Ramachandran (1978) have recorded *S. ranjanae* TEWARI from the Lower and Middle Oligocene of Cutch." We have been unable find a copy of Kaever's paper to verify this observation. Rasheed and Ramachandran's paper is on samples from Quilon in southernmost India, not Kutch in the north west, and it does not mention or show in Plates any form related to *Spiroclypeus* or *Tansinhokella*, and all their samples contain the Miocene planktonic foraminifera *Globigerinoides*. Therefore Adams' evidence for older Oligocene occurrences is currently without support.

Banner and Hodgkinson (1991) erected a new genus that split the previous concept of *Spiroclypeus* into *Spiroclypeus* s.s. and a new taxon *Tansinhokella*. This new genus is the form intermediate between ancestral, involute *Heterostegina* (*Vlerkina*), with no lateral chamberlets, and *Spiroclypeus* s.s., with cubicula replacing lateral chamberlets. Lateral chamberlets are subdivisions of larger chambers where they overlap previous whorls (forming a lateral extension to the otherwise planiform test). Cubicula were defined as morphologically simple, perforate, calcite "cubicles", with no alignment recognisable as the remnant of a primary chamber. Banner and Hodgkinson suggested a single evolutionary series beginning in latest Eocene (Tb) when *H.* (*Vlerkina*) and then *Tansinhokella* evolved in a short period of time, followed in latest Eocene by *Spiroclypeus granulosus* BOUSSAC (a form defined in the type Priabonian; although their range chart mistakenly shows *Spiroclypeus* evolving at base Oligocene). All three genera are shown by them to range to basal Miocene times, although there is uncertainty in that paper about the highest occurrence of *H.* (*Vlerkina*).

This report, and detailed observations by Muhar (1956), differs from Banner and Hodgkinson in that we, like van der Vlerk and Umbgrove (1927), Eames et al. (1962) and Adams (1970), do not have any records of *Tansinhokella* or *Spiroclypeus* in the Tc or Td Letter Stages, in a very large sample set. In addition to this negative evidence, new work in north east Java (Figure 2) has observed an evolutionary datum for *Tansinhokella* within Late Oligocene times.

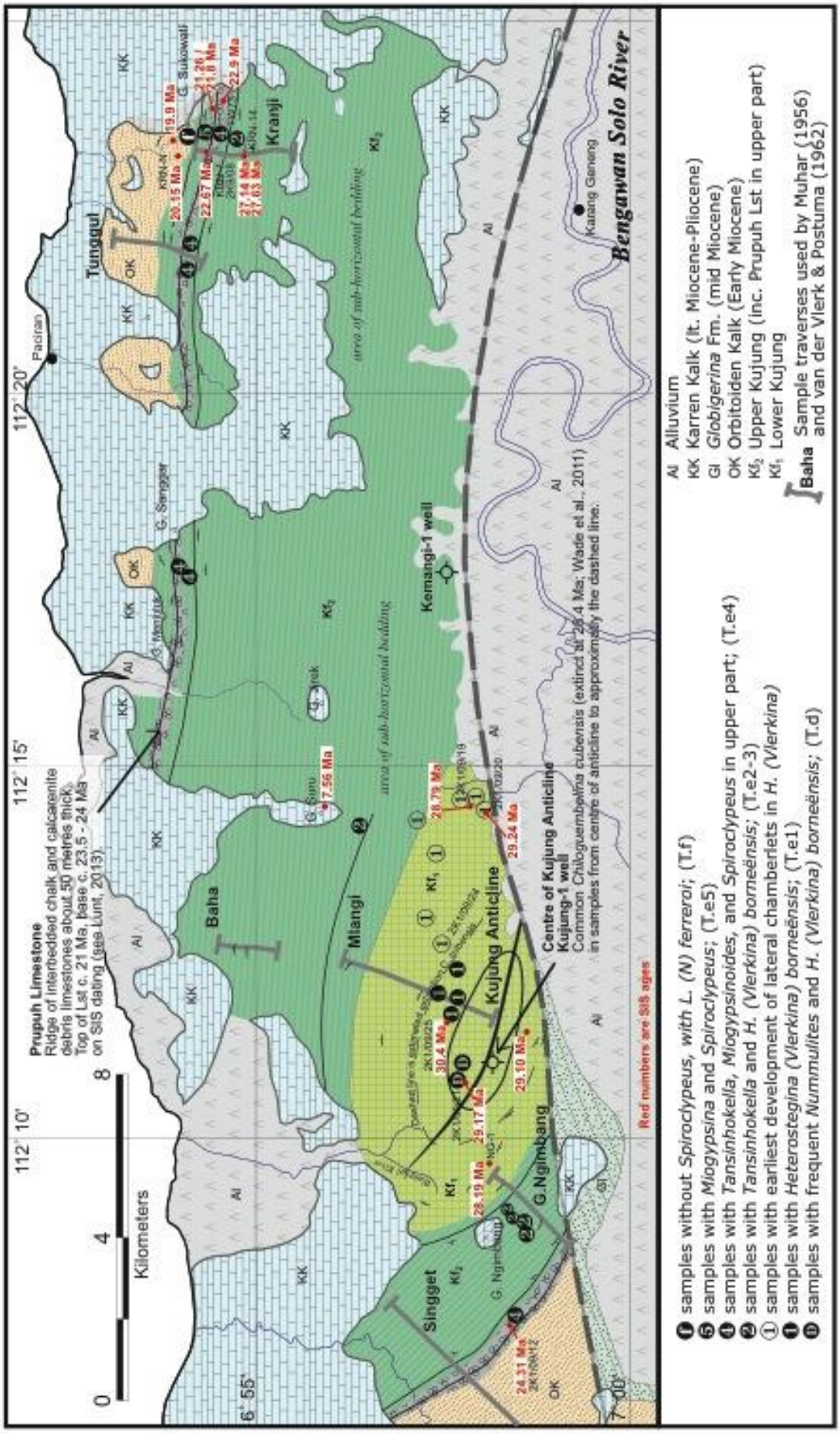



***Figure 2.*** *Occurrence of* Heterostegina (Vlerkina), Tansinhokella *and* Spiroclypeus *in NE Java. The Prupuh Limestone member is condensed and contains Te4 and Te5 Letter Stage assemblages, the latter in a condensed part too thin to distinguish on this map. Tansinhokella forms are present in samples labelled "2" through "5", but not below. Geological base map modified from BPM and GRDC. Kf1 and 2 are mostly mudstones with debris calcarenites. All samples are GPS located.*

We describe, in samples where both internal andexternal views of tests can be seen, a gradual morphological series from *Heterostegina* (*Vlerkina*) to *Tansinhokella* at about 27.5 Ma on SIS or slightly below the top of nannofossil zone NP24, or near top foraminiferal zones P21 [GTS04]. After this *Spiroclypeus* s.s. re-appeared in the stratigraphic record about 3 to 3.5 million years later, shortly before the end of the Oligocene (Figure 3).

This data appears to demonstrate the iterative evolution of both *Tansinhokella* and *Spiroclypeus* s.s., in both cases producing tests that appear identical to the earlier *Tansinhokella* and *Spiroclypeus* forms, and by the rules of nomenclature have to be given the same names. A tentative specific difference is noted between Eocene *T. vermicularis* (TAN) 1937 and *Tansinhokella* of the Late Oligocene – and the type for this genus of *T. yabei* (VAN DER VLERK) 1925. However in most random thin sections of limestone the slight difference is not visible and it may be correct to leave all specimens in *T. yabei* until the specific differentiation is shown to be viable.

The iterative evolution proposed inadvertently by Muhar (who did not know of the Eocene occurrences), and specifically by us, was tested by correlating the evolutionary datum of *Tansinhokella*, and of *Spiroclypeus* s.s., from NE Java to other locations. The hypothesis was that if these apparently evolutionary datums are seen at the same time over a wide area it would emphasise an evolutionary rather than ecophenotypic or migratory cause for the datum. Two areas are noted below to show the synchroneity of this effect, Melinau in Sarawak, and Rajamandala in West Java.
This review therefore validates Muhar's unpublished subdivision of the Lower Te Letter Stage into three parts, with the second evolution of *Tansinhokella* defining the base of Te2-3.

As yet there are no records of latest Eocene *Spiroclypeus* from S.E. Asia comparable to *S. granulosus* from Italy (however the type illustrations of *S. granulosus* apprea to have lateral chamberlets rather than cubicula and might be better placed in *Tansinhokella*, a subject requiring clarification). Across Java and probably Kalimantan, where the best studied sections are, there is a hiatus over the Eocene-Oligocene contact, in shallow marine settings. The Melinau Limestone section reviewed by Lunt (this volume), and a review of Adam's original thin sections from the Melinau Gorge stored in the British Museum, failed to find *Spiroclypeus* even in the latest Tb Eocene preserved there.

## TAXONOMY AFTER THE WORK OF BANNER AND HODGKINSON

Banner and Hodgkinson (1991) developed and completed ideas that were first suggested by Banner as part of the group of Eames et al. (1968), who proposed three subgenera within *Heterostegina*; the extant *Heterostegina*, and two extinct groups; *Vlerkina* in the mid-Oligocene and *Vlerkinella* in the Late Eocene. All three subgenera have approximately the same heterosteginid equatorial section, but in axial section *Heterostegina* (*Vlerkina*) is partly involute, with alar prolongations over the central part of the test, while *Heterostegina* (*Vlerkinella*) was considered completely involute, with long alar prolongations. *Heterostegina* (*Heterostegina*) was noted to be generally much less involute. In 1991 these concepts were revised with *Vlerkina* and *Vlerkinella* being combined on the basis that they were unreliably distinguishable on morphological grounds, with the former name having priority. In this 1991 revision the flat, completely evolute types, which were not considered by Eames et al. in 1968 but are usually called *Heterostegina* by other workers, were placed in the genus *Planostegina*. *Heterostegina* was left containing the *H.* (*Vlerkina*) group that was clearly involute throughout its life cycle and *H.* (*Heterostegina*) for types that were involute in the juvenile phase only (maturo-evolute). *Heterostegina* (*Vlerkina*) was cited as the ancestor of *Tansinhokella*, an evolutionary transition that saw the alar prolongations developed into lateral chambers by simple subdivision. In the ancestral *H.* (*Vlerkina*) the subdivision of the chambers by secondary septa stops at the outer limits of the test on the previous whorl (i.e. chamberlets are present, but they are not in a lateral position). The alar prolongations are undivided, except in specimens found at the transition to the evolutionary appearance of *Tansinhokella* (see Figure 12).

The related late Eocene genus *Grzybowskia*, which is only found in the Far East at high latitudes, on Christmas Island (to the south in Eocene times)and Bonin [Ogasawara] Islands in the north (Lunt 2003, Matsumaru, 1996) is similar to *H.* (*Vlerkina*) but the primary chambers are not subdivided by orthogonal secondary septa, but more complex, arcuate polygons of new chamberlets. Figure 12 of Lunt 2003 shows that these subdivisions do not extend into the alar prolongations and there is no evidence that *Grzybowskia* ever evolved into a morphology comparable to *Tansinhokella*.

This report differs from the work of Banner and Hodgkinson who defined cubicula as partitions having lost any recognisable remnant of the primary chamber septum, and the presence of cubicula to be definitive of *Spiroclypeus* (Table 1). We observe that loss of primary septal traces occurs very soon after the onset of lateral chamberlet formation in the earliest *Tansinhokella* (compare Figures 12 and 13). However this does not undermine the use of *Tansinhokella* as a taxon, as discussed below.

The current status of the taxonomy is not entirely satisfactory, with the same generic name(s) being applied to two apparently separate linages. Ongoing work by Renema seems to indicate differences in stolon systems between Eocene and Oligocene lineages which, if validified, means that the Eocene *Tansinhokella* and *Spiroclypeus* can be given new

generic names. Until a morphological distinction can be demonstrated the existing names should be used, as stratigraphic location is not a valid property on which to base a taxonomic distinction.

## OUTCROP QUALITY AND AGE DETERMINATION

The first sites studied were repeats of the Late Oligocene sections of Muhar (1956) in NE Java (Figure 2). The micropalaeontology of this area was described for the Bataafsche Petroleum Maatschappij (BPM) by Muhar (1956) and his samples were later used by van der Vlerk and Postuma (1967) who compared the ranges in interbedded planktonic and larger foraminifera-rich beds. The area of uplift is referred to as either the Kujung Anticline or the Tuban Plateau. Numerous overlapping sections offer nearly continuous coverage of very thick and rapidly deposited debris-flows bioclastic sands and mudstones in front of an extensive carbonate platform, drilled by many oil wells (Lunt 2013, Figure 150) and ranging in age from the top of the Early Oligocene to basal Miocene. The mid-Oligocene marker *Chiloguembelina cubensis* occurs in samples from the very centre of the anticline, associated with Td larger foram debris [rare *Nummulites fichteli*]. An apparently unbroken, deep marine stratigraphic record continues to above the evolution datums of both *Globigerinoides* and *Miogypsina* (van der Vlerk and Postuma, 1967 and Lunt, 2013). The senior author first examined the micropalaeontology in samples from seismic shot-holes across this area, with the seismic data showing simple structural form (an E-W elongate, flat-topped anticline) with no significant faults. This simple structural form is confirmed by SAR and Shuttle Radar Topography Mapping [SRTM] as the marker limestone beds stand out in relief and are unbroken. The high rate of sedimentation in this area means that any small faults below the resolution of this imaging data will have insignificant effect on the stratigraphic succession. Later, while preparing field trips for the Indonesia Petroleum Association, the area was again sampled by the senior author, with both mudstones examined for planktonic as well as both in-situ smaller and transported larger foraminifera, and the thin debris flow limestone examined in thin section as well as some dating from strontium isotope stratigraphy [SIS].

The Melinau Limestone (Figure 1) was studied and discussed by Adams (1965, 1970), in particular the Melinau Gorge was recognised as an unfaulted, continuous section of shallow marine, low energy platform carbonate some 1200 metres thick (cf. Wannier, 2009). It ranges in age from Ta (latest Middle Eocene) to within the middle of the Late Oligocene. Samples outside the Gorge continue stratigraphic coverage to basal Miocene (see accompanying paper, this volume). The Melinau Gorge seems to have the most complete latest Eocene section in the region and as such it was thought that it might contain *Spiroclypeus* bearing beds similar to those in western Tethys. The senior author has examined the original thin sections of Adams at the British Museum and later had a chance to visit and re-sample the Melinau area. The Gorge section is a single, unbroken cliff-face exposed on the northern side of the Melinau River around 114.9008° East, 4.1406° North. The Melinau Gorge section became the test of the evolutionary model developed in NE Java. Being at a location about 1250 km north of Java, it was almost certainly subject to a very different history of facies control.

***Table 1***. *Summary of generic characters from Banner & Hodgkinson 1991*

<table>
<tr><th>Planostegina</th><th>Heterostegina</th><th>H. (Vlerkina)</th><th>Grzybowskia</th><th>Tansinhokella</th><th>Spiroclypeus</th></tr>
<tr><td>evolute</td><td>maturo-evolute</td><td colspan="4">involute</td></tr>
<tr><td colspan="3">chamberlets subrectangular</td><td>chamberlets polygonal</td><td colspan="2">chamberlets subrectangular</td></tr>
<tr><td>no lateral chamberlets</td><td colspan="4">with lateral chamberlets</td><td>cubicula</td></tr>
<tr><td>no alar prolongation</td><td colspan="3">umbilically unembracing alar prolongation</td><td colspan="2">umbilically embracing alar prolongation</td><td>lateral cubicula</td></tr>
</table>

In Central Java there are three occurrences of Late Eocene larger foraminiferal limestone, primarily at Gunung Gamping (= “Limestone Hill” in Javanese, also called Gamping Barat, i.e. “west Gamping” to distinguish it from an older Eocene location also called “Gamping” nearby to the east). Gamping Barat is a biohermal limestone several tens of metres thick (Gerth 1930; Mohler 1949) and re-sampled for this study. Coring (Lunt 2013) showed this reefal limestone lies above marine ash tuff of Zone P14 age. About 16 km to the west, at the top of the Nanggulan section is a single, thin debris-flow of calcarenite, *Pellatispira*-rich limestone about a metre thick which was originally mentioned by Rothpletz (1943, unpublished) and cited in van Bemmelen (1949). This well-preserved bed is above thick P12-P14 deltaic and volcaniclastic sequences, and below condensed clays of P16 age (Lunt, 2013).

In West Java Late Eocene limestones at Cicarucup and Cimuncang, first described by Koolhoven (1933a, b) have been re-collected or examined from archived material at the Geological Museum in Bandung. These locations are of thin, transported shallow marine lenses in deeper marine mudstones, dated as within planktonic foraminiferal zone P15, probably the lower part as argued below.

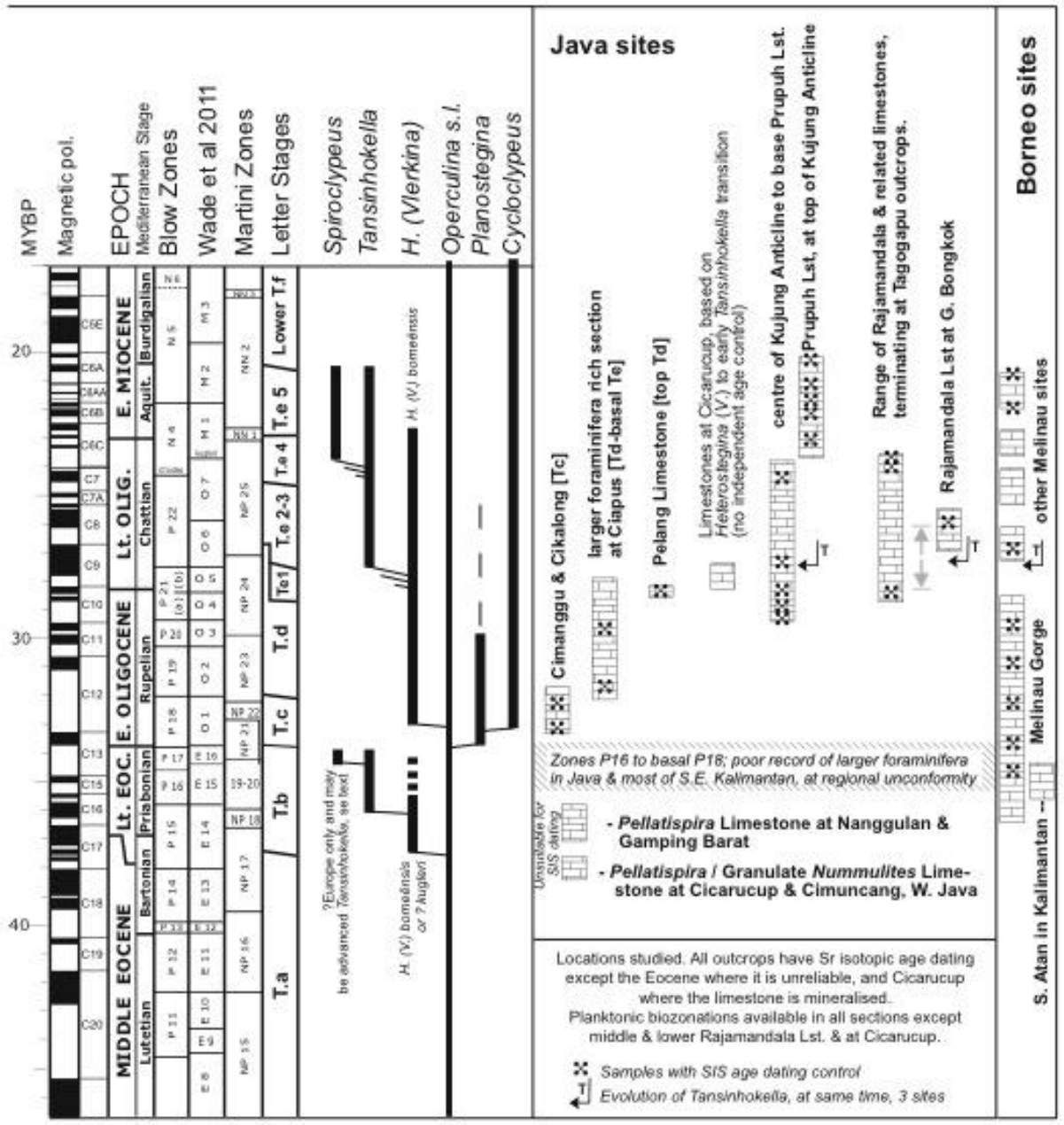



***Figure 3***. *Proposed stratigraphic ranges of* Heterostegina *(*Vlerkina*),* Tansinhokella *and* Spiroclypeus *s.s., plotted against the time scale of Gradstein et al. (2005), with additional data from Java based on strontium isotope stratigraphy (SIS data from CSIRO using sea-water calibration to Gradstein et al. 2004).*

All Late Eocene sites in Java with shallow marine carbonates are overlain by deeper marine clastics devoid of limestones or even any transported carbonate facies bioclasts. The overlying deep marine claystone is latest Eocene (P16-17), with the distinct and short ranging *Turborotalia cunialensis* and *Cribohantkenina inflata* (e.g. Nanggulan, Lunt 2013). This indicates that shallow carbonate facies are not represented in the very latest part of the Late Eocene in Java.

The Cimanggu section in West Java has shallow clastic beds with thin limestones overlying a thick non-marine deltaic sequence (Bayah Formation). The contact is not seen but the lowest fossiliferous beds in the Cimanggu section is in Letter Stage Tc. This oldest fossiliferous site was first sampled by Koolhoven (1933a, samples P204 and P296), and this small site, located at 106.120462˚E, 6.863671˚S (WGS84), has been revisited for this study. A one meter thick muddy sandstone has yielded abundant and well preserved, loose larger foraminifera, rich in heterostegines, and capping this there is a clean coralline limestone. This fossiliferous shallow marine bed overlies Bayah Formation deltaics dated as Eocene, based on the presence of *Proxapertites operculatus*. A few tens of metres vertically above this is the Tc-Td zonal transition, at which point the section can be correlated to the nearby Ciapus river outcrops [Td to lower Te, see below; Lunt, 2013]. The Cimanggu site is the type location of *Planostegina praecursor* (TAN), *P. bantamensis* (TAN) as well as *Cycloclypeus koolhoveni* TAN.

Samples from the basal Ciapus and Cimanggu sections were analysed for SIS but gave very spurious strontium ages where there was significant andesitic sand content, but the least sandy

mudstone and the clastic-free limestone above it gave ages between 33 and 34 Ma (Table 3), consistent with the basal Oligocene age indicated from biostratigraphy (*Pseudohastigerina micra* overlapping with *Cassigerinella chipolensis* and also presence of the nannofossil *Helicosphaera perch-nielseniae/obliqua*).

Most of the Ciapus section (type location of *Cycloclypeus oppenoorthi* TAN) is dated within Letter Stage Td (Lunt, 2013). This section has multiple beds of debris-flow bioclastic sands interbedded with open marine, planktonic-rich mudstones. There is a considerable drop in the abundance of *Nummulites* (? top Td) just below the extinction datum of *Chiloguembelina cubensis*, after which are a few beds with larger forams, but only very rare *Nummulites*. Above this there is a significant fault before the outcrops resume, containing basal Te index fossils.

About 65 km to the east of Cimanggu is the Cikalong section, a deep marine turbidite/ slump facies dominated by muds and silts but with beds of sands to over a metre thick, with rare sandy limestone blocks or olistoliths, rich in Tertiary c larger foraminifera and coral debris (Lunt, 2013). This site has not been dated by SIS due to paucity of calcareous material in the very deep marine facies and clastic contaminants in the limestones. Claystone foraminifera faunas are dominated by deep marine arenaceous species, but the few samples with planktonic faunas have *Chiloguembelina cubensis* and *Cassigerinella chipolensis,* indicating a general Early Oligocene age.

In eastern Java the Pelang Beds are well dated by SIS as about 28.3 Ma (combined precision and correlation error 27.59- 28.89 Ma, Lunt, 2013). The Pelang Beds are composed of a number of thin bioclastic debris-flows with rich Td faunas, overlain by chalky mudstones rich in planktonic foraminifera. The Pelang Beds and the small central area of the Kujung Anticline further east in NE Java are equivalent to the upper part of the Ciapus Td section.

A number of Javanese biohermal limestone formations of Late Oligocene to basal Miocene age have been studied in thin section, and lack the planktonic zonal control at other sites. Around Bandung the Rajamandala limestone was studied by palaeontologists of the Geological Survey (Harting, 1929) as well as being described in Hanzawa (1930). Some loose fossil specimens of *Tansinhokella* with good preservation are available from the Tagogapu site, at the top of this limestone, of very latest Oligocene age, described with isotopic dating (24.6 Ma) and detailed biostratigraphy in Lunt (2013). The Rajamandala Limestone continues west across Java, with many local names (Upper Cijengkol, Citarate and Cimapag Limestones). Its palaeontology was briefly summarized by Koolhoven (1933a,b) and it has also been re-sampled at several locations for this study. Two important mid Oligocene sites in west Java are Gunung Bongkok, a few kilometres west of the coastal town of Cisolok, with SIS dating one of the oldest *Tansinhokella* records in West Java [sample 2K/06/28, See Figure 11] and the basal Rajamandala [sample 2K1/07/12] near Gunung Walat, which was dated by SIS but contains no *Tansinhokella*.

## DISCUSSION OF PALAEONTOLOGY IN STRATIGRAPHIC ORDER

### Late Eocene (Tb)

While in Europe the Late Eocene is now considered equivalent to the Priabonian Stage, in the Indo-Pacific it has long been synonymous with Letter Stage Tb. It appears to be the same as the period from the extinction of multiple planktonic foraminifera at the top of zone P14, and a later extinction at the top of zone P17, a period of about 4 million years (Gradstein et al., 2005, Wade et al., 2011).

Late Eocene samples from Java with larger foraminifera all come from the broad (2.2 Ma) zone P15 [=early Tb], although we can argue, from secondary biostratigraphic markers (the last vestiges of Ta associated morphologies), that one of these samples is lowest P15 and the others from higher in this long-lasting zone. In the wider area around Java and South Makassar there are no known carbonates

***Table 2**. Summary of* Spiroclypeus *specific characters from Baumann 1971*

| Species | *pleurocentralis* | *tidoenganensis* | *margaritatus* | *leupoldi* | *orbitoideus* |
|---|---|---|---|---|---|
| External texture | pustulate | pustulate | pustulate reticulate | reticulate | reticulate |
| Walls between lateral chambers | much thicker than lateral chambers | much thicker than lateral chambers | about the same thickness as the lateral chambers | thinner than lateral chambers | thinner than lateral chambers |
| Shape of lateral chambers | irregular long | irregular long | becoming regular | regular short | regular short |
| Approx numbers of lateral chambers | 1 to 30 | 30 to 70 | 70 to 110 | 110 to 180 | more than 180 |

or larger foraminifera bearing facies of P16-17 age (Matthews and Bransden, 1995, Lunt, 2013). There is evidence for a major tectonic event within the middle part of the Late Eocene (latest part of N15) in this area at that time (Lunt and van Gorsel, 2013), which terminated a geographically widespread suite of carbonates of early Tb age. Overlying these carbonates are deep marine clastics of P16 to P17 age (with *Turborotalia cunialensis* and *Cribohantkenina inflata*). This may be the reason why so many Tb outcrops and well penetrations in S.E. Sundaland have not recorded *Spiroclypeus* s.s. equivalent to *S. granulosus* in Europe. The record of *S. granulosus* in the type Priabonian of Italy is given as localities around "Col de Priabona, du pied S.O. de la butte de la Grenella; route de Campi-Piana, Italy". This is in the immediate vicinity of the stratotype which was studied by Hardenbol (1968), who found zone P16 and P17 planktonic foraminifera there. However specific examination of Adams' many samples and thin sections from this terminal Eocene section in Melinau, plus new samples, did not find any *Spiroclypeus* s.s. in Sarawak. This is a genus that can be recognised from a fragment of the test, in a wide range of random orientations.

In west Java the Late Eocene sites and original samples of Koolhoven (1933a; Bayah Quadrangle mapping) have been re-examined, the former re-located from his sample maps, and the original samples archived at the Indonesian Geological Survey (Badan Geologi) in Bandung. In addition, mudstones associated with the limestone, not examined by Koolhoven and the micropalaeontologists of his day, have been studied and found to contain P15 faunas (Lunt 2013, Cimuncang site). These mudstone sediments are deep marine in origin, while the thin, larger foraminifera bearing limestones are debris-flow calcarenites.

Large numbers of thin sections and the examination of polished surfaces of many hand specimens from the multiple Koolhoven Eocene (basal Tb) limestone sites are all similar, and do not contain *Heterostegina, Tansinhokella* or *Spiroclypeus*. The Cimuncang and Cicarucup sites contain simple *Pellatispira provalei* and *P. fulgeria* types, granulate *Nummulites* species, some forms still with moderate degrees of dimorphism between the A and B generations; characters that mostly became extinct at the top of Letter Stage Ta. However the survival of some granulate species into basal Tb has already been noted by workers in the Middle East (Morley Davies et al., 1971). It was at Cicukangkarang in the Cicarucup area (106.34212˚E, -6.81661˚S) that the type of the granulate *N. hoogenraadi* (DOORNINK) was found and observations were made of *N. djokdjokartae* (MARTIN) (cf. Doornink, 1932; Koolhoven, 1933b), although the latter granulate taxon has not been seen by us and may be based on a slightly different species concept. [Note that the Cimuncang section was known to Doornink as "Tji Haur", see note in Koolhoven (1933a)]. It is the presence of these granulate forms here (and absence in other P15 sites) that suggests Cimuncang and Cicarucup are basal Tb/ basal Late Eocene in age.

Letter Stage Tb samples from Central Java, in field and core samples from the Gamping Barat location (Lunt 2103), have a different fauna to the West Java sites. They have more complex *Vacuolispira* pellatispirids, abundant *Palaeonummulites* with equal-size A and B generations, and lack granulate *Nummulites*. In addition there are frequent *Heterostegina* (*Vlerkina*) specimens and rare *Tansinhokella*. The thin debris flow limestone at Nanggulan is thought to be equivalent to the Gamping Barat bioherm and also has frequent *Heterostegina* (*Vlerkina*) (Figure 4), rare *Tansinhokella* and the same Nummulitid fauna as at Gamping Barat. At Nanggulan the thin larger foraminiferal limestone is immediately below clays with *Turborotalia cunialensis* and, in the upper part, *Cribrohantkenina inflata* (Lunt, 2013).

Processed residues from the Late Eocene of Kalimantan, including "sample 665" collected by Ubaghs on the Soengai (Sungai = river) Atan, are stored in the Museum of Badan Geologi in Bandung. Sample 665 was the type location for *Tansinhokella vermicularis* (TAN). No plankton is in these residues. The overall assemblage of *Nummulites, Discocyclina, Asterocyclina* and various species of *Pellatispira* and *Biplanispira* is not significantly different from the Central Java locations, except for the frequent *Tansinhokella*. Topotypes of *Tansinhokella* are illustrated here (Figures 6 & 7), particularly the axial sections that are not well figured in the type description.

As noted above and in the accompanying paper (Lunt, this volume), the Melinau Gorge site in Sarawak has about 400 metres of Letter Stage Tb exposed. The lower part includes samples with a high proportion of finely fragmented bioclasts, in which it is not easy to identify *Heterostegina* (*Vlerkina*), but the uppermost 130 meters of Tb contain *Tansinhokella vermicularis*, which can be identified even in fragments (Figure 5). The highest few samples of Eocene Tb contain the distinct taxa *Wilfordia sarawakensis*, which Adams defined here and predicted would be found more often in the future because of its distinct appearance, and because in these uppermost Eocene samples it is a common fossil. This has not happened, and to our knowledge Melinau Gorge is the only place this taxon has been found. It is likely that the gap in the carbonate stratigraphic record that affects the southern edge of Sundaland, as noted above, means shallow marine carbonates of latest Eocene (P16-17) age are rare in the region, but Melinau Gorge appears to include a complete Eocene-Oligocene [Tb to Tc] transition. In these latest Eocene samples of Melinau Gorge only the *Tansinhokella* morphotypes are found. Therefore to our knowledge no true *Spiroclypeus* has yet been found in the latest Eocene of the Indo-Pacific.

***Table 3.*** *Samples with strontium isotopic dating, in approximate age order*

| Sample and location | Ratio & error (%) | NIST 987 | Age & measurement precision and key marker foraminifera |
|---|---|---|---|
| Dermawu-1 just above reefal equivalent to the Prupuh Limestone<br>25 km W of the Kujung Anticline<br>111.920972E, 7.012750S | **0.708354** ± 0.0011 | 0.710140 | **19.68** (19.49 to 19.86) **Ma**<br>Foraminifera in marly mudstone c. 50 feet above a Kujung Unit 1 reef. Picked benthic foraminifera analysed. (Slightly deeper, a core in the upper limestone, with a rich Te5 fauna, gave an erroneous SIS age) |
| Kranji section of Muhar [=Kali (river) Suwuk] Sample GB/2K/06/12<br>112.389927E, 6.895659S | **0.708430** ± 0.0017 | 0.710235 | **19.94** (19.68 to 20.31) **Ma**<br>Marly mudstone above outcropping Prupuh Limestone Formation [= planktonic rich equivalent to the Kujung Unit 1) |
| Kranji section of Muhar [=Kali Suwuk]. KRN-N<br>112.382718E, 6.896083S | **0.708416** ± 0.0015 | 0.710235 | **20.15** (19.89 to 20.52) **Ma**<br>Mudstone with *Lenticulina* tests analysed. **Lower Tf** index form *Lepidocyclina ferreroi* present, no *Spiroclypeus* or *Eulepidina* |
| Dander-1 2230', Core at top of Kujung / Prupuh Limestone, 50 km SW of the Kujung Anticline.<br>111.836558, 7.325837S | **0.708296** ± 0.0014 | 0.710140 | **20.68** (20.64 to 21.25) **Ma**<br>Rich Te5 fauna present, including *Tansinhokella* |
| Prupuh section of Muhar (**type Prupuh Limestone**).<br>Sample Prupuh 1, top of Lst,<br>112.451522E, 6.919971S | **0.708356** ± 0.0015 | 0.710235 | **21.26** (21.02 to 21.53) **Ma**<br>Rich Te5 fauna present, including *Tansinhokella* and *Spiroclypeus* |
| Prupuh section of Muhar<br>Prupuh 2, nr top of Lst<br>112.450996E, 6.920137S | **0.708308** ± 0.0015 | 0.710235 | **21.95** (21.73 to 22.16) **Ma**<br>Rich Te5 fauna present, including *Tansinhokella* and *Spiroclypeus* |
| Prupuh section of Muhar<br>Sample 2K/07/56<br>112.449902E, 6.920400S | **0.708318** ± 0.0013 | 0.710235 | **21.8** (21.62 to 21.99) **Ma**<br>Rich Te5 fauna present, including *Tansinhokella* and *Spiroclypeus* |
| Kranji section of Muhar<br>[=Kali Suwuk] Sample KRN-7<br>112.383512E, 6.899693S | **0.708260** ± 0.0012 | 0.710235 | **22.67** (22.47 to 22.87) **Ma**<br>Rich Te5 fauna present, including *Tansinhokella* and *Spiroclypeus* |
| Rembang-2 swc 2682<br>Prupuh Limestone<br>110.640253E, 7.049928S | **0.708234** ± 0.0013 | 0.710235 | **23.12** (22.89 to 23.37) **Ma**<br>Near top of richly fossiliferous Te5 Lst, ? SIS age suspected slightly too old |
| Kranji section of Muhar<br>[=Kali Suwuk] TW73<br>112.395060E, 6.903582S | **0.708151** ± 0.0012 | 0.710140 | **22.91** (22.7 to 23.12) **Ma**<br>Rich Te4 fauna present, including *Tansinhokella* and *Spiroclypeus* but no *Miogypsina* |
| South of Singget section of Muhar<br>Prupuh Limestone; 2K1/09/12<br>112.124528E, 6.974596S | **0.708172** ± 0.0015 | 0.710235 | **24.31** (24.03 to 24.62) **Ma**<br>Rich Te4 fauna present, including *Tansinhokella* |
| Rembang-2 swc 2848.5<br>Lowest part of Prupuh Limestone<br>110.640253E, 7.049928S | **0.708169** ± 0.0019<br>**0.708166** ± 0.0015 | 0.710235 | **24.37** (24.01 to 24.78) **Ma**<br>**24.45** (24.16 to 24.78) **Ma**<br>Rich Te4 fauna present, including *Tansinhokella* |
| Rajamandala Limestone, near top<br>Tagogapu, 2K1/01/03<br>107.46625E, 6.81438S<br>(highest sub-sample at this site) | **0.708197** ± 0.0015 | 0.710235 | **23.84** (23.55 to 24.12) **Ma**<br>Rich Te4 fauna present, including *Tansinhokella* and Zone P22 foraminifera |
| Rajamandala Lst nr top<br>Tagogapu, 2K1/01/02<br>107.46603E, 6.81465S<br>(middle sub-sample) | **0.708190** ± 0.0012 | 0.710235 | **23.97** (23.75 to 24.2) **Ma**<br>Rich Te4 fauna present, including *Tansinhokella* and Zone P22 foraminifera |

| Sample and location | Ratio & error (%) | NIST 987 | Age & measurement precision and key marker foraminifera |
|---|---|---|---|
| Rajamandala Lst nr top<br>Tagogapu, 2K1/01/01<br>107.46603E, 6.81465S<br>(lowest sub-sample at this site) | **0.708158** ± 0.0015 | 0.710235 | **24.60** (24.29 to 24.96) Ma<br>Rich Te4 fauna present, including *Tansinhokella*, Zone P22 foraminifera and NP25 nannofossils |
| Lower Rajamandala,<br>Gunung Bongkok 2K/06/28<br>106.408896E, 6.957554S | **0.708108** ± 0.0014 | 0.710235 | **25.97** (25.56 to 26.51) **Ma**<br>Rich Te2-3 fauna present, including *Tansinhokella* |
| Kranji section of Muhar,<br>KRN-14<br>112.39237E, 6.91172S | **0.708060** ± 0.0015<br>**0.708075** ± 0.0017 | 0.710235 | **27.63** (27.02 to 28.17) **Ma**<br>**27.14** (26.45 to 27.83) **Ma**<br>Te2-3 fauna: The oldest *Tansinhokella* in NE Java, also transitional *Tansinhokella* to *Heterostegina* (*Vlerkina*) forms in this sample |
| Basal Rajamandala Limestone<br>2K1/07/12<br>106.778998E, 6.921483S | **0.708027** ± 0.0015 | 0.710235 | **28.5** (28.15 to 28.87) **Ma**<br>Te1 fauna, including *Halkyardia, Eulepidina, Heterostegina (Vlerkina)* but no *Tansinhokella* |
| Central Kujung Anticline | | | |
| Gunung Ngimbang section of Muhar<br>Sample NG-1<br>112.1590E, 6.9689S | **0.708040** ± 0.0015 | 0.710235 | **28.19** (27.79 to 28.54) **Ma**<br>Frequent *Heterostegina* (*Vlerkina*) and rare possible transitional forms to *Tansinhokella*. *Eulepidina* present |
| 6 km east of Kujung-1 well<br>Sample 2K1/09/19<br>112.240368E, 6.963830S | **0.708015** ± 0.0012 | 0.710235 | **28.79** (28.5 to 29.1) **Ma**<br>Frequent *Heterostegina* (*Vlerkina*) and possible transitional forms to *Tansinhokella*. A single *Nummulites* fragment. Large coral fragments |
| 6 km east of Kujung-1 well<br>Sample 2K1/09/20<br>112.239413E, 6.969822S | **0.707997** ± 0.0015 | 0.710235 | **29.24** (28.87 to 29.62) **Ma**<br>Frequent *Heterostegina* (*Vlerkina*) and possible transitional forms to *Tansinhokella*. |
| Mlangi section of Muhar<br>Sample 2K1/09/25<br>112.216689E, 6.955065S | 0.**707955** ± 0.0023 | 0.710235 | **30.44** (29.72 to 31.15) **Ma** Fragment of *Eulepidina*, *Lepidocyclina, Neorotalia* and *Chiloguembelina cubensis*. Te1 [SIS age probably too old considering *C. cubensis*] |
| Southeast of Kujung-1 well<br>Shot point- 89EJ33A Sp.1241<br>112.193619E, 6.981914S | **0.707908** ± 0.0012 | 0.710140 | **29.1** (28.79 to 29.39) **Ma**<br>Mudstone with good foraminiferal fauna including *Chiloguembelina cubensis, Paragloborotalia opima opima* and fragments of *Lepidocyclina* but no *Tansinhokella* |
| Northwest of Kujung-1 well<br>Sample 2K1/09/21<br>112.181879E, 6.972773S | **0.708000** ± 0.0018 | 0.710235 | **29.17** (28.71 to 29.62) **Ma**<br>Letter Stage Td including *Heterostegina* (*Vlerkina*) and planktonic Zone P21a (*Chiloguembelina cubensis*) |
| Other, older locations | | | |
| Pelang Limestone<br>Multiple samples and thin sections<br>110.751291E, 7.193862S | **0.708040** ± 0.0016 | 0.710235 | **28.19** (27.76 to 28.57) **Ma**<br>Letter Stage Td: *Heterostegina* (*Vlerkina*), frequent *Nummulites fichteli / intermedius*. [?SIS age slightly too young as overlying deep marine marls are NP24 / Lower P22 (Lunt 2013) and also have a falsely young SIS age (25.2 Ma). Also Te1 stage in Melinau is dated as old as 29.86 Ma] |
| Ciapus#5<br>106.216276E, 6.882162S | **0.707942** ± 0.0013 | 0.710235 | **30.83** (30.44 to 31.25) **Ma**<br>Letter Stage Td including *Heterostegina* (*Vlerkina*) and Nummulites fichteli / intermedius |
| Ciapus#4<br>106.216040E, 6.882752S | **0.707915** ± 0.0013 | 0.710235 | **31.71** (31.31 to 32.02) **Ma**<br>Letter Stage Td without *Heterostegina* (*Vlerkina*), rare |

| Sample and location | Ratio & error (%) | NIST 987 | Age & measurement precision and key marker foraminifera |
|---|---|---|---|
| | | | *Nummulites fichteli* |
| Ciapus#1<br>106.215600E, 6.882940S | **0.707909** ± 0.0012 | 0.710235 | **31.86** (31.51 to 32.13) **Ma**<br>Poorly preserved Td fauna (the lowest Td at this site |
| Padi 1. 110.699378E, 7.077168S<br>Good samples in Tc limestone, about 100 metres thick | **0.707893** ± 0.0012 | 0.710235 | **32.22** (32.0 to 32.41) **Ma**<br>Highest sample with Tc fauna in this well with no *Heterostegina* (*Vlerkina*) |
| Padi 1 mid- Tc sample<br>110.699378E, 7.077168S | **0.707885** ± 0.0012 | 0.710235 | **32.37** (32.16 to 32.58) **Ma**<br>Tc fauna with no *Heterostegina* (*Vlerkina*) |
| Padi 1 mid- Tc sample<br>110.699378E, 7.077168S | **0.707860** ± 0.0013 | 0.710235 | **32.84** (32.62 to 33.05) Ma<br>Tc fauna with no *Heterostegina* (*Vlerkina*) |
| Padi 1 lowest Tc sample<br>110.699378E, 7.077168S | **0.707845** ± 0.0013 | 0.710235 | **33.1** (32.89 to 33.32) Ma<br>Lowest sample with Tc fauna in this well with no *Heterostegina* (*Vlerkina*) |
| Cimanggu Cm#5,<br>106.121482E, 6.862400S | **0.707897** ± 0.0011 | 0.710235 | **32.11** (31.86 to 32.25) Ma<br>Highest bed assigned to Tc, with rare *Heterostegina* (*Vlerkina*) [**the lowest record of this genus with good stratigraphic control**] |
| Cimanggu Cm#4<br>106.120474E, 6.863654S<br>Few cms above "296" sample | **0.707841** ± 0.0014 | 0.710235 | **33.15** (32.92 to 33.40) **Ma**<br>Letter stage Tc sample, without *Heterostegina* (*Vlerkina*) but rich in large *Planostegina*. |
| Cimanggu 296<br>106.120474E, 6.863654S. Tan Sin Hok's site at base of Oligocene section | **0.707832** ± 0.0014 | 0.710235 | **33.31** (33.07 to 33.56) **Ma**<br>Letter stage Tc sample, without *Heterostegina* (*Vlerkina*)but rich in large *Planostegina*. |
| Cikolong 248,<br>Museum sample but equivalent found in same area around 106.676E, 7.021S | **0.707792** ± 0.0011 | 0.710235 | **34.03** (33.82 to 34.29) **Ma**<br>Rich Tc fauna without *Heterostegina* (*Vlerkina*) but with several large *Planostegina*. |

$^{87}Sr/^{86}Sr$ ratios normalised to $^{86}Sr/^{88}Sr$ =0.1194
Ages calculated from McArthur & Howarth (2004)

## Earliest Oligocene (Tc)

Basal Oligocene [Tc] assemblages are dominated by *Nummulites fichteli*, flat evolute *Operculina*, *Planostegina*, and small numbers of a maturo-evolute form called *Heterostegina* cf. *depressa* by both Tan Sin Hok (1932) in West Java and Adams (1965) in Melinau Tc. This *Heterostegina* (*Heterostegina*) form has been observed in new samples from the original location of Tan (Figure 8), where it is noted to have a larger size than the more compact, wholly involute *Heterostegina* (*Vlerkina*) that appears in the overlying samples.

There were no observations of *Tansinhokella* or *Spiroclypeus*, both of which can be identified from fragments due to their distinctive test architecture, in any of the Tc samples examined. These include multiple field samples from Cimanggu and Cikalong (details in Lunt, 2013), a few poorer field samples at Gunung Walat (type Batu Asih Fm; Lunt, 2013) and oil exploration wells Rembang-1 and Kujung-1in NE Java, with cuttings core and sidewall core material examined in detail by the senior author. It is considered significant that about 30 samples from Tc, roughly 12 samples from Td and about 30 more samples from lowest Te in the Melinau Gorge, often examined with multiple thin sections for each sample by Adams (1965), had no indication of *Tansinhokella*.

## Early Oligocene (Td)

The transition to from zone Tc to Td, i.e. the first observations of *Eulepidina, Nephrolepidina* and *Neorotalia mecatepecensis*, is seen in the Cimanggu section of West Java. Good Td assemblages are also seen in the nearby Ciapus section, and in both locations there is good planktonic biozonation for the Tc-Td boundary at about 32 Ma [SIS], lowest P19 and NP23 (Lunt, 2013). The Pelang limestone of eastern Java has been well studied by us, as has the central part of the Kujung Anticline (Figure 2) that includes the transition from Td to Te. The data set from this zonal interval in NE Java is quite detailed,

and mostly comprises allochthonous debris-flow limestones which tend to mix bioclasts from many shallower habitats. In many dozens of large format thin sections and examination of cut faces of hand specimens, there were common *Heterostegina* (*Vlerkina*) but no sign of *Tansinhokella*.

## Late Oligocene to basal Miocene (Te)

In NE Java there is apparently continuous stratigraphic coverage over nearly the entire Te Letter Stage. The Kujung Anticline or Tuban Plateau area (Figure 2) yields a good record of the *Heterostegina* (*Vlerkina*) to *Spiroclypeus* lineage both in thin section of debris-flow limestone and as occasional individual tests in the mixed mudstone/ calcarenite facies. In these samples there are lower samples with only *Heterostegina* (*Vlerkina*), above which are samples with forms that are morphologically transitional to *Tansinhokella,* and above these transitional forms *Tansinhokella* is common. *Spiroclypeus* is only found in the uppermost part of the section, in the harder limestones of the Prupuh Beds that straddle the Oligocene-Miocene, Lower to Upper Te, boundary.

The same location was studied by Muhar (1956) who came to the same conclusion: that *Heterostegina* (*Vlerkina*) is present lower than *Tansinhokella*. This also follows the regional observation of Leupold and van der Vlerk (1931), but neither of these workers distinguished *Tansinhokella* from *Spiroclypeus*.

The transitional forms to *Tansinhokella* are identified by the onset of subdivision of the alar prolongations in the ancestral *Heterostegina* (*Vlerkina*) in the later adult stages only (Figure 12). The subdivision of the alar prolongation into chamberlets differ from the perpendicular septula in the outer flanges (median layer) in that they are irregular and angular so that the primary septum is no longer straight. In a very short stratigraphic period a reticulate mesh of chamberlets is developed (Figure 13) and all sign of the primary septal traces is lost from what is left of the alar prolongations. This type of chamberlet formation also extends over the axis of the umbo, which in the previous morphological stage would have been the origin of the primary septa. By extending over the centre of the umbo these lateral chamberlets begin to stack up in a fashion that is independent of the whorls of growth. This is the morphological divide when the genus *Tansinhokella* has been reached (Figures 11 & 13). Figure 10 is the host rock from which the specimen enlarged in Figure 11 is obtained (Gunung Bongkok, 25.97 Ma on SIS) and this facies is rich in *Heterostegina* (*Vlerkina*) but has only rare *Tansinhokella*. In carbonate samples stratigraphically above this *Tansinhokella* is frequent to common and *Heterostegina* (*Vlerkina*) becomes increasing rare.

Outcrop samples from the Rajamandala and equivalent limestones in western Java do not yield the quality of material as observed in NE Java, but these beds have good basal assemblages rich in *Heterostegina* (*Vlerkina*), without any *Tansinhokella* or *Spiroclypeus*. Some early *Tansinhokella* specimens are illustrated here from lower Citarate Limestone near Bayah (Figure 13). Throughout the middle and upper oarts of the Late Oligocene Rajamandala Limestone are *Tansinhokella* (Figures 16 &17), and in the upper part also some *Spiroclypeus*. The upper part can be studied as thin section and in loose material at Tagogapu near Rajamandala, with SIS data on the top and bottom of this limestone given in Lunt (2013).

Stratigraphically further up in the Kujung Anticline the adult *Tansinhokella* specimens have much smaller equatorial flanges projecting outside the now multi-layered umbonal area, even in flat specimens. The general rate of coiling is not changed much from *Heterostegina* (*Vlerkina*), with about 3 complete whorls in the adult, but the sub-layers of reticulate chamberlets grow independently of the main radial chamber addition. These lateral chamberlets also extend beyond the outer circumference of the previous whorl, so that the umbonal thickening is extended and increased (compare the two extremes, Figure 11 and Figures 15b or 17).

In some adults of *Tansinhokella* there is a gerontic stage of thin-walled cubicula (Figure 15B). Banner and Hodgkinson defined cubicula as lateral chamberlets that have lost all sign of the primary septal trace and hence are no longer recognisable as subdivisions of a larger chamber. As noted above, this morphological divide is untenable as it occurs near the base of evolution of *Tansinhokella*, and hence is cannot be used as a distinguishing character for *Spiroclypeus*. The end-members of the *Tansinhokella* - *Spiroclypeus* lineage are very distinct but the morphoseries is unfortunately gradual. However there is fairly abrupt transition to very thin walled chamberlets which are considered here cubicula. In axial sections of *Tansinhokella* the remnants of spiral sheets are clear, even though they may be partially discontinuous. The very thin wall of cubicula prevents any recognition of spiral sheets, and this is the divide used here for cubicula and the onset of a *Spiroclypeus* morphology, even though it appears as a gerontic stage first, before dominating the test. As a result of the loss of the spiral sheets the *Spiroclypeus* tests become generally similar to *Lepidocyclina* (*Nephrolepidina*) in axial section, and examination of the median layer is required to see the very stunted alar prolongations (Figure 15C and 18)

The type for *Spiroclypeus* is *S. orbitoideus*, a species defined on microspheric specimens (cf. Banner and Hodgkinson, 1991). Illustrations of clearly macrospheric specimens dominated by cubicula are rare, or of poor quality in old publications, suggesting the possibility that *Spiroclypeus* s.s. - if microspheric only - could be an intra-specific dimorphic feature and unsuitable for use in a taxonomic classification. We can confirm and illustrate here that cubicula are not just restricted to

the microspheric generation (Figure 18 here, see also Plate 3- figure 3 of Krijnen, 1931 and Plate 10- figure 4 of Banner & Hodgkinson, 1991). Both *Tansinhokella* and *Spiroclypeus* occur in the Prupuh Limestone of NE Java as young as 20 to 20½ Ma (SIS dating in Lunt 2013). SIS dating in the table below has a small gap in outcrop on the dip slope of the condensed Prupuh limestone (Figure 2) which covers the top of Te and the extinction of both genera.

As noted above and in the accompanying paper, the Melinau Limestone also includes the evolutionary transition from *Heterostegina* (*Vlerkina*) to *Tansinhokella*, although the stratigraphic position is just above the end of the Melinau Gorge outcrop. The highly indurated carbonates make examination of transitional forms to *Tansinhokella* difficult and dependent on random thin-sections, so good intermediates are not as easy to find as in the samples from NE Java illustrated here. *Tansinhokella* is found in the Te5 samples between the Gorge and the Mulu Park Headquarters, and in the Mulu Quarry area (Te2-3 and Te4). The age of the oldest *Tansinhokella* in Melinau is 26.7 Ma based on SIS, while the oldest *Tansinhokella* in NE Java (sample Kranji KRN-14) is 27.14 Ma (same SIS lab and normalisation/ calibration). There is a data gap below the lowest *Tansinhokella* in Melinau (the next oldest SIS age is 29.86 Ma), but assuming the accuracy [machine precision and observation repeatability] of the SIS technique for dating is between half and one million years, then this is a good age correlation independent of biostratigraphy. This suggests that the up-section re-appearance of *Tansinhokella*, in geographically separate sites, is an evolutionary event, and not the end of some environmental or biological exclusion on a continuous, Eocene-sourced, population, exiled for more than 6 Ma in some un-sampled, peripheral site.

## TAXONOMIC NOTES AND UNCERTAINTY IN SPECIES CONCEPTS

Banner and Hodgkinson (1991) noted six or seven legally valid, and not obviously synonymous, species of *Heterostegina* (*Vlerkina*) which, in order of seniority, are:
*H.* (*V.*) *borneensis* VAN DER VLERK 1929 [late Oligocene, Lower Te, Kalimantan];
*H.* (*V.*) *assilinoides* BLANCKENHORN 1937 [basal Miocene, Te5, Turkey];
*H.* (*V.*) *texana* GRAVELL & HANNA 1937, [Late Oligocene Texas, USA];
*H.* (*V.*) *pusillumbonata* COLE 1954, [late Oligocene, Lower Te Bikini Island];
*H.* (*V.*) *pleurocentralis* (CARTER 1957) [late Oligocene, Lower Te- see Banner & Hodgkinson Oman);
*H.* (*V.*) *qatarensis* KUPPER 1957 [Recent Middle East Gulf];
*H.* (*V.*) *kugleri* EAMES ET AL. 1968 [late Eocene, Caribbean]

Of these, Banner and Hodgkinson (1991) noted that *H.* (*V.*) *qatarensis* may be maturo-evolute and not eligible for this subgenus, the matter requiring more study on un-abraded specimens. Note that the majority of species were defined in the Late Oligocene, and the last to be defined was *H.* (*V.*) *kugleri* in the Late Eocene. In the author's experience late Eocene samples with *Heterostegina* (*Vlerkina*) are relatively rare. It is therefore suggested that the Late Eocene transition through *H.* (*V.*) to *Tansinhokella* was rapid. This contrasts with the much slower succession of *Heterostegina* (*Vlerkina*) to *Tansinhokella* during the late Oligocene: about 4 Ma of *Heterostegina* (*Vlerkina*) without *Tansinhokella*. Of these species Banner and Hodgkinson (1991) selected *H.* (*V.*) *assilinoides* and *H.* (*V.*) *pleurocentralis* as having distinct morphological differences from the type *H.* (*V.*) *borneensis*. They describe *H.* (*V.*) *assilinoides* as having squarer chamberlets and weaker ornamental pillars and a smaller megalospheric proloculus, while *H.* (*V.*) *pleurocentralis* has long, narrow rectangular chamberlets and weak pillars. As Banner and Hodgkinson noted, the microspheric generation of this genus is not yet known, although microspheric forms are seen in the descendant *Tansinhokella* (cf. Krijnen 1931). Within the approximately 9 Ma duration of the Oligocene range of *Heterostegina* (*Vlerkina*), our observations see no stratigraphic pattern, restriction, or trend in the species used by Banner and Hodgkinson, so the proposed morphological variations might be ecophenotypic or within the range of monospecific variation. We see no need to use species other than *Heterostegina* (*Vlerkina*) *borneensis* at the moment.

*Heterostegina* (*Vlerkina*) *pleurocentralis* (CARTER) was one of the five species of *Spiroclypeus* recognised by Krijnen (1931). Only one of his species stays in *Spiroclypeus* s.s as used here (*S. orbitoideus*), and two are re-assigned to *Tansinhokella*. Only *pleurocentralis* is transferred to *Vlerkina*. The complex and confused nomenclatural history of this form was dealt with in Banner and Hodgkinson (1991), who elected a neotype and topotypes from the same Taqah Limestone (Lower Te, Late Oligocene; Adams and Frame 1979 and Adams pers comm. in Banner and Hodgkinson 1991), at the same location as Carter, in Oman.

Krijnen noted microspheric and macrospheric generations for all his species of *Spiroclypeus* s.l., except *S. orbitoideus*, which was described only in the microspheric form. It should be borne in mind that Krijnen assigned microspheric forms to species with macrospheric holotypes based on shared morphological features that have not been proven to be linked to a valid species concept. As noted above microspheric forms in *Heterostegina* (*Vlerkina*) are rare and have not yet been encountered by the present authors. The microspheric forms Krijnen noted for what would now be considered *H.* (*V*). *pleurocentralis* are probably not members of this taxon, following the work on neotype and topotype material of that species by Banner and Hodgkinson.

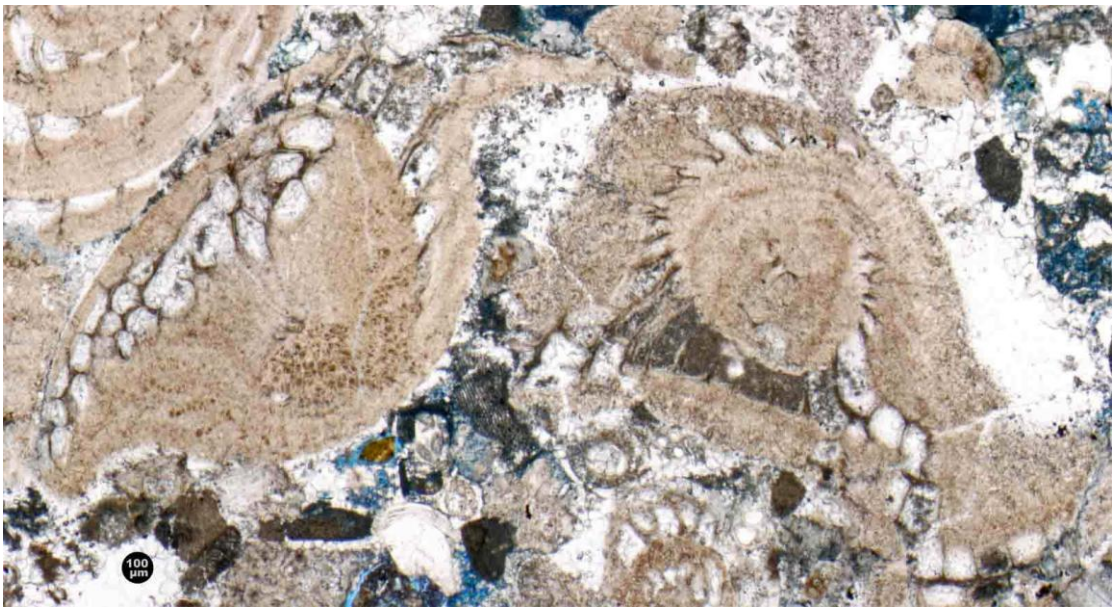



***Figure 4***. *Two oblique sections through Heterostegina (Vlerkina) in a Tb limestone found at the top of the Nanggulan section in Java (110.18664˚E, 7.73837˚S). Age of this thin limestone is lower or mid Tb as the upper Tb equivalent in this area (Zones P16, P17) is deep marine planktonic-rich clay, without larger foraminifera (Lunt, 2013). In these specimens the main chamber spaces in the equatorial flanges are clearly subdivided by secondary septa, but these do not extend into the alar prolongations that extend over preceding whorls. (100µm scale dot in lower left corner)*




***Figure 5***. *One of Adams' (1985) thin sections from S10085c in the Melinau Gorge, Sarawak (British Museum (NH) collection). This sample from the top of the Eocene Tb Letter Stage contains Tansinhokella, assigned to T. vermicularis. The irregular vermiculate or "worm-like", partly reticulate pattern of chamberlets in the broadly developed alar prologations can be seen in the oblique section, centre bottom of image. (100µm scale dot in upper right corner)*

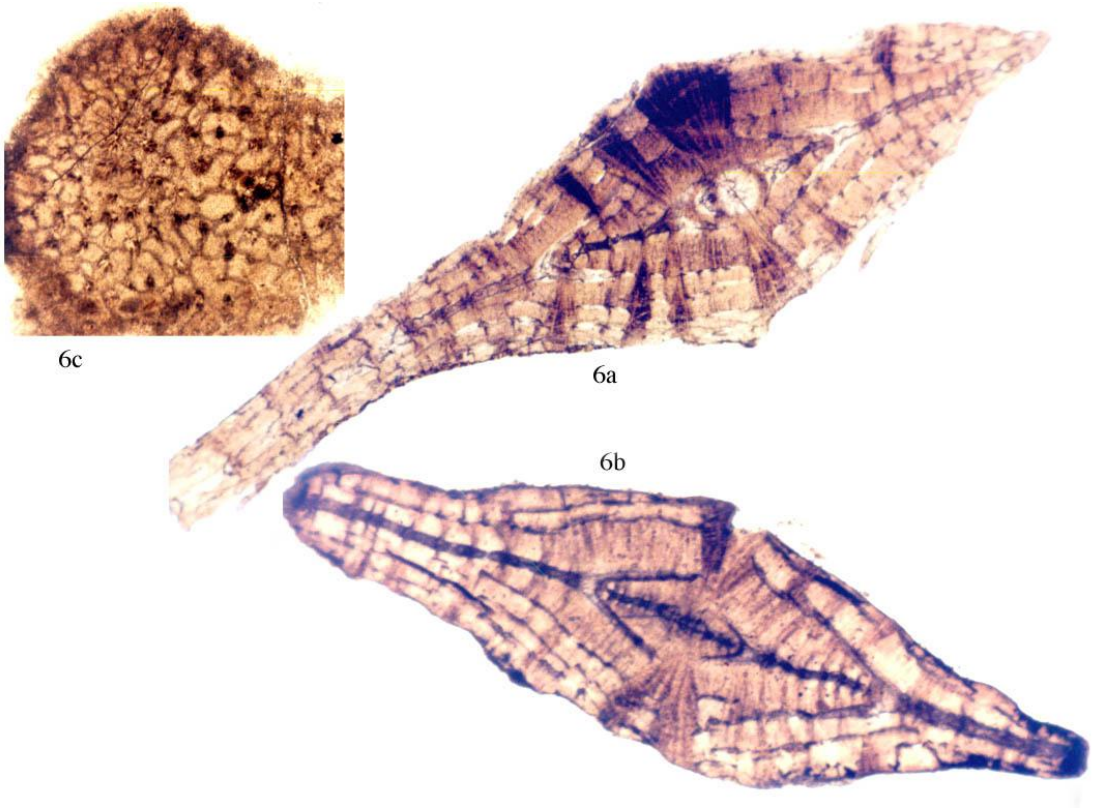



***Figure 6a, b, c.*** *Tansinhokella vermicularis (Tan). Topotype material from sample 665 of Ubaghs (1936), Soengai Atan (Atan River), Kalimantan. In the same sample as Nummulites, Discocyclina, Pellatispira and Biplanispira.* ***(a)*** *axial section of macrospheric form, 3.58 mm maximum dimension.* ***(b)*** *Near axial section, diameter 2.9 mm, reported as a microspheric form.* ***(c)*** *Section though worm-like or vermicular-shape lateral chamberlets, which is subtly different from the more regular, reticulate pattern of septal traces in the lateral chamberlets of Late Oligocene- basal Miocene Tansinhokella.*

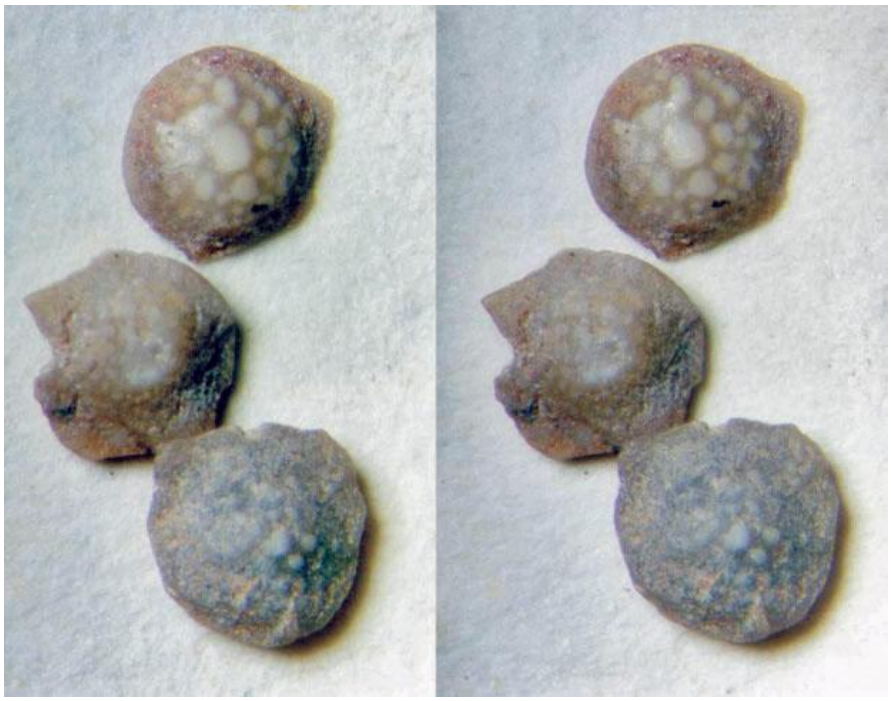


***Figure 7.*** *Stereopaired image of* Tansinhokella vermicularis *topotype material from sample 665 of Ubaghs (1936), Sungai Atan, Kalimantan. External views. Compared to the sections above from the same sample, the equatorial flanges have been reduced by abrasion. Maximum diameter of the upper test is 1.85mm. The uppermost test is cut in half and has its exterior polished to show the pillar ornament. This specimen appears, in the cut face facing the paper, to be microspheric and has the thickest central or umbonal area of any of the tests. The lower two specimens are assumed to be macrospheric and have profiles similar to the axial thin section in Figure 6a above.*



***Figure 8****. Letter Stage Tc limestone at Cimanggu, W Java (106.120462˚E, 6.863671˚S), a thin carbonate bed above soft sandy mudstone bed; "sample 296" of Koolhoven (1933). This is the type locality of Planostegina bantamensis, P. praecursor (Tan) and Cycloclypeus koolhoveni (Tan). On the right is P. praecursor; completely evolute and therefore lacking alar prolongations, in spite of the strong umbonal swelling or pillar. On the left is the form logged as Heterostegina cf. depressa by Tan (1932), which is maturo-evolute, as can be seen by the rapid reduction in thickness of the equatorial flange from intermediate to adult stage. The alar prolongations are very small in this species.*



***Figure 9.*** *Maturo-evolute* Heterostegina *cf.* depressa *sensu Tan (1932) of Letter Te1 age from the Cicarucup site in West Java (106.331770˚E, 6.828270˚S), with small alar prologations, unlike* P. praecursor*, which has a similar outline. The Te index* Eulepidina *is also in this image. While* Heterostegina *(*Vlerkina*)* borneensis *is known from sediments of this age, the large, flat* Heterostegina *cf.* depressa *is here associated with other large flat foraminifera, suggesting environmental influence on the distribution of members of the genus* Heterostegina*. The discoid, involute,* Heterostegina *(*Vlerkina*)* borneensis *is not seen in this association.*



***Figure 10.*** *Sample from Gunung (mount) Bongkok in West Java (106.408896˚E, 6.957554˚S). On the published map of Koolhoven (1933) this was mapped as Cimapag Limestone, but on the original sample map it was mapped as Citarate Lst (Cimapag, Citarate and Upper Cijengkol limestones are all equivalent to the Rajamandala Lst to the NE; Lunt, 2013). A single* Eulepidina *is present in the centre of this image. The sample is rich in* Heterostegina *(*Vlerkina*)* borneensis *with deep alar prolongations, and in some of them it seems that the number of septal traces suggests secondary septa may be present. See Figure 11 for an illustration of* Tansinhokella *from this same sample demonstrating this sample is Letter Stage Te2-3, probably the basal part.*

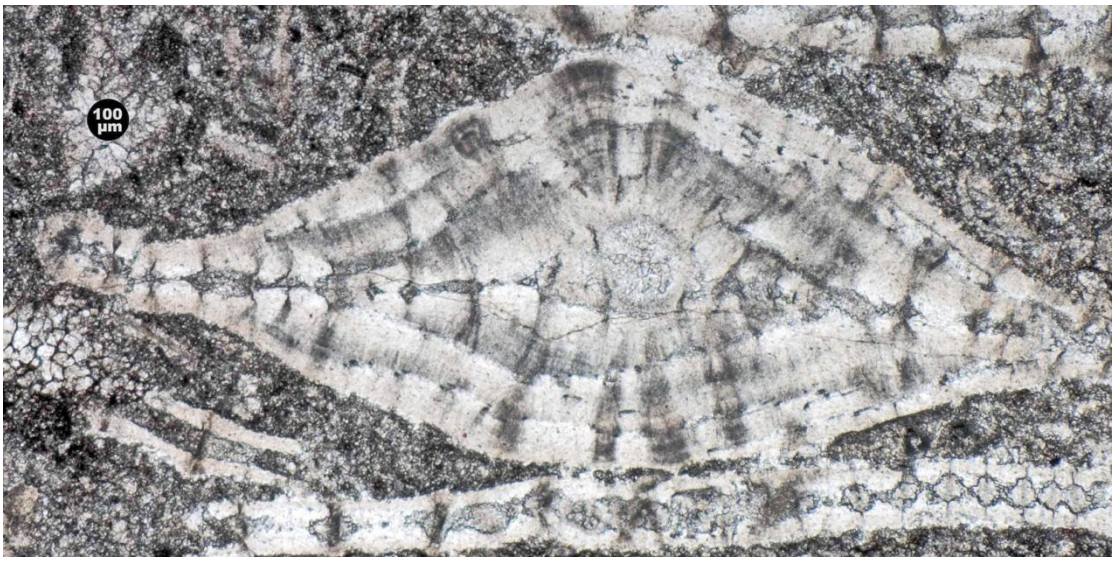



***Figure 11.*** *Gunung Bongkok West Java, same sample as Figure 10. In the minority in the fauna are some specimens of* Tansinhokella*, as shown here, with clear development of several levels of lateral chamberlets. Note that each whorl can be traced to a wall between levels of lateral chamberlets (i.e. a simple spiral sheet), and the alar prolongations that gave rise to the lateral chamberlets now extend over the center of umbo.*




***Figure 12.*** *Mudstone sample 2K1-9-24, 3 km ENE of Kujung-1 well. (112.209120˚E, 6.960842˚S; map Figure 2)*
*Mudstone samples closer to the well-site contain the index planktonic foraminifera* Chiloguembelina cubensis*, so this sample is dated as slightly younger than its 28.4 Ma extinction datum (Wade et al 2011).*
*This is one of the oldest samples containing subdivision of chambers into chamberlets within the alar prolongations. The mudstone-type preservation has stained these specimens brown but the septal traces are still white. Note the alar prolongations are still roughly radial (curved) over most of the umbonal area, certainly more so than the reticulate divisions seen in the following and slightly younger images (Figures 13a, b). The morphology of the subdivided alar prolongations does not suggest stacking of alar prolongations into layers of lateral chamberlets. Thin sections of calcarenites beds at this site contain just* Heterostegina *(*Vlerkina*).*

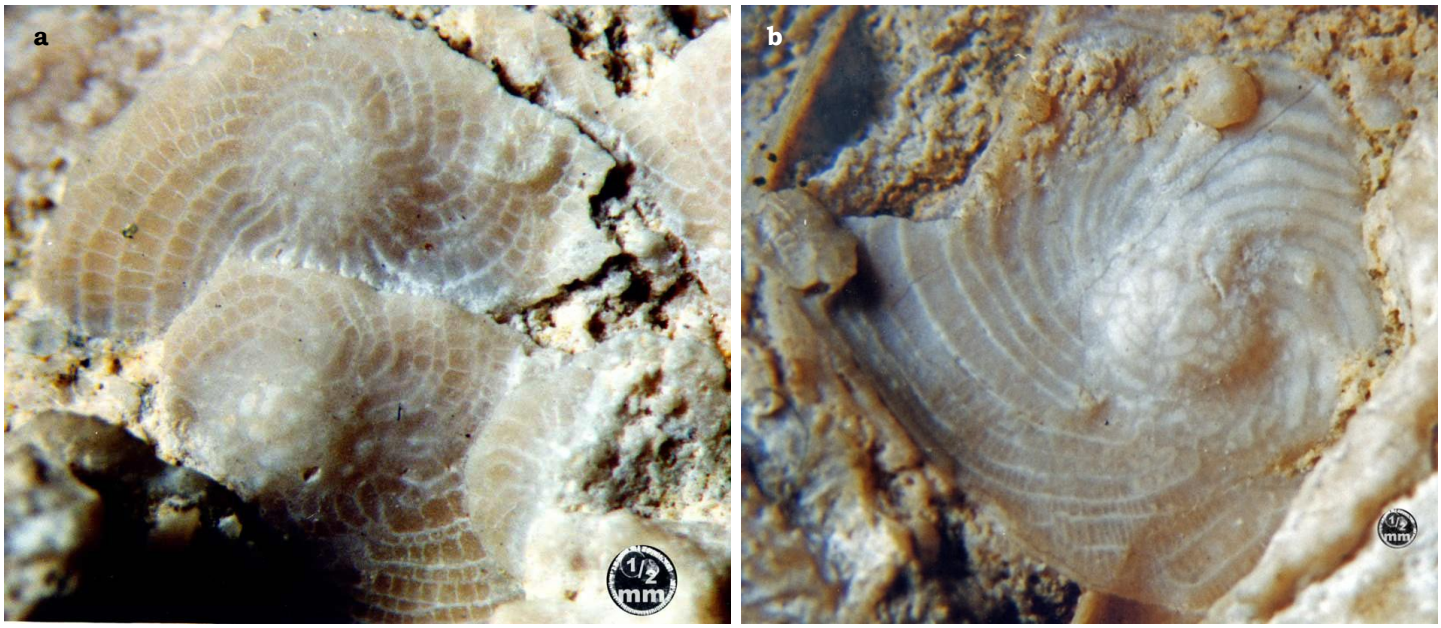



***Figure 13a, b.*** *Two images of sample155 collected by Koolhoven in map sheet 14 (Blad 14; roughly 106.2947˚E, 6.9727˚S). Samples from the Citarate Limestone, a local name for the Rajamandala Limestone. This site is roughly on-strike with the Gunung Bongkok samples (Figures 10 & 11). This site is also Letter Stage Te2-3 age, probably lower part. These large specimens are well preserved and show how the lateral chambers now form reticulate meshes that cover the umbo, and it is hard to identify any sign of a radial axis from which primary septa might originate. The extension of layers of secondary chamberlets extend over the central umbonal area would inevitably lead to overlapping layers of such chamberlets, with each whorl added, and thereby will be Tansinhokella. This genus is seen in thin sections from this and adjacent sites*

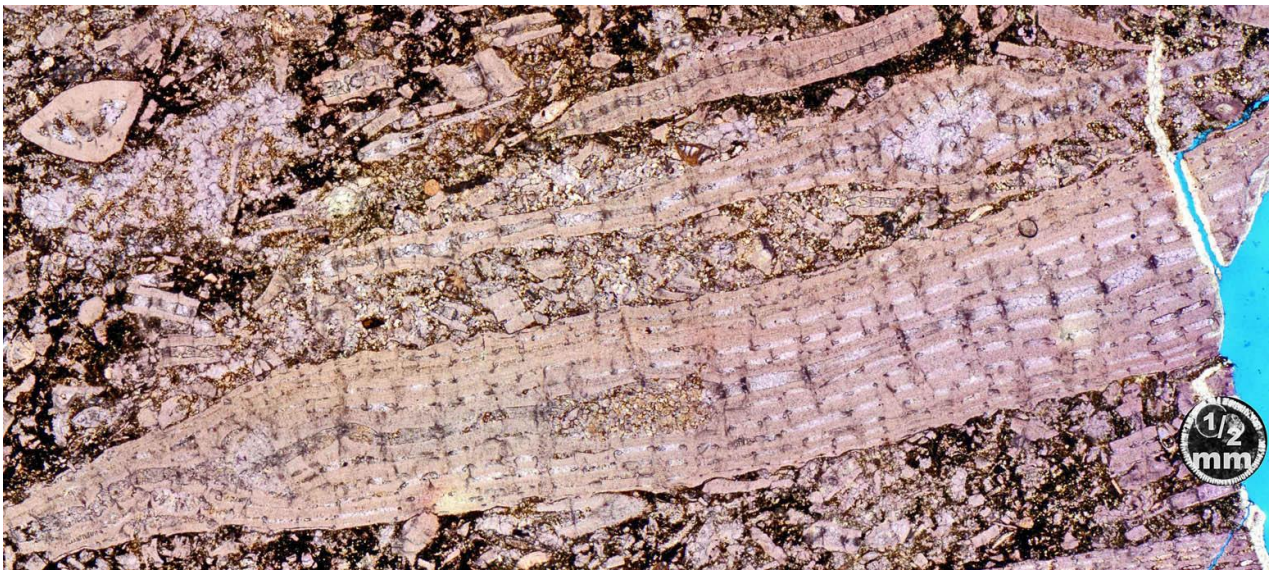



***Figure 14.*** *Thin section of Suwuk 2K/9/08, Kranji section, just below the main ridge of harder Prupuh limestone (112.386269˚E, 6.909183˚S). Large flat foraminifera dominate, probably for environmental reasons, and are a mixture of* Tansinhokella *and* Eulepidina *the former being distinguished as the whorls of growth are still visible, present in the median layer complete with nummulitic cord.* Miogypsinoides *is absent, but appears slightly higher in the sections so this sample is therefore considered upper Letter Stage Te2-3.*
*Note how in the particularly thin macrospheric test the single layer of lateral chamberlets extends a long way out from the umbonal area. This contrasts with specimens in Figures 13a, b, from the lower part of Te2-3, where lateral chamberlets are restricted to the central area over the umbonal swelling.*

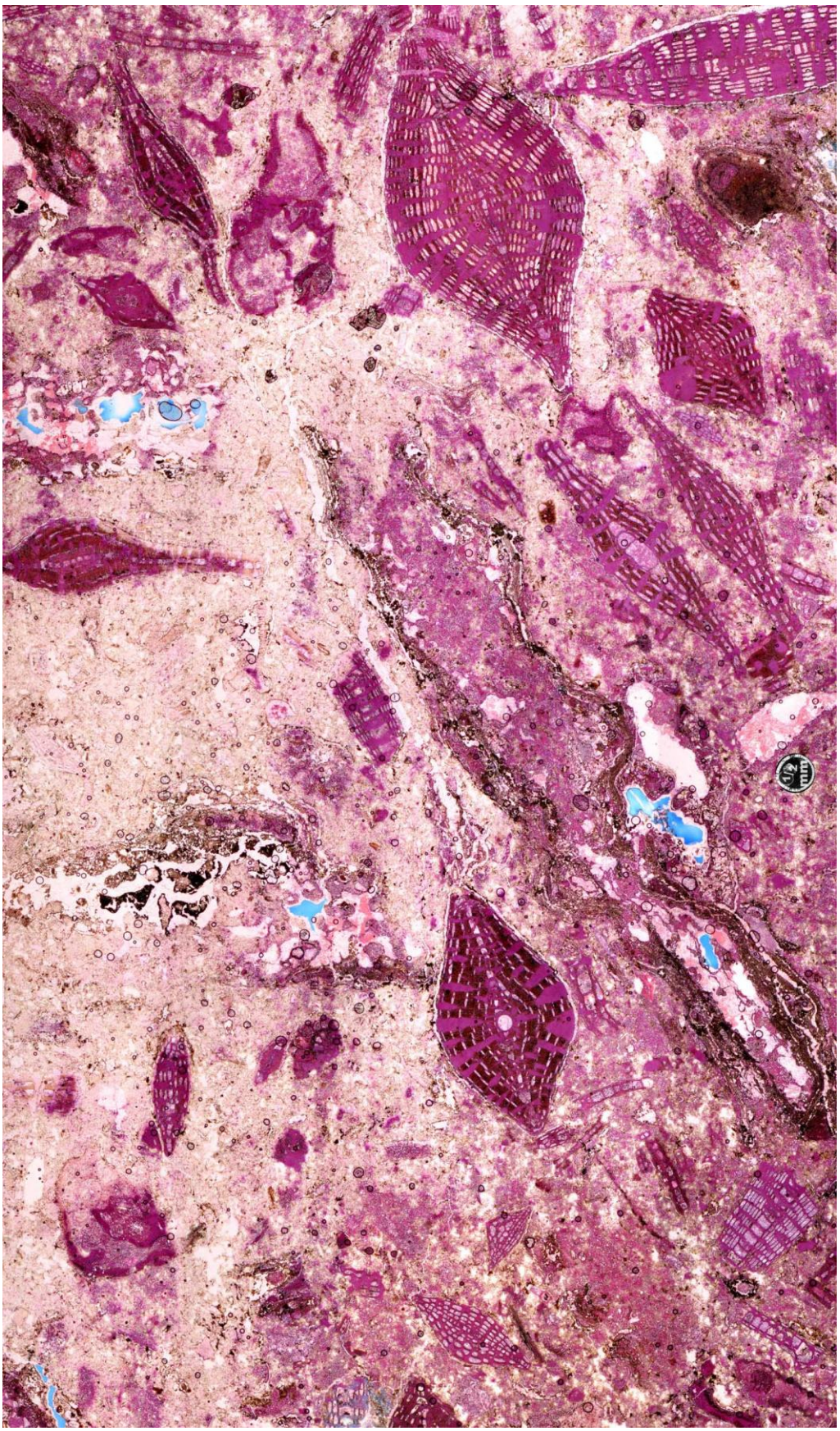


***Figure 15a.*** *Sample S27, type Prupuh limestone (just east of map in Figure 2, 112.445214˚E, 6.921136˚S), latest Oligocene just below the evolutionary appearance of* Miogypsina *(its ancestor* Miogypsinoides *is present in this slide). Shows range of advanced Tansinhokella and Spiroclypeus specimens, with* Eulepidina *and* Lepidocyclina *(*Nephrolepidina*). With the development of cubicula* Spiroclypeus *s.s are very similar to* Lep. *(*N*) but can be distinguished as the whorls of growth are visible, preserved in the median layer complete with nummulitic cord.* Spiroclypeus *now has many more layers of cubicula than whorls of growth. Some of the specimens here have about 20 layers of cubicula but only 4 or 5 whorls of the median layer. The layers of cubicula pinch out over the breadth of the test, but this high ratio of cubicula to whorls shows that growth is now focused and accelerated in the enlarged umbonal area*

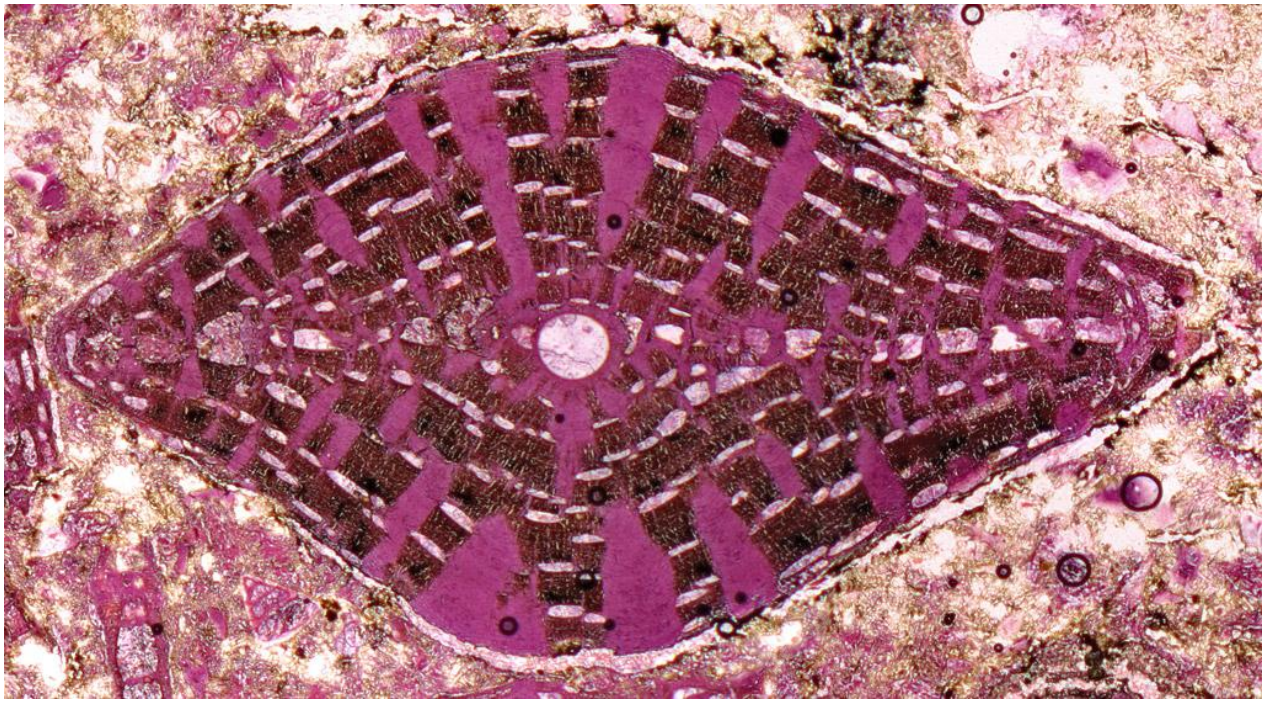


***Figure 15b.*** *Close up of* Tansinhokella *?*leupoldi*, from thin section in Figure 15a. Diameter of specimen is 3.25mm. Note on parts of the outer test a very thin walled final layer of "lateral chamberlets" or early cubicula is present, suggesting the geronitic stage may be transitional to* Spiroclypeus*. The number of layers of lateral chamberlets slightly exceeds the number of whorls*

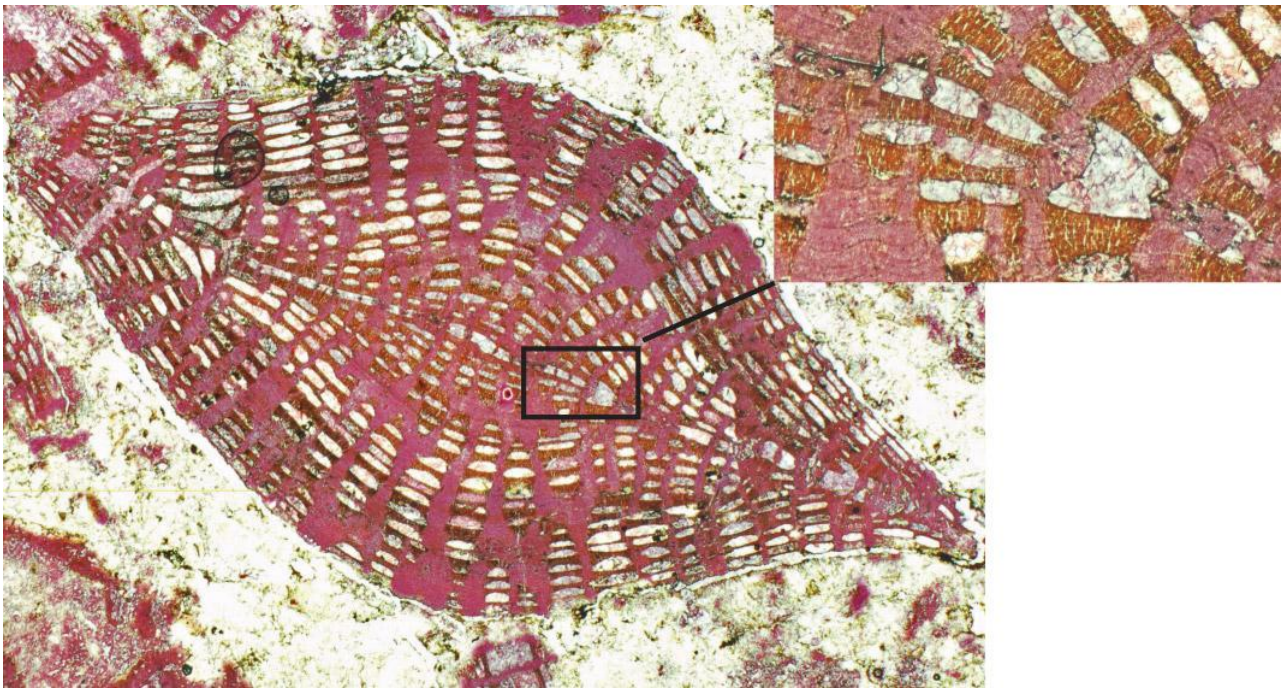


***Figure 15c.*** *Close-up of* Spiroclypeus *s.s. from thin section in Figure 15a, latest Oligocene. Diameter of specimen 4.78mm. True cubicula are present as a high number of stacked layers, greatly exceeding the number of whorls. Close examination of the median layer reveals a marginal cord, without which this specimen might be hard to distinguish from* L. *(*Nephrolepidina*). This is the largest specimen in the thin section, and may actually be a microspheric form.*

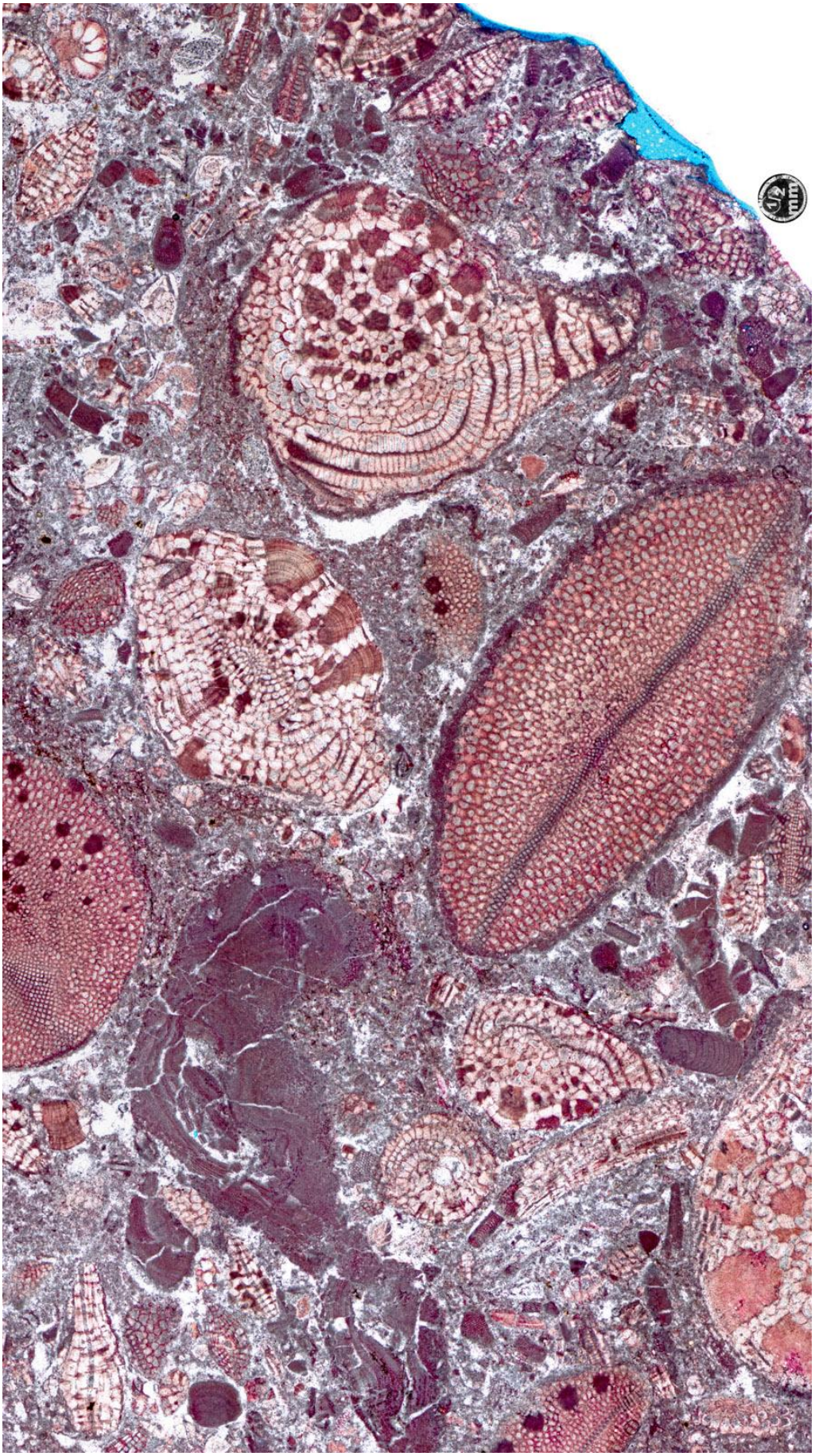


***Figure 16.*** *Rajamandala Limestone, West Java (2K/08/02 at 107.418830˚E, 6.833910˚S). Good illustration of advanced* Tansinhokella *from Letter Stage Te4 with reticulate divisions of the lateral chamberlets, but the views of axial sections shows these are within recognisable alar prologations roughly one layer of lateral chamberlets per whorl (e.g. upper left). However the specimen at the center of the slide might be microspheric and appears to have more layers of lateral chamberlets / cubicula than whorls. Reticulate pattern made by subdivision of the alar prolongation is of similar sized polygons, lacking the occasional elongate "worm-like" chamberlets seen in the Tb* Tansinhokella vermicularis*.*




***Figure 17.*** *Near top Rajamandala Limestone, West Java (107.359220˚E, 6.865160˚S, sample 2k/8/5 at the top of the Cisambeng River section). Letter Stage Te4, occurring with* Miogypsinoides*. A specimen of* Tansinhokella *where the thickness of the lateral walls is still greater than the thickness of the lateral chamberlet spaces. However the final whorl, identifiable from the presence of the nummulitic cord, can be traced back to some of the earlier, inner levels of chamberlets in the umbonal area. This suggests the later adult (gerontic) stage is dominated by rapid growth of chamberlets over the central umbonal areas during a time of reduced whorl addition.*

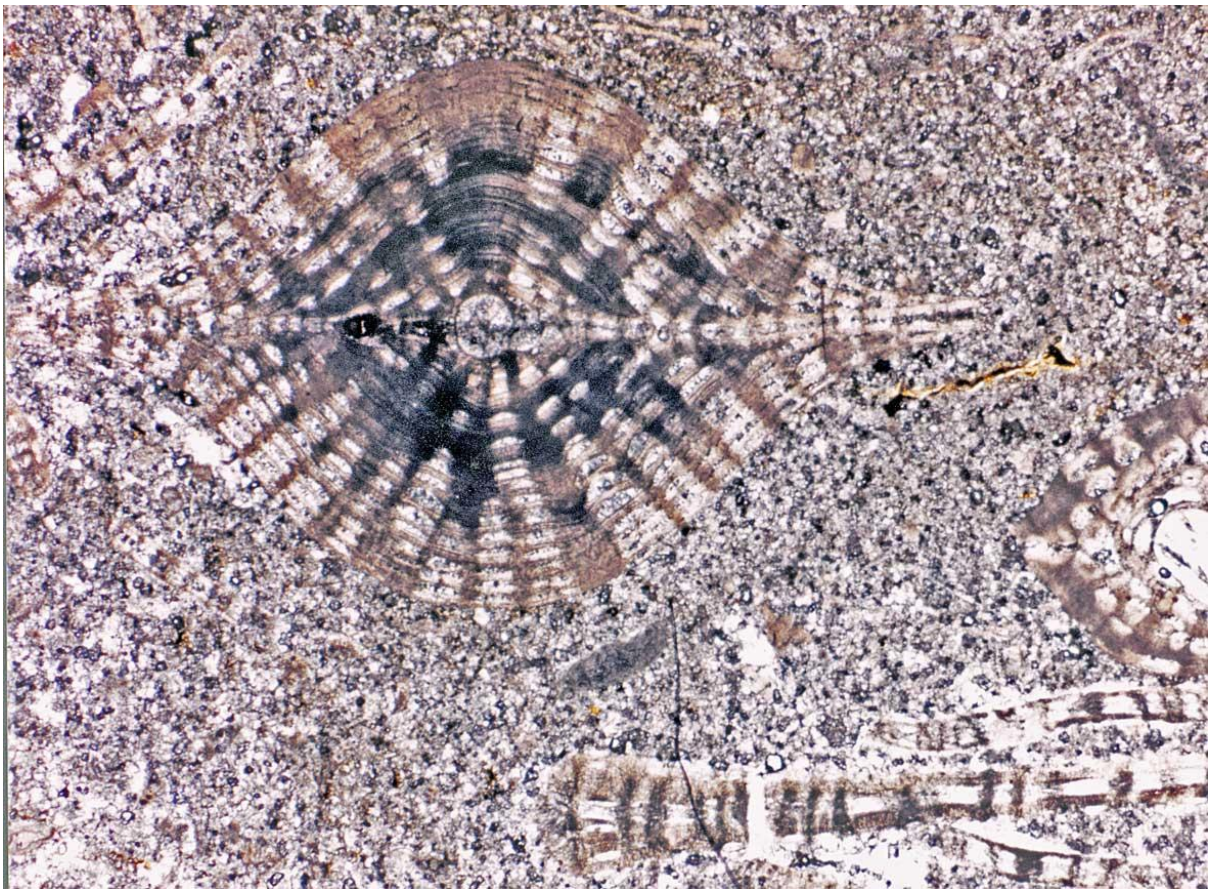


***Figure 18.*** *Macrospheric* Spiroclypeus *from Te5 in Bukit Panjang-1 well, north of Madura (113.268500˚E, 6.777821˚E). Max diameter of test visible is 4.1mm. As with Figure 15c this form looks superficially similar to* Lepidocyclina *(*Nephrolepidina*) except remnants of alar prologations can be seen. In this specimen the nummulitic cord is reduced and not clear. On the lower right are some other fragments of* Spiroclypeus*.*

In spite of this uncertainty of species concepts an important trend can be seen. This is the progression from a macrospheric-dominated population (with no discernible difference in overall size between generations) to a population with both A and B generations (where the microspheric [B] generation is overall larger and distinct). This morphological change occurs close to the *Heterostegina* (*Vlerkina*) to *Tansinhokella* transition. After this there was an increase in abundance in the microspheric generation, locally dominant, in the descendant *Spiroclypeus* s.s.

Within the genus *Tansinhokella* we use the name *T. vermicularis* for a Late Eocene form that may be morphologically distinct, with the vermicular form of the lateral chambers being locally developed (Figure 6c) and arguably more pervasive that in Oligocene forms, where tests have more regular shaped chamberlets (Figures 13 & 16). This morphological distinction is considered tentative. *Tansinhokella yabei* is the type species for the genus. This was considered a junior synonym of *"S" pleurocentralis* by Krijnen, but the work by Banner and Hodgkinson, mentioned above, resolved this synonymy.

The species of *Spiroclypeus* s.l. used by Krijnen (1931) were defined on the presence or absence of pillars and the overall shape (flat, discoid, inflated). In addition the taxon *margaritatus* was noted to have thin test walls, revealing the median layer. The taxa *pleurocentralis* and *tidoenganesis* had maximum test thickness lying well off-center in the test. Microspheric forms were assigned to the macrospheric types by sharing these basic physical properties.

In 1971 a guide to larger foraminifera was made by Paul Baumann and reproduced through Lemigas in Jakarta, and, while not formally published, it became a widely distributed and influential guide on foraminifera identification amongst oil industry workers in SE Asia. This table (Table 2) covered the five species of Krijnen, but included factors not mentioned by Krijnen, specifically the shape of lateral chambers which at "regular short" for *leupoldi* and *orbitoideus* represents the modern concept of cubicula. The data presented in Baumann's table matches the plates in Krijnen. The taxon *pleurocentralis*, now placed in the ancestral *Heterostegina* (*Vlerkina*), appears (probably by chance considering the taxonomic history) to be the morphologically simplest of the morphotypes in this series. After the "ancestral" *pleurocentralis* the trend seems as might be expected; gradually towards smaller cubicula. However much of the detail in this table is tautological as shorter individual chamberlets must result in more of them in a test of the same size, and also shortness requires simplicity in shape.

Our current opinion is that both *S. orbitoideus* and *S. leupoldi* are members of *Spiroclypeus* s.s., with the former being the senior name, defined on a microspheric form and the latter being defined on a macrospheric specimen (a drawing of the axial section - see later comments on paucity of illustrated macrospheric *Spiroclypeus* tests). The name *S. orbitoideus* is arguably an adequate name to use for all members of this genus in Asia until better species concepts are established.

## CONCLUSIONS

New analyses, in addition to those of previous workers (Muhar 1956, Adams 1970) suggest that neither *Tansinhokella* nor *Spiroclypeus* occur in deposits of Early Oligocene age, in Tc or Td Letter Stages. Observation indicates a succession from probably *Operculina* to *Heterostegina* (*Vlerkina*) then *Tansinhokella* and reportedly *Spiroclypeus* (at least in western Tethys) during the Late Eocene, then disappearance at a time of mass foraminiferal extinction [c. 33.8 Ma]. This was followed by a period with only the evolute *Planostegina* and rare maturo-evolute *Heterostegina* (*Heterostegina*), after which was a repeated evolution from *Heterostegina* (*Vlerkina*) to *Tansinhokella* to *Spiroclypeus*. The occurrence of intermediate, transitional, forms is important in proving that the interim period with no record of the taxa was due to a true extinction event, and not just temporary migration of species to an un-sampled refuge. Also the coeval timing of the re-appearance of *Tansinhokella* and then *Spiroclypeus* in three widely spaced locations indicates an evolutionary, not facies or biologically controlled migratory, cause (although, for comparison, the migration of *Eulepidina*, *Nephrolepidina* and *Neorotalia mecatepecensis* out of the Americas and across the Tethyan Ocean at base Td seems to have been a remarkably rapid migration and a biostratigraphic datum).

The second, iterative evolution of *Tansinhokella* is seen in the stratigraphic record at about 27 to 27.5 Ma in the three widely spaced locations studied. We have highlighted some uncertainty on the generic classification of *Spiroclypeus granulosus* from the Priabonian of Italy, and certainly the type illustration is of a form not as morphologically advanced as the Te4-Te5 *Spiroclypeus* forms illustrated here. In spite of a deliberate search, *Spiroclypeus* s.s. has still not yet been recorded in the Indo-Pacific Eocene. Its (?re-) evolution in the latest Oligocene of the Indo-Pacific is not as accurately dated as for *Tansinhokella*, but seems to be in the latest Oligocene, roughly at 24.5 Ma, after the evolution of *Miogypsinoides,* but before the evolution of *Miogypsina*. *Heterostegina* (*Vlerkina*) became extinct very close to the Lower Te (Te1-4)-Upper Te (Te5) boundary, with a few reliable records of this species overlapping with the Te5 marker *Miogypsina*, roughly 22 to 22.5 Ma. *Spiroclypeus* and *Tansinhokella* became extinct [along with *Eulepidina*] in an event that defines the top of Te Letter Stage, at about 20½ Ma; Lunt and Allan 2004)

As Eames et al (1962) pointed out, there is a record of *Heterostegina* (*Vlerkina*) *borneensis* with *Miogypsina* in Te5 in the Solomon Islands, SW

Pacific (Coleman and McTavish, 1964), but in SE Asia, during the regional, carbonate-rich "Bebuluh Transgression" of Te5 (Umbgrove, 1938, Tan 1939) there are no verified records of *Heterostegina* (*Vlerkina*). However *Heterostegina* (*Vlerkina*) *assilinoides* was found with *Miogypsina* (Te5) at the type location, in southern Turkey, as noted in Banner and Hodgkinson (1991, p. 266). As a result it is thought that *Heterostegina* (*Vlerkina*) became extinct in basal Te5 times.

At the moment there are no morphological criteria to separate the Late Eocene *Heterostegina* (*Vlerkina*), *Tansinhokella* or *Spiroclypeus* from the later Oligocene forms, so the same name must be used for both occurrences.

This study supports Muhar's (1956) reintroduction of the mid Oligocene evolution of *Tansinhokella* as defining the base of Te2 which, as noted above, is now placed at about 27.5 Ma (GTS04).

If this evidence, from good sample coverage of a gradually evolving and particularly distinct morphology, is taken as proof of iterative evolution, it leads to the hypothesis that this phenomenon could be more common than currently thought in genetically simple organisms; but possibly unrecognised if morphologies lack gradual stages. Iterative evolution has long been described in foraminifera (e.g. Cifelli 1969, Haq and Boersma, 1978) where the repeated occurrence of simple features (keels, clavate chambers, cortex, secondary apertures etc.) has been plotted through time. The repeated evolution of simple test forms is seen in the well-known example of *Globigerinoides subquadratus* and *G. ruber* (Cordey 1967, Blow 1979; Stainforth et al. 1975, Bolli & Saunders 1985). However there is an almost tautological inevitability that if a test is simple enough (lacking distinct features) then variation over time must involve repeated expression of apparently identical features. Secondary apertures are hard to evolve with any distinct (differentiating) characteristics and might, or might not, be repeated playing-out of the same gene. On the other hand, keels seem to be an artificial, homeomorphic rather than iterative group, as Norris (1991) and others have shown that there are five different ways to build a keel. However Norris also concluded that "since the same type of keel structure evolved independently in closely related lineages, similar genetic rules for keel construction may have been inherited repeatedly from unkeeled common ancestors."

The importance of this example, from *Heterostegina* (*Vlerkina*) to *Spiroclypeus*, is that it adds significant weight to the notion of true iterative evolution of a genetic series, and not just basic, almost unavoidable, homeomorphism. The iterative series described here shows repetition of the well-known evolutionary processes seen in larger foraminifera, including heterochrony, increased [presumed haploid/ diploid] dimorphism, and the orthogenetic trend towards the radial, three-layered "orbitoid" test.

The distinct features of larger foraminifera, such as the orbitoid test, might allow this group to become a comparative benchmark for possible examples of iterative evolution in other microfossil groups. By proving the concept could other studies tentatively recognise the possibility of iterative evolution in simpler morphologies that lack gradualism, but have interrupted stratigraphic ranges. Such candidate interruptions are currently ignored or explained as "re-working".

Examination of a range of microfossils and smaller macrofossils could address the question: is there a level of increased morphological complexity (as a proxy for genetic complexity) at which such interesting phenomena (iterative, gradual and orthogenetic evolution) disappear?

The example of foraminiferal evolution given here contrasts with recent ideas on evolution of microscopic tests evolving at random, not subjected to evolutionary pressures ("neutral morphologies"; Bonner 2013). Bonner suggests radiolarian tests shapes could be time-persistent random exaptations, (a term defined by Gould & Vrba in 1982; a feature that is an unselected consequence of selection elsewhere in the organism). The data discussed in this paper suggest evolutionary pressure is acting on microfossil tests, but this pressure is perhaps weak, as shown by the length of time it takes to go through gradual stages, and apparently at different rates in the two iterations.

Bonner proposed that the rules of evolution appear to change with physical scale; a general feature that foraminiferal data supports (e.g. gradualism over geological time and orthogenesis; both features rare or absent in the macrofossil fossil record). This paper highlights the important role that larger foraminifera, with their excellent fossil record and detailed morphologies, can play in contributing to an active area of biological research.

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