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A larger benthic foraminiferal zonation for the Eocene of the Caribbean and central American region

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Abstract: We have undertaken a study of the larger benthic foraminifera (LBF) of the Eocene of Jamaica that involved collecting free specimens and calibrating their occurrence against chronostratigraphy using calcareous nannofossils identified from sample splits or adjacent samples. The results have been plotted stratigraphically and allow a detailed zonation of the Eocene (14 zones) to be developed based largely on lepidocyclinids and similar forms. The zonation can be shown to be applicable to the Americas extending from northern South America, to Central America, the Caribbean and southern North America. The LBF biostratigraphy is based on the evolution of various groups. Three zones are recognized in the Ypresian, six zones in the Lutetian, three zones in the Bartonian, and two zones in the Priabonian. In order to classify the LBF we have revised the important groups used for the zonation scheme that occur in the Eocene and figure numerous examples. Our revision rearranges described genera into evolutionary, monophyletic clades to which we give the hierarchy of family and subfamily. We provide remarks on published taxa explaining how they are recognized and describe all the new taxa (two families, one subfamily, four genera and five species). The following families, genera and species are new: *Butterliniana* gen. nov., Helicosteginidae fam. nov., *Helicostegina minor* sp. nov., *Helicostegina jamaicensis* sp. nov., *Helicostegina jeannemairae* sp. nov., Pseudolepidinidae fam. nov., Orbitoininae subfam. nov., *Planorbitoinella* gen. nov., *Polyorbitoinella* gen. nov., *Polyorbitoinella lilyfieldensis* sp. nov., *Orbitoina wrighti* sp. nov., and *Nephronummulites* gen. nov.

Key-words:
- Lepidocyclinidae;
- Nummulitidae;
- Helicosteginidae;
- Eocene;
- biostratigraphy;
- American Larger Benthic Foraminifer (LBF) zones

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Résumé : *Zonation de l'Éocène de la région des Caraïbes et de l'Amérique centrale à l'aide des grands foraminifères benthiques.-* Le matériel de notre étude des grands foraminifères benthiques (GFB) de l'Éocène de la Jamaïque provient de la récolte de spécimens dégagés. Leur distribution a été calée sur une échelle chronostratigraphique fondée sur les nannofossiles calcaires identifiés à partir de broyats des mêmes échantillons ou d'échantillons adjacents. Les résultats de ce calibrage biostratigraphique permettent d'élaborer une zonation détaillée de l'Éocène, soit 14 zones fondées en grande partie sur les lépidocyclinides et formes affines. On démontre que cette zonation peut s'appliquer aux Caraïbes et aux Amériques, depuis la partie septentrionale de l'Amérique du Sud et, via l'Amérique centrale, jusqu'à la partie méridionale de l'Amérique du Nord. La biostratigraphie par GFB s'appuie sur l'évolution des différents groupes. Trois zones sont ainsi identifiées pour l'Yprésien, six pour le Lutétien, trois pour le Bartonien et deux pour le Priabonien. Afin d'organiser taxinomiquement ces GFB, nous avons révisé les groupes importants présents à l'Éocène et utilisés dans notre zonation. Ils sont pour la plupart abondamment figurés. Notre révision réorganise les genres décrits en clades évolutifs et monophylétiques auxquels nous attribuons le niveau hiérarchique de famille et sous-famille. Nous fournissons des précisions sur les taxons publiés en donnant les critères qui ont servi à leur identification. Quelques taxons nouveaux (deux familles, une sous-famille, quatre genres et cinq espèces) sont introduits ici ; il s'agit de *Butterliniana* n. gen., Helicosteginidae n. fam., *Helicostegina minor* n. sp., *Helicostegina jamaicensis* n. sp., *Helicostegina jeannemairae* n. sp., Pseudolepidinidae n. fam., Orbitoininae n. subfam., *Planorbitoinella* n. gen., *Polyorbitoinella* n. gen., *Polyorbitoinella lilyfieldensis* n. sp., *Orbitoina wrighti* n. sp. et *Nephronummulites* n. gen.

Mots-clefs :
- Lepidocyclinidae ;
- Nummulitidae ;
- Helicosteginidae ;
- Éocène ;
- biostratigraphie ;
- zones de Grands Foraminifères Benthiques (GFB) américains

1. Introduction

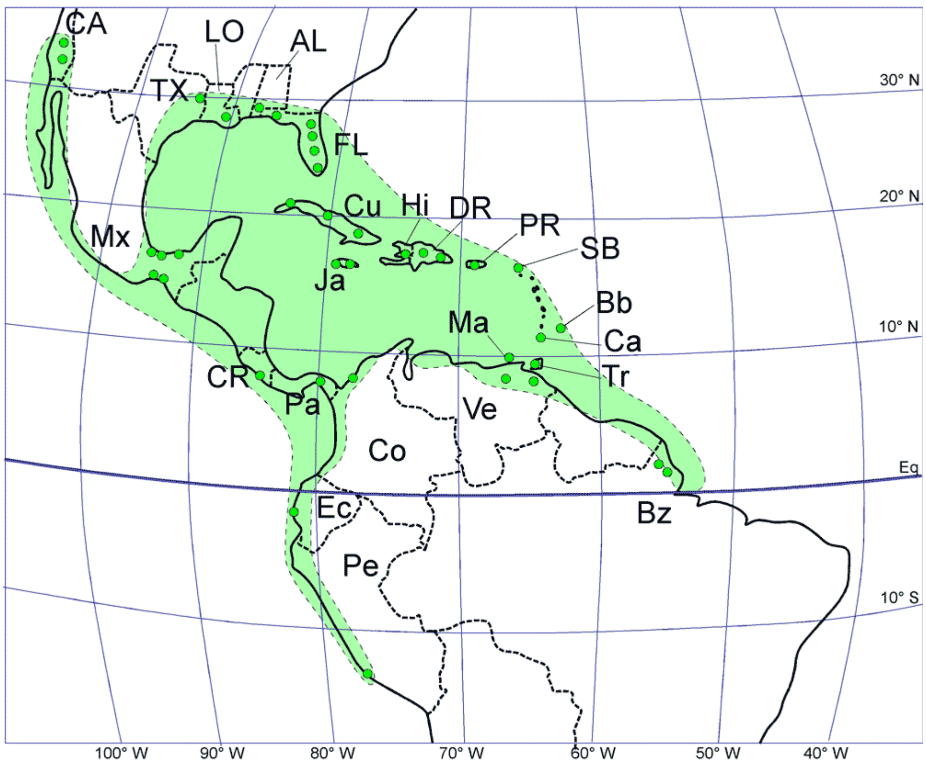
With a duration of 22.1 Myr the Eocene is the longest epoch in the 66 Myr-long Cenozoic and is traditionally zoned using planktic foraminifers (*e.g.*, Bolli, 1957a, 1957b; Bolli & Saunders, 1985; Wade *et al.*, 2011; Vandenderghe *et al.*, 2012; Ogg *et al.*, 2016; Speijer *et al.*, 2020) and calcareous nannofossils (*e.g.*, Martini, 1971; Bukry, 1973, 1975; Okada & Bukry, 1980; Vandenderghe *et al.*, 2012; Agnini *et al.*, 2014; Ogg *et al.*, 2016). Yet these groups are difficult to use in shallow-water platform limestones because they are either rare or absent, or because of the generally lithified nature of these deposits. In the Old World (*i.e.*, Europe and the Middle East), a high-resolution, larger benthic foraminiferal (LBF) zonation has been developed for the shallow-water Tethys Paleogene and early Neogene (Cahuzac & Poignant, 1997; Serra-Kiel *et al.*, 1998; Less & Özcan, 2012; Papazzoni *et al.*, 2017), yet no comparable scheme has been developed for the New World (Americas), although LBF have been used to biostratigraphically calibrate successions.

Work in Florida (P.L. Applin & E.R. Applin, 1944; Cole, 1941, 1942, 1944, 1945; Cole & E.R. Applin, 1964) suggested a series of guide fossils for the Eocene. Later work showed that the ranges of many of these 'guide fossils' were stratigraphically more extensive in the Caribbean (*e.g.*, Cole & Gravell, 1952), probably due to diachroneity of facies.

In Jamaica, Matley (1925) had attempted to zone the White Limestone using LBF, and Hose and Versey (1956) had recognised a series of zones and fossil bands, many of which were based on foraminifers that had been evaluated by Cole (1956). Robinson (1977, 1988, 1993) suggested a series of zones for the Eocene of central Jamaica, and subsequently Robinson and Jiang (1995) and Robinson (1996, 1997) demonstrated the value of evolution as a high-resolution biostratigraphic tool within the *Eulinderina-Polylepidina-Lepidocyclina* lineage in Florida and Alabama, as well as in parts of the Caribbean. In 1999, Robinson and Mitchell suggested a series of LBF assemblages for the Eocene and early Oligocene of Jamaica, and in 2004, Robinson presented a range chart showing the stratigraphic distribution of Cenozoic LBF species for Jamaica.

Elsewhere in the American region, Butterlin (1961, 1971, 1981) studied the LBF and suggested a zonation for the Eocene of Mexico (Butterlin, 1981). He recognized one subzone (B2: *Pseudophragmina zaragosensis* subzone) in the lower Eocene, four subzones (Ca: *Helicostegina dimorpha* subzone; C2: *Lepidocyclina (Polylepidina) antillea* subzone; C3: *Lepidocyclina (Neolepidina) ariana* subzone; C4: *Lituonella grandicamerata* subzone in the C: *Discocyclina marginata* zone) in the middle Eocene, and two subzones (D1: *Dictyoconus Americana* subzone, D2: *Heterodictyoconus cookei* subzone in the D: *Asterocyclina minima* zone) in the upper Eocene. The middle Eocene zonation followed that recognized in Florida by Cole and E.R. Applin (1964), whereas the upper Eocene zonation followed Robinson (1977).

A zonation has also been proposed for northeastern Brazil (Mello e Sousa *et al.*, 2003), however, many of the specimens illustrated are random sections and some species (*e.g.*, *Helicostegina dimorpha* and *Amphistegina lopeztrigoi*) do not seem to be correctly identified.



◀ **Figure 1:** Map of the distribution of Larger Benthic Foraminifers in the American (Caribbean) lepidocyclinid bio-geographical province using the current plate configuration. Dots indicate selected occurrences of LBF. AL, Alabama; Bb, Barbados; Bz, Brazil; CA, California; Co, Colombia; CR, Costa Rica; Ca, Carriacou; Cu, Cuba; DR, Dominican Republic; Ec, Ecuador; Fl, Florida; Hi, Haiti; Ja, Jamaica; LO, Louisiana; Ma, Margarita; Mx, Mexico; Pa, Panama; Pe, Peru; PR, Puerto Rico; SB, St Bartholomew; Tr, Trinidad; TX, Texas; Ve, Venezuela.

While all these schemes allow some biostratigraphic resolution for parts of the Eocene, it is far below that of the comparable scheme in the Old World. In this paper we develop a high-resolution biostratigraphic zonation for the Eocene based on LBF and chronostratigraphically calibrate it using calcareous nannofossils. We have studied sections in Jamaica that expose a more-or-less complete Eocene succession in a variety of deposition environments: shallow-water platform deposits, platform edge deposits and shelf and basin deposits. Although small unconformities are developed in the shallow-water platform successions, the deeper-water successions appear to be more complete, although some short hiatuses (or faults?) have been recognized in this study. Jamaica also lies in the centre of the evolutionary area for many of the LBF used in the zonation, and therefore Jamaica seems ideally suited to develop a zonation scheme based on LBF for the Eocene. Our zonation has a comparable resolution to the zonation developed in the Old World at least for the late Ypresian to Priabonian (Serra-Kiel *et al.*, 1998).

In this paper, we describe our methodology, describe sections used in Jamaica to define the Eocene scheme, and lay out the zonation scheme. We then show how the scheme can be used for the Eocene in selected areas of the American biogeographical province using our own observations and previous published data. Finally, we provide an updated taxonomy of the LBF used in the zonation.

2. Methodology

LBF are abundant in shallow-water Eocene rocks of the Caribbean and middle American region (Fig. 1) and range from shallow-water restricted environments to the deeper parts of the photic zone (Eva, 1976; Wright, 1974; Robinson & Mitchell, 1999; Table 1). Those inhabiting the platform margin and shallow-water photic zone (*e.g.*, lepidocyclinids and nummulitids) have the widest palaeoecological distribution (Fig. 2) and are selected as the principal taxa for the development of a zonation scheme in this paper.

Extensive new material (about 100 samples) has been collected from Jamaica over the last 15 years, which we integrate with previously collected material from Jamaica and elsewhere within the Caribbean-American region (Fig. 1). In general we have tried to collect free specimens of LBF so that external ornamentation can be recorded, and orientated sections (equatorial and axial) can be cut. This allows us to evaluate whether species can be determined in random orientations in thin sections cut from rock samples.

◆

Table 1: Foraminiferal biofacies from the Eocene of Jamaica. In situ assemblages (EB) and transported assemblages (EB-t) can be recognized. Based on EVA (1976), WRIGHT (1974), and ROBINSON and MITCHELL (1999) with amendments.

Biofacies	Description and interpretation
EB1	Foraminiferal assemblage consists of planktic and smaller benthic foraminifers. LBF absent except as transported assemblages in turbidites and storm beds (EB2-t, EB3-t and EB4-t). Deposition below the photic zone (lower ramp).
EB2 (EB2-t as transported assemblage down slope)	LBF dominated by diverse assemblages of orthophragmines together with generally small numbers of Asterigerinoidea and other taxa (*e.g.*, dictyoconids, nummulitids). Deposition in lower part of the photic zone (middle ramp).
EB3 (EB3-t as transported assemblage down slope)	LBF dominated by lepidocyclinids and nummulitids with only a low diversity (but often high abundance) assemblage of orthophragmines (notably *Stenocyclina*). Middle photic zone (middle ramp)
EB4 (EB4-t as transported assemblage down slope)	LBF dominated by lepidocyclinids (orthophragmines absent) and some nummulitids. Middle to upper photic zone, middle to upper ramp and open shelf edge.
EB5	LBF assemblage comprises lepidocyclinids and platform interior forms (typically *Yaberinella*) in broadly equal abundance. Upper photic zone, inner ramp, and protected platform edge settings.
EB6	LBF assemblage dominated by platform interior forms (*Yaberinella*, *Pseudofabularia*, *Fabularia*, dictyoconids, miliolids, etc.). Upper photic zone, inner platform settings.

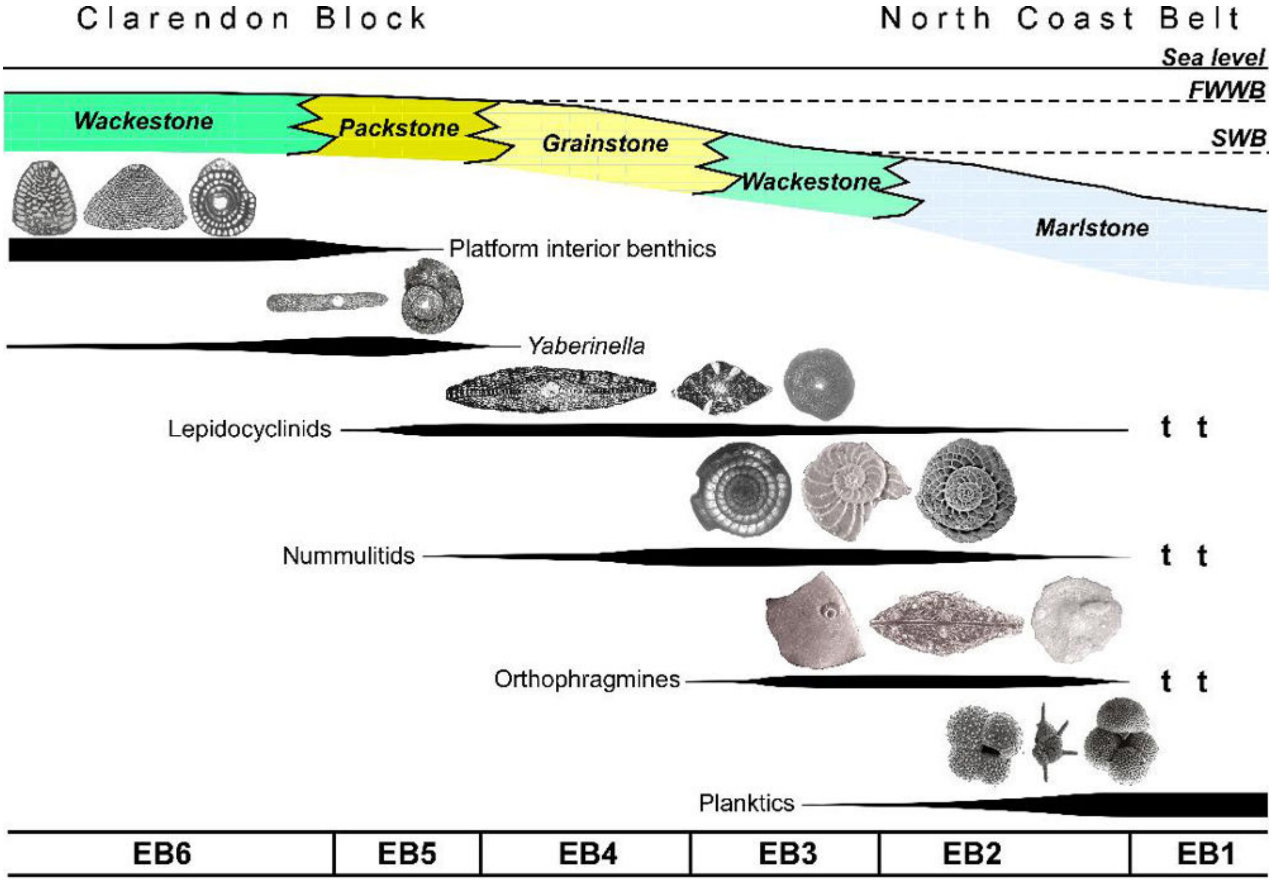


Figure 2: Palaeoecological distribution of selected Larger Benthic Foraminifers in the Eocene based on transects across the Clarendon Block and North Coast Belt of Jamaica. Revised from EVA (1976), WRIGHT (1974), and ROBINSON and MITCHELL (1999). T – specimens transported in turbidites/debris flows.

Typically large samples (a one US gallon or 3.78 litre sized bag) were collected by one of us (SFM, labelled WL) or by two of us (SFM and EÖ, also labelled WL) and broken down by drying and soaking in water, or by repeated freeze-thaw cycles in water. Following breakdown, samples were washed through a 0.5 mm sieve and the LBF were picked. For samples with low yields (or low yields of critical species) further samples were collected and disaggregated. Specimens were sorted into morphospecies based on exterior characteristics and selected specimens were then cut on a glass plate with 600 grade corundum grit to provide orientated equatorial and axial sections. During the cutting process observations were also made of the presence of features (*e.g.*, lateral chamberlets and piles/pillars) that would not be present in the final orientated equatorial thin-section. UWIGM.WL samples are preserved in the collections of the University of the West Indies Geological Museum, Jamaica. EO.WL samples are preserved in the paleontological collections of the Geological Engineering Department of İstanbul Technical University, Turkey. USNM refers to specimens housed in the Smithsonian Institute, Washington - DC. Additional material

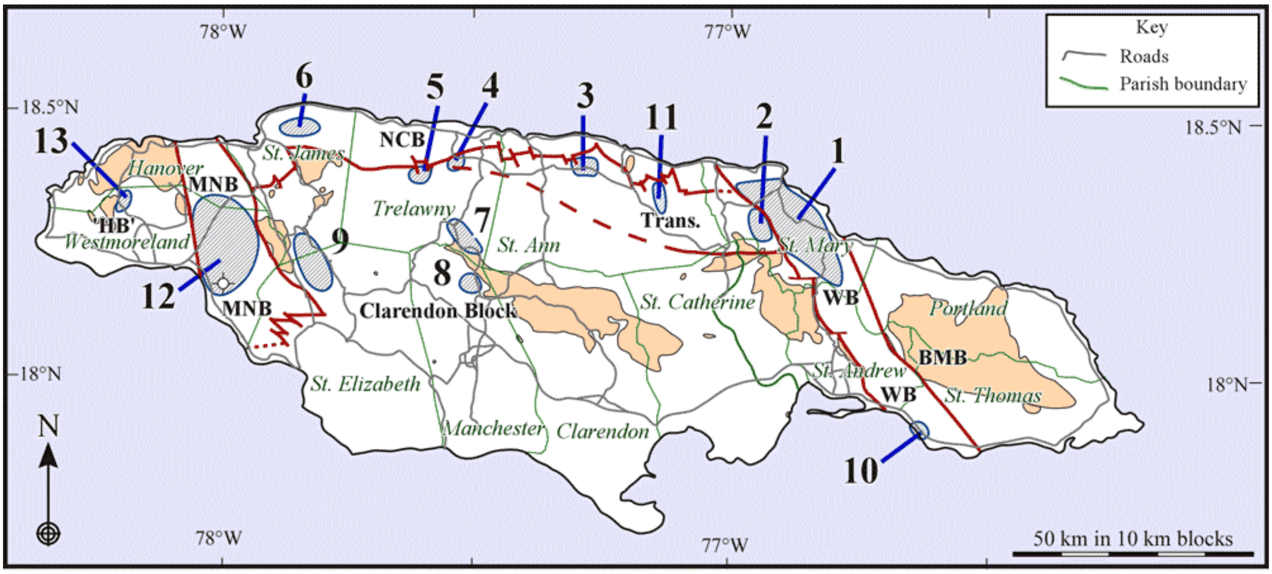


Figure 3: Eocene areas in Jamaica studied for the development of the zonation. 'HB' - Hanover Block; BMB - Blue Mountains Block (Cretaceous rocks, same colour elsewhere); MNB - Montpelier-New Market Belt; NCB - North Coast Belt; Trans. - Transitional zone between North Coast Belt and Clarendon Block; WB - Wag Water Belt. Areas studied: **1**, northern Wag Water Belt; **2**, Rio Sambre; **3**, Lilyfield-Bamboo area; **4**, Swanswick-Clarks Town area; **5**, Sherwood Content area; **6**, Salt Spring - Flower Hill area; **7**, Albert Town-Litchfield area; **8**, Coleyville area; **9**, Western Clarendon Block; **10**, Grants Pen area (St Thomas); **11**, N-S Highway (St Ann); **12**, Montpelier-New Market Belt; **13**, Jerusalem Mountain area.

collected by two of us (ER and NR) is also used in this study, this is prefixed by the letters 'ER' and 'R' respectively. The ER material was collected at various times between the late 1950s and 2005. The NR material was collected in 2017-2018. Some of the ER and NR material includes orientated sections, but most is of unorientated specimens in thin section. A detailed list of samples is provided in the sections below.

Selected samples were also studied for nannofossils. These either represented samples from continuous sections or spot samples associated with particular LBF assemblages. Previous work on nannofossils (*e.g.*, Jiang & Robinson, 1987; Robinson & Jiang, 1997) has been updated for inclusion in this work.

3. Investigated sections in Jamaica

We present brief details of the investigated sections here together with the lithostratigraphic schemes currently in use. Sections are included either because they contain intervals with both LBF and nannofossils, because they yielded free specimens of LBF, or because they are important historically for the descriptions of LBF. We correlate these sections using our LBF zones (American Benthic Zones or ABZ) that are calibrated to the chronostratigraphy using calcareous nannofossils. This paper is concerned with the Eocene which covers zones AE3 to AE16 (Fig. 4) and zones for the Paleocene and Oligocene to Miocene will be presented elsewhere. The zones are formally described after the description of the sections. A revision of the lithostratigraphic units will be presented elsewhere, as it is beyond the scope of this paper. Numbers for localities refer to Fig. 3.

Area 1. Northern Wag Water Belt (parish of St Mary): Ypresian to Priabonian

This area of the northern part of the Wag Water Belt (Fig. 3) consists of small-scale tectonic blocks separated by faults. As such, a continuous stratigraphy is not present. The lithostratigraphy follows Burke *et al.* (1969) and Mann and Burke (1990). LBF have been recovered from the Wag Water Formation, Richmond Formation and the Yellow Limestone (Palmetto Grove and Preston Hill formations) and White Limestone ("Bonny Gate" Formation) groups. The LBF typically occur as transported specimens in turbidites in deep-water shales and marlstone-limestone deposits, which we consider are broadly contemporaneous with the sedimentary rocks they are found in. Chronostratigraphic correlation is based on updated previous nannofossil records (Jiang & Robinson, 1987; Robinson, 1996, 2004) together with additional samples investigated in this work. The samples are listed in Table 2 (with details of the nannofossils in Appendix 1) and a correlation of the formations in this area is shown in Fig. 4.

A calcareous conglomerate in the Wag Water Formation (at Devon Pen) yielded a LBF assemblage characterised by *Tremastegina* with orthophragmines (Jiang & Robinson, 1987). This would indicated ABZ3. The Richmond Formation yields LBF in turbidites or shell beds (Robinson & Mitchell, 1999) and indicate zones ABZ3 and ABZ4. Samples from the Richmond Formation around Albany yield ABZ3 foraminifers with nannofossils indicating Zone NP12 (Jiang & Robinson, 1987). Samples from mudstones around Langley yield LBF indicating ABZ4 and nannofossils indi-

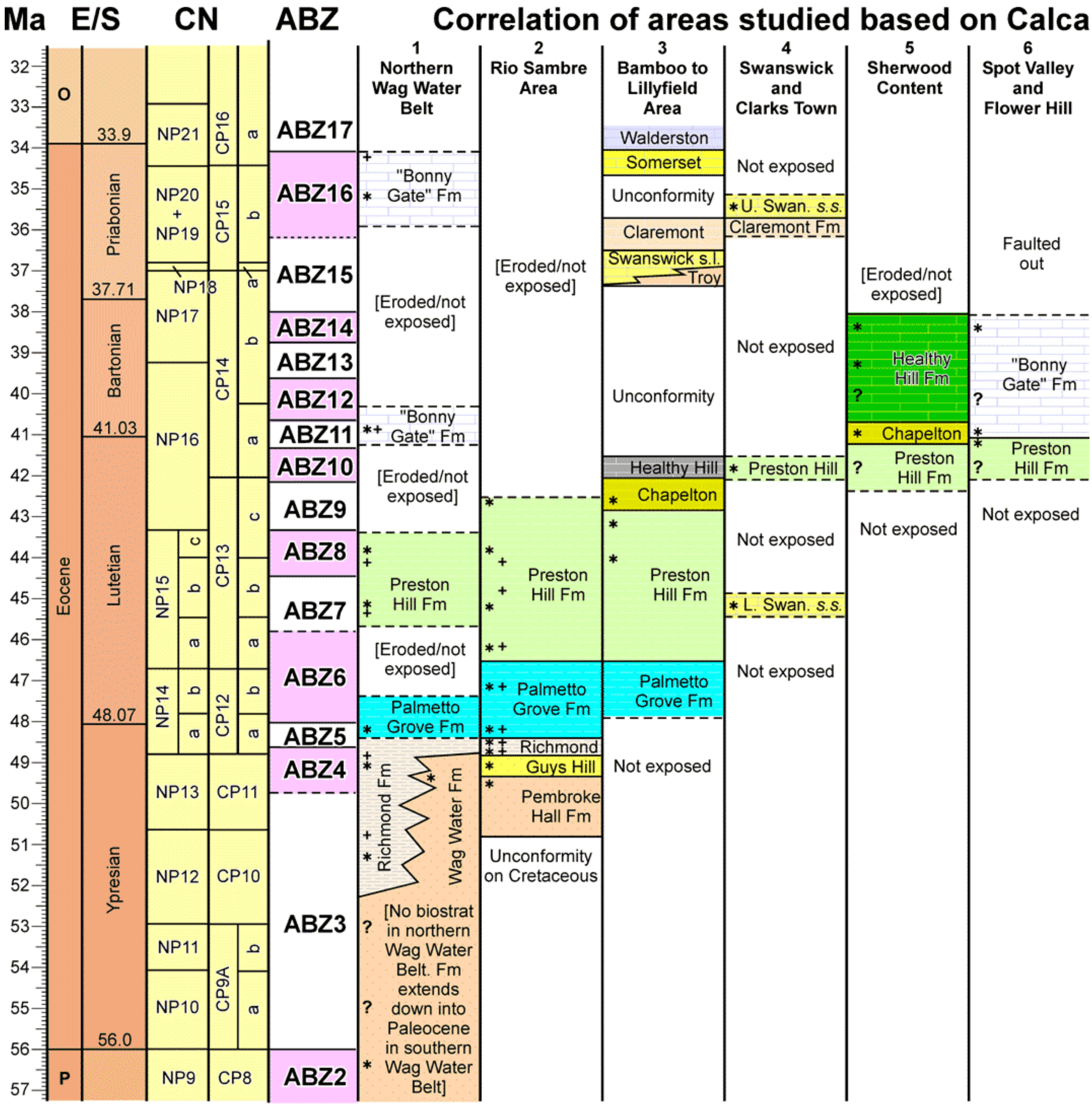
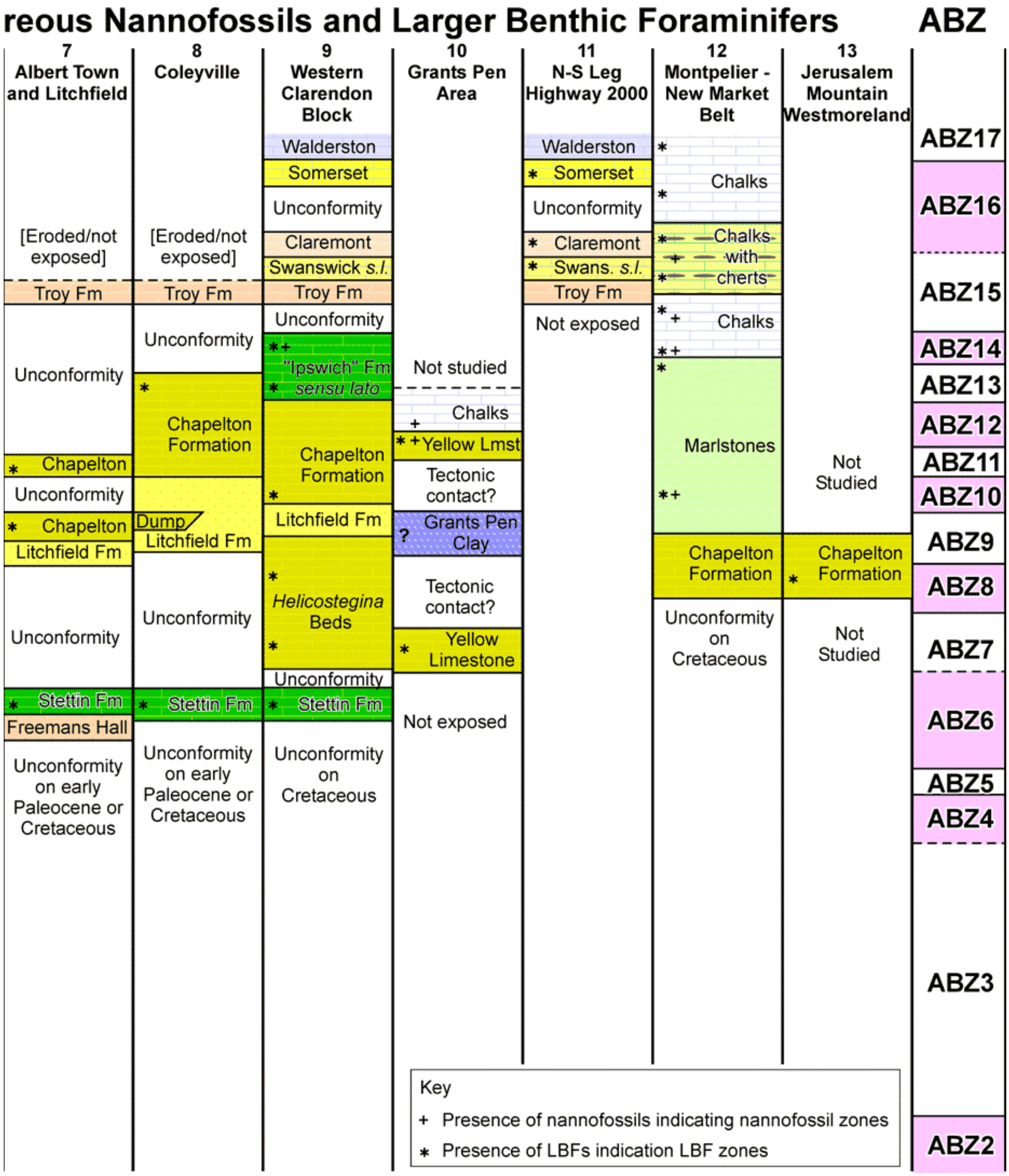


Figure 4: Correlation of formations across Jamaica using Larger Benthic Foraminifers (see zonation below) and calcareous nannofossils. Numbers as in Fig. 3. The diagram uses the 2020 timescale and zonations (Speijer *et al.*, 2020).

cating Zone NP14a (Jiang & Robinson, 1987; Appendix 1). The Wag Water Formation and Richmond Formation, at least in this area, must interfinger; with the Wag Water Formation representing slope deposits that pass into the basinal sandstones and shales of the Richmond Formation (Mitchell, 2021).

The Yellow Limestone Group is represented by the Palmetto Grove and Preston Hill formations (Burke *et al.*, 1969; Robinson & Mitchell, 1999). One sample was collected from the Palmetto Grove Formation (WL3315) and four samples were collected from the Preston Hill Formation (ER152 (= original ER sample R78), ER161, WL4869 and WL4870). No nannofossil data are available for WL3315 (which contains ABZ5 LBF) or ER152/R78 (which contains ABZ7 LBF). Planktic foraminiferal and nannofossil data were published for ER161 (P11, upper NP15, and CP13-lower CP14a; ABZ7-ABZ8 transition) by Robinson (1996). Nannofossil data for samples WL4869 and WL4870, which yield *Eulinderina guayabalensis* and *Planorbitoinella ecuadorensis* n. gen. et sp., indicate lower Zone NP15b (Table 2, Appendix 1).

The "Bonny Gate" Formation in this area has also yielded some useful samples. These are referred to the early Bartonian (WL3416: ABZ11) and late Priabonian (ER176, WL4865, ABZ16). Nannofossil data for ER176 (zone NP21) were published by Robinson (2004).



Area 2. North Coast Belt, Rio Sambre Gorge, and area around (parish of St Mary): Ypresian to Lutetian

This is among the most important areas for establishing the succession of faunas from the late Ypresian to the late Lutetian because of the continuous nature of the successions and quality of the exposures present. The lower part of the succession (Guys Hill, Richmond, and lower Palmetto Grove formations) is exposed in the bed and banks of the Rio Sambre, about 0.5 to 2 km downstream from the bridge between Palmetto Grove and Kilancholly, and the upper part (upper Palmetto Grove and Preston Hill formations) is exposed in road cuts between Farm Turn, Kilancholly and Palmetto Grove in St Mary (Fig. 3). The section in the Rio Sambre has been the subject of several reports (*e.g.*, BURKE *et al.*, 1969; WISE & CONSTANS, 1976; ROBINSON & MITCHELL, 1999). Detailed geological mapping indicates that the section begins with the Pembroke Hall Formation (of BURKE *et al.*, 1969), passes through the Guys Hill, Richmond and Palmetto Grove formations and terminates in the Preston Hill Formation. A summary section of the Richmond and Palmetto Grove formations was published in ROBINSON and MITCHELL (1999, p. 38-39).

Table 2: Details of LBF and calcareous nannofossil zone for samples from area 1 (northern Wag Water Belt). Column 1 indicates LBF zone assignment based on proximity of samples or fauna. WL GPS positions were measured in the field (ER GPS positions picked from georeferenced original field maps).

Zone	Sample	Lat/Long	Location	Formation	Nanno zone	LBF zone
ABZ3	Devon Pen	c. 18°12.3'N; 76°48.9'W	Devon Pen	Wag Water	-	ABZ3 *
"	WL3157	18°17.789'N; 76°52.263'W	Albany	Richmond	-	ABZ3
"	WL3156	18°17.444'N; 76°53.085'W	Albany	Richmond	-	ABZ3
"	WL3304	18°17.720'N; 76°51.768'W	Albany	Richmond	-	ABZ3
"	ER1547	c. 18°17.62.N; 76°50.95'W	Albany	Richmond	NP12 *	-
"	ER1548	c. 18°17.72'N; 76°51.10'W	Albany	Richmond	NP12 *	-
"	ER1549	c. 18°17.17'N; 76°51.88'W	Albany	Richmond	NP12 *	-
"	ER1550	c. 18°17.59'N; 76°51.81'W	Albany	Richmond	NP12 *	-
"	ER1551	c. 18°18.32'N; 76°51.83'W	Albany	Richmond	NP12 *	-
ABZ4	WL3158	18°15.176'N; 76°52.748'W	Richmond	Richmond	-	ABZ4
"	WL3159	18°14.507'N; 76°52.666'W	Richmond	Richmond	-	ABZ4
"	WL3160	18°14.507'N; 76°52.666'W	Richmond	Richmond	-	ABZ4
"	WL3148B	18°13.353'N; 76°50.987'W	Rock River	Wag Water - Richmond transition	NP14a	-
"	WL3394A	18°19.056'N; 076°55.387'W	Langley	Richmond	NP14a	ABZ4
"	WL3154	18°18.649'N; 76°54.904'W	Langley	Richmond	-	ABZ4
ABZ5	WL3155	18°18.252'N; 76°55.237'W	Hampstead	Palmetto Grove	-	ABZ5
"	WL3316	"	"	"	-	ABZ5
"	WL3381	"	"	"	-	ABZ5
"	WL3155	"	"	"	-	ABZ5
ABZ7	ER152 (R78)	c. 18°23.24'N; 76°54.25'W	Grants Town	Preston Hill	-	ABZ7
"	WL4869	18°23.242'N; 76°54.247'W	Grants Town	Preston Hill	Lower NP15b	ABZ7
"	WL4870	18°23.257'N; 76°54.314'W	Grants Town	Preston Hill	Lower NP15b	ABZ7
"	ER161	c. 18°19.57'N; 76°55.81'W	Preston Hill	Preston Hill	Upper NP15+	ABZ7/8
ABZ11	WL3416	18°20.116'N; 076°59.907'W	Rio Nuevo, Gayle	'Bonny Gate'	-	ABZ11
ABZ16	ER176	c. 18°20.08'N; 76°59.05'W	Dressike	'Bonny Gate'	NP21 *	ABZ16
"	WL4865	18°20.079'N; 76°59.045'W	Dressike	'Bonny Gate'	-	ABZ16

* Data from JIANG & ROBINSON (1987); + Data from ROBINSON (1996).

We have re-measured and recollected this entire section. Three separate sections were logged in the Rio Sambre. Section 1 (18° 17.411" N; 76° 56.039" W) extends from the Richmond Formation (samples WL4054-WL4056: ABZ4) into the lower part of the Palmetto Grove Formation. Section 2 (18° 16.903" N; 76° 55.547" W to 18° 16.991" N; 76° 55.618" W) extends from the Richmond Formation (WL4071-4070, WL4033, WL4035, WL4037, WL4041: ABZ4) into the lower Palmetto Grove Formation (samples WL4049, WL4026: ABZ5). Section 3 (18° 16.930" N; 76° 55.621" W to 18° 16.903" N; 76° 55.547" W) extends from the Richmond Formation (samples WL4057, WL4027, WL4058: ABZ4; sample WL 4025: ABZ5) into the lower Palmetto Grove Formation (samples WL4059, WL4024, WL4023: ABZ5). The different sections can be correlated using turbidites (Fig. 5) which can be traced between sections. Samples were collected for calcareous nannofossils to chronostratigraphically calibrate the succession. This indicates the presence of zone NP14a and basal NP14b. Additionally upsection reductions in the abundances of small *Toweius* spp. and *Discoaster lodoensis* suggest that nearly the entire thickness of Zone NP14a is present (Fig. 5). The appearance of *Blackites inflatus* near the top of the section (Fig. 5) indicates the base of the Lutetian. Details of all samples are provided in Fig. 5 and Table 3.

The upper part of the succession is limited to small exposures along roads around Farm Turn, and Kilancholly, where the upper part of the Palmetto Grove Formation and the lower part of the Preston Hill Formation are exposed. Spot samples along these roads have been analysed for their LBFs and zones ABZ6 to ABZ8 are represented (Table 3). These samples have been tied into the chronostratigraphy using calcareous nannofossil identifications from sample splits. Very rich assemblages of LBF are present including dictyoconids, orthophragmines, helicosteginids, nummulitids and *Fabiania*, amongst others. Table 3 shows the breakdown of sample numbers and zone based on LBF and calcareous nannofossils for samples above the Rio Sambre section. Details of the nannofossils are given in Appendix 1.

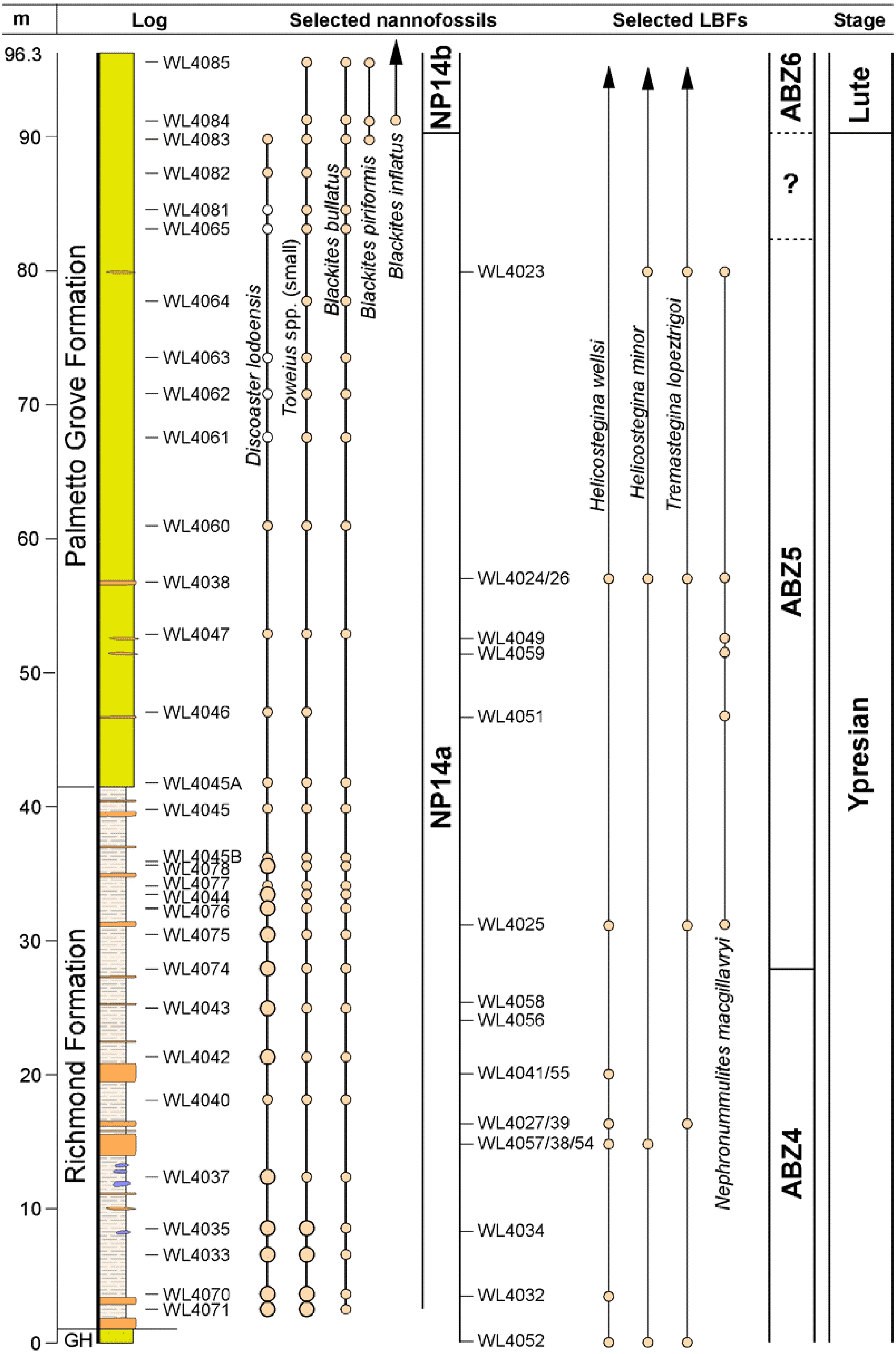


Figure 5: Composite of logged sections for the Rio Sambre Gorge showing distribution of selected nannofossils and Larger Benthic Foraminifers. Dot sizes for nannofossils indicates relative abundance; white dots indicate sporadic occurrences. Dots for foraminifers indicate presence.

Table 3: Details of LBF and calcareous nannofossil zone for samples (above the Rio Sambre section) from area 2 (western St Mary).

Zone	Sample	Lat/Long	Location	Formation	Nanno zone	LBF zone
ABZ6	WL4066	18°17.351'N; 76°55.645'W	Farm Turn	Palmetto Grove	NP14b	-
"	WL3307	18°17.267'N; 76°55.667'W	Farm Turn	Preston Hill	-	-
"	WL3317	18°17.603'N; 76°55.499'W	Farm Turn	Preston Hill	NP14b	-
"	WL3308A	18°17.324'N; 76°55.566'W	Farm Turn	Preston Hill	NP14b	ABZ6
ABZ7	WL3305	18°17.212'N; 76°55.611'W	Farm Turn	Preston Hill	-	ABZ7
"	WL3306	18°17.221'N; 76°55.619'W	Farm Turn	Preston Hill	-	ABZ7
"	WL2098	18°17.542'N; 76°55.452'W	Farm Turn	Preston Hill	-	ABZ7
"	WL3309	18°17.542'N; 76°55.452'W	Farm Turn	Preston Hill	NP15b	ABZ7
"	WL3309A	18°17.542'N; 76°55.452'W	Farm Turn	Preston Hill	-	ABZ7
"	WL3310	18°17.632'N; 76°55.487'W	Farm Turn	Preston Hill	NP15b	ABZ7
"	WL3310A	18°17.632'N; 76°55.487'W	Farm Turn	Preston Hill	-	ABZ7
"	WL2099	18°17.632'N; 76°55.487'W	Farm Turn	Preston Hill	-	ABZ7
"	WL3311	18°17.648'N; 76°55.438'W	Farm Turn	Preston Hill	NP15b	ABZ7
"	WL4068	18°17.872'N; 76°55.127'W	Farm Turn	Preston Hill	-	ABZ7
"	WL3405	18°16.642'N; 76°55.304'W	Kilocholly	Preston Hill	NP15b	ABZ7
"	WL4028	18°16.638'N; 76°55.153'W	Kilocholly	Preston Hill	-	ABZ7
"	WL4029	18°16.861'N; 76°55.105'W	Kilocholly	Preston Hill	-	ABZ7
"	WL3030	18°16.890'N; 76°55.078'W	Kilocholly	Preston Hill	-	ABZ7
"	WL4031	18°16.941'N; 76°55.100'W	Kilocholly	Preston Hill	-	ABZ7
"	WL3695	18°16.631'N; 76°55.289'W (Series of samples taken along road way)	Kilocholly	Preston Hill	NP15b	ABZ7
"	WL3696	"	Kilocholly	Preston Hill	NP15b	ABZ7
"	WL3697	"	Kilocholly	Preston Hill	NP15b	ABZ7
"	WL3698	"	Kilocholly	Preston Hill	NP15b	ABZ7
"	WL3699	"	Kilocholly	Preston Hill	NP15b	ABZ7
"	WL3700	"	Kilocholly	Preston Hill	NP15b	ABZ7
"	WL3701	"	Kilocholly	Preston Hill	NP15b	ABZ7
"	WL3423	18°16.631N; 76°55.289'W	Kilocholly	Preston Hill	-	ABZ7
ABZ8	WL3312	18°17.664'N; 76°55.416'W	Farm Turn	Preston Hill	NP15b	ABZ8
"	WL2100	18°17.664'N; 76°55.416'W	Farm Turn	Preston Hill	-	ABZ8
"	WL3314	18°17.605'N; 76°55.295'W	Farm Turn	Preston Hill	NP15b	ABZ8
"	WL4069	18°17.606N; 76°55.291'W	Farm Turn	Preston Hill	-	ABZ8
"	WL3313	18°17.661N; 76°55.353'W	Farm Turn	Preston Hill	-	ABZ8

Area 3. Lilyfield-Bamboo Area (North Coast Belt, parish of St Ann): Lutetian

This area is historically significant because Cole (1956, 1963) presented information on the LBF from here. Özcan *et al.* (2019, 2022a) also presented data on the orthophragmines from here. This area (Fig. 3) yields good faunas from the Preston Hill and "Chapelton" formations. Above this is a typical shallow-water Clarendon Block stratigraphy which consists of the Troy, "Swanswick" *s.l.* (see area 4 below), Claremont and Somerset formations; these are hard limestones and were not sampled for LBF because they lack free specimens (they are included on Fig. 4 for completeness). We did not carry out any nannofossil analyses for this area, because this part of the stratigraphy was covered in the area around Farm Turn (Area 2) and the LBF allow a straight forward correlation (Fig. 4). Zones ABZ8 and ABZ9 are represented in this area (Fig. 4). Details of the samples, LBF zones and nannofossil zone are given in Table 4 and Appendix 1.

Area 4. Swanswick and Clarks Town (North Coast Belt/Clarendon Block): Lutetian, Bartonian and Priabonian

This area is significant because it contains the type section of the Swanswick Formation of Hose and Versey (1956 - see also Versey in Zans *et al.*, 1963, where the type section is defined). Unfortunately, the faunas from the type Swanswick Formation do not correlate with the Swanswick Formation as mapped across much of Jamaica (*e.g.*, Versey in Zans *et al.*, 1963; Robinson & Mitchell, 1999; Mitchell, 2013a, 2016). The type Swanswick section contains two different stratigraphic intervals: the lower level consists of yellow-brown impure wackestones (a typical Yellow Limestone lithology) and yields *Helicostegina gyralis* in association with *Linderina floridensis* and nummulitids (Wright & Switzer, 1971; Robinson & Mitchell, 1999; herein) and can be assigned to the early Lutetian (ABZ7); in contrast, the upper part of the succession consists of pale cream packstones and yields *Heterostegina*

Table 4: Details of LBF zone for samples from area 3 (Lilyfield area). (Nannofossils were not studied from this area.)

Zone	Sample	Lat/Long	Location	Formation	Nanno zone	LBF zone
ABZ8	WL3427	18°25.288'N; 077°16.427'W	Elgin Hall/Lilyfield	Preston Hill Fm	-	ABZ8
"	WL2086	18°23.581'N; 077°14.094'W	Elgin Hall/Lilyfield	Preston Hill Fm	-	ABZ8
"	WL3426	18°25.150'N; 077°16.452'W	Elgin Hall/Lilyfield	Preston Hill Fm	-	ABZ8
"	WL2048	18°25.074'N; 077°16.641'W	Elgin Hall/Lilyfield	Preston Hill Fm	-	ABZ8
"	WL2047	18°25.049'N; 077°16.674'W	Elgin Hall/Lilyfield	Preston Hill Fm	-	ABZ8
"	WL2047A	18°25.035'N; 077°16.677'W	Elgin Hall/Lilyfield	Preston Hill Fm	-	ABZ8
ABZ9	WL2049	18°25.043'N; 077°16.549'W	Elgin Hall/Lilyfield	Preston Hill Fm	-	ABZ9
"	WL2049B	18°25.035'N; 077°16.543'W	Elgin Hall/Lilyfield	Preston Hill Fm	-	ABZ9
"	WL2049C	18°25.042'N; 077°16.549'W	Elgin Hall/Lilyfield	Preston Hill Fm	-	ABZ9
"	WL2046A	18°24.993'N; 077°16.692'W	Elgin Hall/Lilyfield	Chapelton Fm	-	ABZ9
"	WL2046	18°24.992'N; 077°16.693'W	Elgin Hall/Lilyfield	Chapelton Fm	-	ABZ9
"	WL2045A	18°24.975'N; 077°16.700'W	Elgin Hall/Lilyfield	Chapelton Fm	-	ABZ9
"	WL2045A	18°24.975'N; 077°16.700'W	Elgin Hall/Lilyfield	Chapelton Fm	-	ABZ9
"	WL2045C	18°24.968'N; 077°16.701'W	Elgin Hall/Lilyfield	Chapelton Fm	-	ABZ9
"	WL2044	18°24.944'N; 077°16.699'W	Elgin Hall/Lilyfield	Chapelton Fm	-	ABZ9
"	WL2041	18°24.800'N; 077°16.743'W	Elgin Hall/Lilyfield	Chapelton Fm	-	ABZ9
"	WL4379	18°24.464'N; 077°15.792'W	Elgin Hall/Lilyfield	Chapelton Fm	-	ABZ9

Table 5: Details of LBF and calcareous nannofossil zone for samples from area 4 (type Swanswick Formation).

Zone	Sample	Lat/Long	Location	Formation	Nanno zone	LBF zone
ABZ7	WL3275	18°24.982'N; 077°31.915'W	Swanswick House	Yellow Limestone	-	ABZ7
"	WL3275A	18°24.982'N; 077°31.915'W	Swanswick House	Yellow Limestone	-	ABZ7
ABZ9	WL3277	18°23.845'N; 077°32.206'W	Clarkes Town	Preston Hill	-	ABZ9
ABZ16	WL3265	18°24.917'N; 077°31.983'W	Swanswick House	Swanswick *s.s.*	-	ABZ16

Table 6: Details of LBF and calcareous nannofossil zone for samples from area 5 (North Coast Belt, parish of Trelawny).

Zone	Sample	Lat/Long	Location	Formation	Nanno zone	LBF zone
ABZ11	WL3958	18°24.464'N; 77°36.151'W	Sherwood Content	Chapelton	-	ABZ11
ABZ13	WL3772	18°23.912'N; 77°37.500'W	Sherwood Content	Chapelton	-	ABZ13
ABZ15	R.1068	18°24.043'N; 77°37.517W	Sherwood Content	Chapelton	-	ABZ14
"	R.1072	18°24.070'N; 77°37.515'W	Sherwood Content	Chapelton	-	ABZ14
"	WL3774	18°24.071'N; 77°37.514'W	Sherwood Content	Chapelton	-	ABZ15

ocalana and very rare *Fabularia verseyi* allowing a correlation with ABZ16 (Fig. 4); an interval between consists of lime mudstones and is best assigned to the top of the Claremont Formation. Across much of the Clarendon Block, the white grainstones that have been mapped as Swanswick Formation occur between the Troy Formation (dolostones and recrystallized limestones) and the Claremont Formation (predominately lime mudstones: MITCHELL, 2004, 2013a), which yield an ABZ15 LBF assemblage. Thus the type Swanswick (here designated as "Swanswick" *s.s.*) includes only early Lutetian (ABZ7) and late Priabonian (ABZ16) LBF with a probable fault (maybe an unconformity) between, whereas the widely mapped Swanswick Formation (designated here as "Swanswick" *s.l.*) yields a lower ABZ15 LBF assemblage. It is notable that to the south of Clarkes Town (SW of Swanswick itself) the Preston Hill Formation is exposed and yields late Lutetian LBF (ABZ10, herein) indicating that the Yellow Limestone in the lower part of the type Swanswick Formation is a limestone level developed within the Preston Hill Formation. A revision to the lithostratigraphy is required, and this will be published elsewhere. No nannofossil work was undertaken by us on these successions because of the numerous faults and the generally indurated nature of the limestones. Samples are listed in Table 5.

Area 5. Sherwood Content (North Coast Belt, parish of Trelawny): Lutetian and Bartonian

Sherwood Content lies in the transition zone between the Clarendon Block and the North Coast Belt (Fig. 3) and faunas were described from here by VAUGHAN (1928) and COLE (1956). The succession consists of three units: the Preston Hill Formation, Chapelton Formation and Healthy Hill Formation. LBF assemblages indicate a succession through the Bartonian (Fig. 4) with ABZ11, ABZ13 and ABZ14 represented. No nannofossil work was undertaken in this area because much of the succession here consists of indurated limestones. Samples are indicated in Table 6.

Table 7: Details of LBF and calcareous nannofossil zone for samples from area 6 (Spot Valley and Flower Hill, North Coast Belt, parish of St James).

Zone	Sample	Lat/Long	Location	Formation	Nanno zone	LBF zone
ABZ11	WL2837	18°29.525'N; 77°51.791'W	Salt Spring	Preston Hill	-	ABZ11
"	WL4234	18°29.526'N; 77°51.793'W	Salt Spring	Preston Hill	Barren	ABZ11
"	WL2836	18°29.627'N; 77°51.622'W	Salt Spring	'Bonny Gate'	-	ABZ11
"	WL4236	18°29.679'N; 77°51.373'W	Salt Spring	'Bonny Gate'	NP16	ABZ11
"	WL4237	18°29.621'N; 77°51.203'W	Salt Spring	'Bonny Gate'	NP16	ABZ11
ABZ12	WL4241	18°30.401'N; 77°47.827'W	Spot Valley	'Bonny Gate'	Barren	ABZ12
"	WL4243	18°30.422'N; 77°47.710'W	Spot Valley	'Bonny Gate'	Barren	ABZ12
ABZ14	WL2819	18°29.135'N; 77°50.385'W	Flower Hill	'Bonny Gate'	-	ABZ14

Table 8: Details of LBF and calcareous nannofossil zone for samples from area 7 (Albert Town and Litchfield, Clarendon Block, parish of Trelawny).

Zone	Sample	Lat/Long	Location	Formation	Nanno zone	LBF zone
ABZ6	WL3666	18°17.225'N; 77°31.959'W	Stettin	Stettin	-	ABZ6
"	WL3667	18°17.318'N; 77°31.886'W	Stettin	Stettin	-	ABZ6
"	WL3458	18°12.508'N; 77°30.051'W	Coleyville	Stettin	-	ABZ6
ABZ9	WL3444	18°17.519'N; 77°32.634'W	Albert Town	Chapelton	-	ABZ9
ABZ11	WL3445	18°17.566'N; 77°32.780'W	Albert Town	Chapelton	-	ABZ11
"	ER1356	c. 18°17.66'N; 77°32.85'W	Albert Town	Chapelton	NP16 *	ABZ11
"	WL3447	18°17.659'N; 77°32.853'W	Albert Town	Chapelton	-	ABZ11
"	WL4195	18°15.271'N; 77°29.995'W	Litchfield	Chapelton	-	ABZ11

* Data from ROBINSON (1996).

Table 9: Details of LBF and calcareous nannofossil zone for samples from area 8 (Coleyville, Clarendon Block, parish of Manchester).

Zone	Sample	Lat/Long	Location	Formation	Nanno zone	LBF zone
ABZ6	WL3458	18°12.508'N; 77°30.051'W	Coleyville	Stettin	-	ABZ6
ABZ13	WL4109	18°11.570'N; 77°30.798'W	Coleyville	Chapelton	-	ABZ13

Area 6. Spot Valley, Salt Spring and Flower Hill (North Coast Belt): Bartonian

Eocene rocks belonging to the Yellow Limestone and White Limestone groups occur in a structurally complex area to the SE of Montego Bay (Fig. 3) in what has been called the Montego Bay Anticline (MEYERHOFF & KRIEG, 1977). There is a transition here from marlstones of the Preston Hill Formation to the overlying chalks of the "Bonny Gate" Formation (Fig. 4), which occurs in ABZ11. The overlying chalks of the "Bonny Gate" Formation have yielded LBF indicating ABZ12 (at Spots Valley) and ABZ14 (south of Flower Hill). Nannofossil samples were taken from the marlstone-chalk sequence in ABZ11 (indicating zone NP16 and CP14a) and from the chalks in ABZ12 at Spots Valley (which were barren). Correlations are shown in Fig. 4. Samples and LBF and nannofossil zones are listed in Table 7 and Appendix 2.

Area 7. Yellow Limestone around Albert Town and Litchfield (Clarendon Block): late Lutetian and early Bartonian

The Yellow Limestone around the northwestern margin of the Central Inlier (MITCHELL, 2013b; Fig. 3) consists of four formations: Freemans Hall, Stettin, Litchfield and Chapelton formations (Fig. 4) (ROBINSON, 1996; ROBINSON & MITCHELL, 1999; MITCHELL, 2016). Samples from the Stettin Formation yield *H. minor* in the absence of nummulitids and can be assigned to the earliest Lutetian lower ABZ6 (Fig. 4). The overlying Litchfield Formation lacks zonally significant LBF, but the Chapelton Formation contains LBF indicating zones ABZ9 and ABZ11, indicating a hiatus representing ABZ10 (Fig. 4). Some nannofossil work on the Chapelton Formation has previously been presented by ROBINSON (1996) for this area and indicates zone NP16. Samples are detailed in Table 8.

Area 8. Yellow Limestone at Coleyville (Clarendon Block): Bartonian

The area around Coleyville (Fig. 3) has a similar lithostratigraphy to that of the area around Albert Town and Litchfield, although the LBF assemblages are different (further from the platform edge). Zonal indicators are largely absent (except for very rare *H. minor* in the Stettin Formation) until the upper part of the Chapelton Formation. The upper part of the Chapelton Formation at the Forest Reserve yields abundant lepidocyclinids indicating ABZ13. No nannofossil work was undertaken here and correlations are shown in Fig. 4. Samples are described in Table 9.

Table 10: Details of LBF and calcareous nannofossil zone for samples from area 9 (western Clarendon Block, parishes of St James and St Elizabeth).

Zone	Sample	Lat/Long	Location	Formation	Nanno zone	LBF zone
ABZ6	WL3520	18°22.470'N; 077°51.220'W	Springvale	Yellow Lmst	-	ABZ6
ABZ9	ER1575	c. 18°21.54'N; 77°49.11'W	Point	Yellow Lmst	-	ABZ9
"	ER3031	c. 18°21.54'N; 77°49.11'W	Point	Yellow Lmst	-	ABZ9
ABZ10	WL2921	18°09.880'N; 77°44.270'W	Elderslie	Chapelton	-	ABZ10
ABZ13	WL2564	18°12.019'N; 77°50.771'W	Ipswich	Ipswich	-	ABZ13
"	WL2635	18°11.603'N; 77°49.246'W	Ipswich	Ipswich	-	ABZ13
"	WL3501	18°11.631'N; 77°48.959'W	Railway cutting	Ipswich	-	ABZ13
"	WL3503	18°11.700'N; 77°49.354'W	Railway cutting	Ipswich	-	ABZ13
"	WL3507	18°09.880'N; 77°44.270'W	Appleton	Ipswich	-	ABZ13

Table 11: Details of LBF and calcareous nannofossil zone for samples from area 10 (Grants Pen, parish of St Thomas).

Zone	Sample	Lat/Long	Location	Formation	Nanno zone	LBF zone
ABZ7	WL3572	17°54.730'N; 76°38.107'W	Grants Pen	Yellow Lmst	-	ABZ7
"	WL3714	17°54.732'N; 76°38.107'W	Grants Pen	Yellow Lmst	-	ABZ7
"	WL3715	17°54.784'N; 76°38.213'W	Grants Pen	Yellow Lmst	-	ABZ7
"	WL4631	17°54.749'N; 77°38.113'W	Grants Pen	Yellow Lmst	-	ABZ7
"	WL4631	17°54.753'N; 76°38.114'W	Grants Pen	Yellow Lmst	-	ABZ7
ABZ12	WL3571	17°54.590'N; 76°37.906'W	Grants Pen	Yellow Lmst	-	ABZ12
"	WL3711	17°54.589'N; 76°37.907'W	Grants Pen	Yellow Lmst	-	ABZ12
"	WL4628	17°54.540'N; 77°36.888'W	Grants Pen	Yellow Lmst	NP17	Barren
"	WL4629	17°54.589'N; 77°37.904'W	Grants Pen	Yellow Lmst	Barren	ABZ12
"	WL4630	17°54.589'N; 77°37.904'W	Grants Pen	Yellow Lmst	NP16	ABZ12

Table 12: Details of LBF and calcareous nannofossil zone for samples from area 11 (road cuts along northern N-S leg of Highway 2000).

Zone	Sample	Lat/Long	Location	Formation	Nanno zone	LBF zone
ABZ15	WL3876	18°21.538'N; 77°09.500'W	Highway2000	'Swanswick *s.l.*'	-	ABZ15
"	WL3876A	18°21.538'N; 77°09.500'W	Highway2000	'Swanswick *s.l.*'	-	ABZ15
"	WL4182	18°22.800'N; 77°09.517'W	Highway2000	'Swanswick *s.l.*'	-	ABZ15
"	WL4095	18°20.790'N; 77°08.917'W	Highway2000	Claremont	-	ABZ16
ABZ16	WL3931	18°19.905'N; 77°08.525'W	Highway2000	Somerset	-	ABZ16

Area 9. Western side of the Clarendon Block, St Elizabeth and St James: Lutetian and Bartonian

Rocks of the Yellow Limestone Group occur in a series of inliers in northern St Elizabeth and southern St James where the rocks of the White Limestone Group have been eroded (Fig. 3). The succession has similarities with the succession around the Central Inlier, but the Bartonian has thickened substantially and can be mapped in more detail. The formations present here need revision, but are currently assigned to the Stettin Formation, *Helicostegina*-beds, Litchfield Formation, Chapelton Formation, Healthy Hill Formation, and 'Ipswich' Formation (VERSEY, 1957; ATKINSON, 1969). The 'Ipswich' Formation can be divided into three distinct mappable units: a lower unit of pale, thickly-bedded wackestone with a platform-type LBF assemblage; a series of brown and locally red packstones and grainstones carrying a lepidocyclinid assemblage (the type Ipswich Formation of VERSEY, 1957), and an upper unit passing back into wackestones with some lepidocyclinids and platform interior LBF.

ABZ6 is found in the Stettin and basal part of the *Helicostegina*-beds, zones ABZ7 - ABZ8 in the middle and upper parts of the *Helicostegina*-beds, ABZ10 in the Chapelton Formation, and zones ABZ13 to ABZ14 are represented in the middle and upper 'Ipswich' Formation (Fig. 4). The Yellow Limestone is overlain by a typical lower White Limestone succession which includes the Troy, 'Swanswick' *sensu lato*, Claremont and Somerset formations (Fig. 4). This demonstrates that the Ipswich Formation is demonstrably older than the Swanswick Formation, although the two were mapped as a single unit by the Jamaican Geological Survey (BATESON, 1972). Limited nannofossil data has been provided by ROBINSON *et al.* (2018). Samples are listed in Table 10.

Area 10. Grants Pen, St Andrew (SW Wag Water Belt): Bartonian

The Grants Pen area of St Thomas (Fig. 3) is a complex area which has overturned beds and probably significant faulting. The area contains a suite of Yellow Limestone marlstones that are overlain by chalks with at least one chert band. The area is important because it yields LBF.

Table 13: Details of LBF and calcareous nannofossil zone for samples from area 12 (Montpelier-New Market Belt).

Zone	Sample	Lat/Long	Location	Formation	Nanno zone	LBF zone
ABZ14	WL4444	18°16.742'N; 77°59.423'W	Cold Spring	Marlstones	-	ABZ14
"	WL4445	18°16.725'N; 77°59.440'W	Cold Spring	'Bonny Gate'	NP17	
"	WL4449	18°16.697'N; 77°59.636'W	Cold Spring	'Bonny Gate'	-	ABZ14
ABZ15	WL4618	18°18.267'N; 78°01.061'W	Haddo	'Bonny Gate'	NP18	ABZ15
"	WL4620	18°18.172'N; 78°01.122'W	Haddo	'Bonny Gate'	NP18	ABZ15
"	WL4621	18°17.887'N; 78°01.275'W	Haddo	'Bonny Gate'	NP18	ABZ15
"	WL4622	18°17.864'N; 78°01.285'W	Haddo	'Bonny Gate'	NP18	ABZ15
ABZ16	WL4602	18°11.493'N; 78°00.770'W	Bath	'Bonny Gate'	NP19	ABZ16
"	WL4624A	18°16.938'N; 78°01.605'W	Line Gate	'Bonny Gate'	NP19	ABZ16
"	WL4617	18°18.383'N; 78°00.957'W	Mackfield	'Bonny Gate'	NP19	ABZ16
"	WL4616	18°18.735'N; 78°00.795'W	Mackfield	'Bonny Gate'	NP19	ABZ16

Table 14: Details of LBF and calcareous nannofossil zone for the sample from area 13 (Jerusalem Mountain - Upper Rock Spring, parish of Westmoreland).

Zone	Sample	Lat/Long	Location	Formation	Nanno zone	LBF zone
ABZ9	WL3641	18°20.757'N; 77°13.870'W	Rock Spring	Chapelton	-	ABZ9

Pseudolepidina trimera occurs in a hard limestone that cannot be dated using calcareous nannofossils; whereas *Lepidocyclina ariana* (ABZ12) occurs in a Yellow Limestone marlstone which has been chronostratigraphically calibrated using nannofossils to zone NP16 in this work (Appendix 2). Correlations are shown in Fig. 4, and samples are listed in Table 11.

Area 11. Highway 2000 around the Golden Vale Junction, parish of St. Ann (Clarendon Block): Priabonian

The road cuts created during the construction of the North-South Leg of Highway 2000 in the parish of St Ann (Fig. 3) showed good sections through the Swanswick *s.l.*, Claremont, Somerset, and Walderston Formations. The lower three of these were composed of relatively weakly cemented limestones from which free specimens of LBF could be extracted. These sections were close to the shelf edge in Late Eocene time and contain rich lepidocyclinid assemblages. These were used to understand the succession of lepidocyclinids through the Priabonian, with zones ABZ15 and ABZ16 represented (Fig. 4). No nannofossil work was undertaken on these samples. Samples are described in Table 12.

Area 12. The central and southern Montpelier-New Market Belt: late Bartonian to Priabonian

The succession in the Montpelier-New Market Belt (Fig. 3) covers the interval from the late Lutetian to the Priabonian. Samples were used from the Content-1 well which penetrated the lower part of the succession (Chapelton Formation and overlying marlstones) and from surface outcrops. Surface outcrops can be divided into five Eocene units: Chapelton Formation, marlstones, lower unit of chalks, unit of chalks with cherts, and upper unit of chalks. New road cuts associated with the improvement work on the Mackfield to Ferris Cross main road facilitated the collection of samples from weakly indurated, freshly exposed rocks. A series of nannofossil samples was analysed from here from the late Bartonian into the mid-Priabonian. ABZ10 (samples from the Content Well: Eva, 1980), ABZ14, ABZ15 and ABZ16 are represented in this area (Fig. 4). Samples are listed in Table 13 and nannofossil records are included in Appendix 2.

Area 13. Jerusalem Mountain - Upper Rock Spring Area (parish of Westmoreland)

The Chapelton Formation is exposed around Rock Spring to the north of the Jerusalem Mountain Inlier (Fig. 3; Mitchell & Edwards, 2016). The Chapelton Formation here yields abundant free specimens of *Helicostegina jeannemairae* associated with *Operculinoides* sp. and can be assigned to ABZ9 (Fig. 4). No nannofossil work was carried out here, and the sample is listed in Table 14.

4. Zonation scheme

We develop a zonation scheme for the Eocene of the American biogeographic province based on the stratigraphic distribution of selected taxa. The zonation is based on the first appearance datum (FAD) and last appearance datum (LAD) of selected taxa. Planktic foraminiferal zones are indicated by the prefixes 'P' (Berggren *et al.*, 1995) and 'E' (Pearson *et al.*, 2006) and calcareous nannofossil zones by the prefixes 'NP' (Martini, 1971), 'CN' (Okada & Bukry, 1980) and 'CNE' (Agnini *et al.*, 2014). The American Benthic Zones (ABZs) are defined below, and their ages are constrained largely using calcareous nannofossils related to the 'NP' zonation. The zonation scheme for the Eocene is shown in Fig. 6 and consists of 14 zones (ABZ3 to ABZ16). The fourteen Eocene zone are defined below, and the zonation for the Paleocene, Oligocene and early to middle Miocene will be presented in a separate paper.

ABZ3. *Tremastegina lopeztrigoi* Zone. From the LAD of *Ranikothalia catenula* (which defines ABZ2) to the FAD of *H. wellsi*. Small specimens tentatively assigned to *T. lopeztrigoi* are found in the Nonsuch Formation of Jamaica where they co-occur with *Ranikothalia* (Robinson & Jiang, 1990; Robinson & Wright, 1993). ABZ3 is recognised by the presence of *T. lopeztrigoi*, in the absence of either *Ranikothalia* (ABZ2) or *Helicostegina wellsi* (ABZ4). The associated LBF assemblage is characterised by long-ranging forms, particularly orthophragmines, such as *Orbitoclypeus*, *Stenocyclina*, *Pseudophragmina* and *Asterocyclina* (see Özcan *et al.*, 2019, 2022a, for a revision of the orthophragmines). The reference section for the zone is in the Richmond Formation near Albany, northern Wag Water Belt, Jamaica (Fig. 3), and is assigned to NP12 (Fig. 6; Jiang & Robinson, 1987). Blanco-Bustamentel *et al.* (1999) suggested that *Ranikothalia* and *Eoconuloides* (= *Helicostegina* herein) *wellsi* occurred throughout the lower Eocene, but these results have not been proved elsewhere and a reassessment of these successions in Cuba is needed.

ABZ4. *Helicostegina wellsi* Zone. From the FAD of *H. wellsi* to the FAD of *Nephronummulites macgillavryi*. In shelf edge localities, the LBF of this zone are dominated by *H. wellsi* and *T. lopeztrigoi*, locally with *H. minor*, *Fallotella* and *Cushmania*. In the deeper shelf succession of the Richmond Formation the zone contains common *H. wellsi* and *T. lopeztrigoi* along with a high-diversity LBF assemblage including orthophragmines (*Asterocyclina*, *Stenocyclina*, *Pseudophragmina* and *Orbitoclypeus*), *Fabiania*, *Cushmania*, *Fallotella* and *Eorupertia*, and locally *H. minor*. The reference locality for the zone is in the Rio Sambre section, parish of St Mary, Jamaica (Robinson & Mitchell, 1999; Fig. 5). Our nannofossil determinations indicate that ABZ4 belongs to the lower part of Zone NP14a (Fig. 6; Appendix 1). This is consistent with previous age assignments (NP14 and P9: Wise & Constans, 1976; Robinson & Mitchell, 1999). We tentatively place the boundary between ABZ3 and ABZ4 within Zone NP13 as we do not have LBF assemblages indicating Zone NP13. It is unclear if NP13 is absent due to a hiatus, or, more likely, cut out by faulting.

The occurrence of *H. wellsi* (as *Amphistegina elliotti*) in Ecuador as recorded by Cushman and Stainforth (1946) is a typical shallow-water occurrence, where *H. wellsi* is the only species present. *H. wellsi* is a distinctive species and can easily be recognised in random thin sections. The presence of *Tremostegina senni* and *H. minor* in the absence of *Operculinoides* (Senn, 1940; Caudri, 1972; Jones, 2009) in the Murphy's Beds of Barbados (Upper Scotland Group) suggests assignment to ABZ4 (or possibly lower ABZ6).

ABZ5. *Nephronummulites macgillavryi* Zone. From the FAD to LAD of *N. macgillavryi*. The reference section lies in the upper part of the Richmond Formation and lower part of the Palmetto Grove Formation in the Rio Sambre Gorge, parish of St Mary, Jamaica (Figs. 5 - 6). In the lower part of the zone, *N. macgillavryi* co-occurs with *H. wellsi*, whereas *H. minor* occurs throughout the zone. The zone is here correlated with the upper part of the Ypresian (upper Zone NP14a below the entry of the nannofossil *Blackites inflatus* in Zone NP14b (Figs. 5 - 6). The zone is recognized in Cuba (Rutten, 1935), Jamaica (Robinson & Wright, 1993; herein), and Nicaragua (Andji *et al.*, 2018). Many assemblages are characterised only by *N. macgillavryi* (as reported by Rutten, 1935; Robinson & Wright, 1993; Andji *et al.*, 2018), and these probably represent shelf edge assemblages lacking the deeper-water orthophragmine component of the fauna. *N. macgillavryi* is a distinctive species and can easily be recognised in hand specimen and in random thin sections.

ABZ6. *Helicostegina minor* Zone. From the LAD of *N. macgillavryi* to the FAD of *Operculinoides* spp. This is a low diversity interval above the Lower-Middle Eocene boundary, and amongst the Asterogerinoidea only *Helicostegina* and *T. lopeztrigoi* are present; longer ranging taxa include orthophragmines (including *Stenocyclina advena* and *Asterocyclina* spp.), *Fallotella* and *Cushmania*. There is a succession of species of *Helicostegina*, *H. minor* occurs in the lower part of the zone and *H. gyralis* in the upper part of the zone (Fig. 6) and thus it can be divided into lower (ABZ6A) and upper (ABZ6B) parts. The reference locality for the zone lies in the upper part of the Palmetto Grove Formation above the Rio Sambre in the parish of St Mary, Jamaica. The zone also occurs in shelf edge assemblages where *H. minor* occurs in association with inner platform LBF (*Verseyella jamaicensis* (Cole, 1956), *Coleiconus zansi* Robinson, 1993, and *Fabularia colei* Robinson, 1969) in the Stettin Formation of the Central Inlier (Robinson & Wright, 1993; Robinson & Mitchell, 1999). In the Rio Sambre section, the entire zone yields the nannofossil *Blackites inflatus* indicating Zone NP14b (Fig. 6; Appendix 1). Zone NP15a has not been recorded in samples from transects in this area, nor elsewhere in Jamaica, and there appears to be a minor hiatus (representing zone NP15a) between ABZ6 and ABZ7 in Jamaica.

In Cuba, Cole and Bermúdez (1944) recorded an identical assemblage of LBFs from the Peñon Formation, which we can assign to the upper part of ABZ6 based on the presence of *H. gyralis* in the absence of *Operculinoides* spp. Torres-Silva *et al.* (2018) recorded a second assemblage from the Peñon Formation in Cuba in which *Operculinoides* spp. occurred with *H. wellsi* (reported as *E. wellsi*), which we would place in ABZ7.

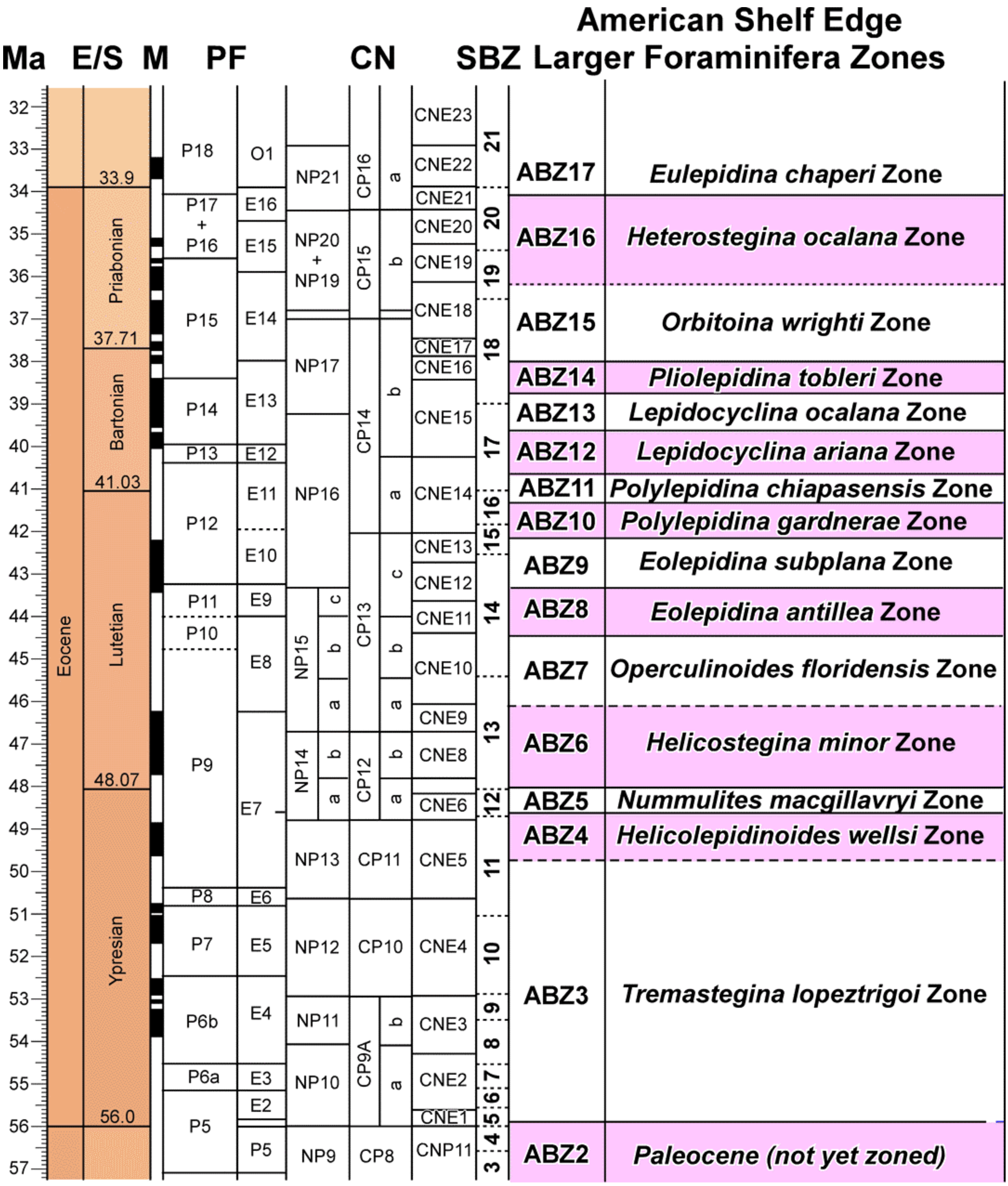
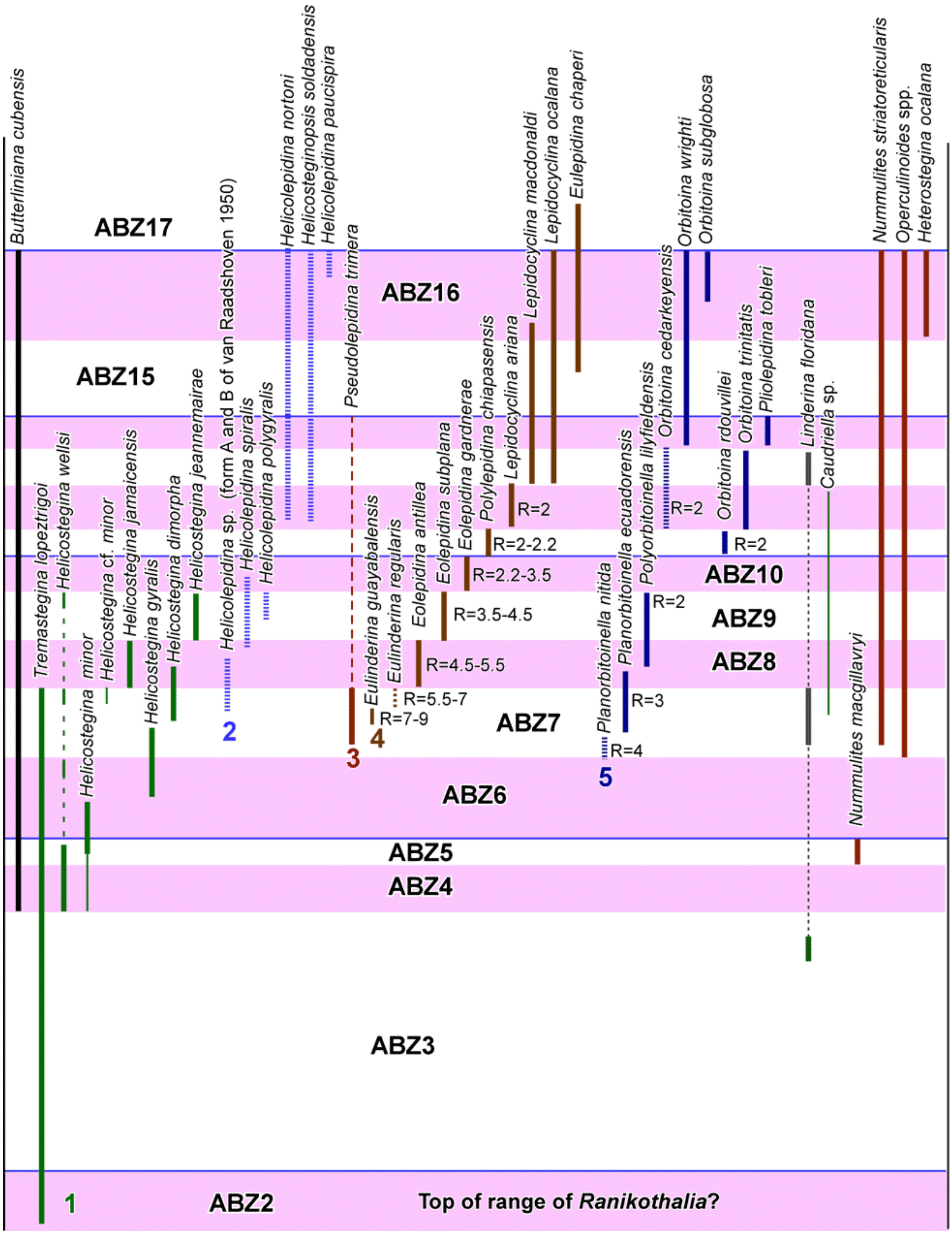


Figure 6: Distribution of selected Larger Benthic Foraminifers in relation to the Eocene zonation scheme calibrated against planktic foraminifers and calcareous nannofossil zonations. The Standard Benthic zonation (SBZ) scheme for the Tethys is shown for comparison (SERRA-KIEL *et al.*, 1998; SPEIJER *et al.*, 2020).



ABZ7. *Operculinoides* spp. Zone. From the FAD of *Operculinoides* ex gr. *floridensis* and *Nummulites* ex gr. *striatoreticulatus* to the FAD of *Eolepidina antillea* (with Ṝ < 5.5). The reference section lies on the road from Farm Turn to Hampstead, parish of St Mary, Jamaica. The zone sees the appearance of numerous taxa including *Eulinderina guayabalensis*, *Planorbitoinella ecuadorensis* and *Pseudolepidina trimera* suggesting an important migration event at this time. The area from where these taxa migrated from is unknown, but could be in the Pacific, and it represents the most significant faunal change in the Eocene of the Americas. *Helicostegina gyralis* occurs in the lower part of the zone, whereas *H. dimorpha* occurs in the upper part of the zone.

The appearance of *Operculinoides* ex gr. *floridensis* (*e.g.*, *Op. jennyi* Barker) and *Nummulites striatoreticulatus* (*e.g.*, *N. guayabalensis* Barker) in large numbers is particularly conspicuous and the genera can easily be recognized in random thin sections. In the Rio Sambre area *Operculinoides* ex gr. *floridensis* appears at the base of Zone NP15b, but Zone NP15a is missing. We tentatively put the ABZ6/ABZ7 boundary within Zone NP15a (Fig. 6), pending further research. In Mexico, *Eu. guayabalensis* occurs in association with *Operculinoides prenummulitiformis* and *Nummulites guayabalensis* (Barker, 1939, p. 325) indicating ABZ7. The association of *H. wellsi* and *T. senni* (cited as *Eoconuloides senni*) with *Operculinoides* sp. in Calyx wells 50 and 50A in Trinidad (Caudri, 1996, Fig. 7) also suggests assignment to ABZ7.

ABZ8. *Eolepidina antillea* Zone. From the FAD of *Eo. antillea* (with Ṝ < 5.5) to the FAD of *Eo. subplana* (with Ṝ < 4.5). The reference section lies on the road from Farm Turn to Hampstead, parish of St Mary, Jamaica. At Farm Turn (Rio Sambre area) the transition from ABZ7 to ABZ8 occurs in the upper part of Zone NP15b (Fig. 6; Appendix 1). Robinson (1996) reported that a sample from the type locality of the Preston Hill Marl (his locality 2c, ER161) contained *Eolepidina* with Ṝ = 5.5 (n = 14), which is at the transition between *Eu. guayabalensis* and *Eo. antillea* (*i.e.*, the ABZ7/ABZ8 boundary) as defined here. This locality has yielded the following plankton correlations: P11, upper NP15, and CP13-lower CP14a (Robinson, 1996) which is consistent with the upper part of Zone NP15c. We therefore place the boundary between ABZ7 and ABZ8 in the upper part of Zone NP15b (Fig. 6). Sample USGS 6897 (collected by S.B. Senn) from St. Bartholomew was reported (Robinson, 1996) to have *Eo. antillea* with Ṝ = 5.08 (n = 12) and was very tentatively attributed to Zone P11/P12 (Westercamp & Andreieff, 1983; Robinson, 1996); it is consistent with the age of ABZ8 as determined here.

ABZ9. *Eolepidina subplana* Zone. From the FAD of *Eo. subplana* (with Ṝ < 4.5) to the FAD of *Eolepidina gardnerae* (with Ṝ = 3.5 or less). The type section lies at Lilyfield in the parish of St Ann, Jamaica. The zone can be recognised in Alabama (Robinson & Jiang, 1995), St. Bartholomew (Robinson, 1996), Jamaica (Robinson, 1996), Mexico (Barker & Grimsdale, 1936), and Margarita Island, Venezuela (Caudri, 1974). A sample from Albert Town (ER1366 from Robinson, 1996, locality 2B) containing *Eo. subplana* (indicating ABZ9) yielded a few calcareous nannofossils, including *Sphenolithus furcatolithoides*, *Pemma papillatum* and *Discoaster barbadiensis* and was assigned to Zone NP16 (Robinson, 1996). In the Bay Minette Corehole (Baldwin County, Alabama) *Eo. subplana* with Ṝ = 4 occurs in samples at depths of 529.7 m, 543.2 m and 644.4-646.6 m and the nannofossils indicate assignment to Zone NP16 (Robinson & Jiang, 1995). We therefore place the boundary between ABZ8 and ABZ9 at about the NP15/NP16 boundary (Fig. 6). Sample ER1485 from St. Bartholomew (Sample 3A: Robinson, 1996) from the "Upper Group" (near Lurin) was reported (Robinson, 1996) to have a Ṝ = 3.82 (n = 11) and was tentatively attributed to Zone P12 (Westercamp & Andreieff, 1983; Robinson, 1996), which is consistent with the age of ABZ9 as determined here. On Margarita Island, Venezuela (Caudri, 1974), the following species are present (identifications updated from Caudri, 1974): *Eo. subplana* (= *Lepidocyclina (Polylepidina) antillea* of Caudri, 1974), *Orbitoina* sp., *Helicolepidina polygyralis* and *Operculinoides* spp. and can be assigned to ABZ9.

ABZ10. *Eolepidina gardnerae* Zone. From the FAD of *Eolepidina gardnerae* (with Ṝ < 3.5) to the FAD of *Polylepidina chiapasensis* (with Ṝ > 2.2). The reference section lies at a depth of 3327 feet (= 1037.6 m) in the Content #1 Well, at Content, parish of Westmoreland, Jamaica. *Eolepidina* from here (as *Polylepidina*) have been described by Eva (1980) and Robinson (1996) and are also figured here. Robinson (1996) recorded biostratigraphic data from the level that yielded *Eo. gardnerae* in the Content-1 Well (his locality 2A): core samples from depths of 1010.4 m, 1030.8 m, 1040.6 m and 1070.8 m had rich, but overgrown, nannofossils (including *Sphenolithus furcatolithoides*, *Cribrocentrum reticulatum*, *Reticulofenestra umbilica*, *Helicosphaera compacta*, *Dictyococcites bisectus* (small form; = *D. scrippsae*) and *Pemma papillatum*: Robinson & Jiang, 1995; Robinson, 1996) that indicate Zone NP16; whereas a sample from 1040.6 m had calcareous nannofossils (including *Sphenolithus furcatolithoides*, *Pemma papillatum* and *Reticulofenestra umbilica*) and was assigned to Zone CP14a (determinations by W.E. Steinkraus in Robinson, 1996). In the Bay Minette Corehole (Baldwin County, Alabama) *Eo. gardnerae* (ABZ10) with Ṝ close to 3 occurs in three samples collected at depths of 515.1 m, 518.8 m and 522.1 m. These samples are assigned to Zone NP16 (Robinson & Jiang, 1995; Robinson, 1996), but the appearance of *Cribrocentrum reticulata* at 518.8 m (Robinson & Jiang, 1995) means that the uppermost sample that yielded *P. gardnerae* can be assigned to a level in Zone CP14a. This means that the boundary between zones ABZ9 and ABZ10 must occur within Zone NP16, probably within the upper part of Zone CP13c (Fig. 6).

ABZ11. *Polylepidina chiapasensis* Zone. From the FAD of *Polylepidina chiapasensis* (with $\bar{R}$ = 2 - 2.2) to the FAD of *Lepidocyclina ariana*. The reference section lies on the road from Salt Spring to Flower Hill in the parish of St James, Jamaica. Samples WL4234 and WL4236 from the Preston Hill Formation (Salt Spring to Flower Hill transect) yield *Po. chiapasensis* and have yielded nannofossils indicating Zone NP16 and CP14a (Appendix 1). We therefore assign the ABZ10 - ABZ11 boundary to an interval within Zone NP16 (within Zone CP14a) (Fig. 6).

ABZ12. *Lepidocyclina ariana* Zone. From the FAD of *Lepidocyclina ariana* to the FAD of *Lepidocyclina ocalana*. At Grants Pen in St Thomas (Jamaica), *L. ariana* (Sample WL4630) occurs with nannofossils indicating upper Zone NP16 (CP14a) whereas a slightly higher sample without LBF (WL4628) yielded nannofossils possibly indicating Zone NP17 (Appendix 1). In the Bay Minette Corehole (Baldwin County, Alabama) *L. ariana* occurs with nannofossils indicating Zone NP17 (Robinson & Jiang, 1995). We therefore place the ABZ11- ABZ12 boundary in the upper part of Zone NP16 (CP14a). The reference section for the zone lies at Grants Pen in St Thomas, Jamaica.

This zone is widely developed being found in Jamaica, Alabama (Robinson & Jiang, 1995; Robinson, 1997), Florida (Cole, 1944) and Margarita Island, Venezuela (Caudri, 1974). In Margarita Island the LBF assemblage consists of advanced *L. ariana*, *Orbitoina* spp., *Helicolepidina spiralis trinitatis* [= *nortoni* Vaughan], *Helicosteginopsis soldadensis*. *Caudriella ospinae* and *Operculinoides* spp. (Caudri, 1974, identifications updated); this assemblage occurs with the planktic foraminifer *Orbulinoides beckmanni* indicating Zone P13 (Caudri, 1974) - this is in complete agreement with the age calibration of ABZ12 herein based on calcareous nannofossils (Fig. 6).

ABZ13. *Lepidocyclina ocalana* Zone. From the FAD of *L. ocalana* to the FAD of *Pliolepidina tobleri*. The assemblage is characterised by the appearance of species of *Lepidocyclina* with adauxiliary chambers, in contrast to the assemblage present in ABZ12. The reference locality for the zone is in the "Ipswich" Limestone in the Ipswich area, parish of St Elizabeth, Jamaica. A sample from the Ipswich Limestone (ER3103) yielded a sparse nannoflora, including *Chiasmolithus grandis* and small *Cribrocentrum reticulatum*, indicating a range from upper Zone NP16 to Zone NP17 (Robinson *et al.*, 2018). Strontium isotope ratios from this level (Robinson *et al.*, 2018) suggest an age in the range 31.25-38.8 Ma consistent with Zone NP17. We therefore correlate ABZ13 primarily to lower-mid Zone NP17 (Fig. 6).

ABZ14. *Pliolepidina tobleri* Zone. From the FAD of *Pl. tobleri* to the LAD of *Pl. tobleri*. The reference locality of this zone lies around the marlstones/chalk boundary at Cold Spring in the Montpelier-New Market Belt, parish of Westmoreland, Jamaica. A sample (WL4444) from the marlstones at Cold Spring, just below a sample (WL4449) with common *Pl. tobleri* yielded a nannoflora indicating zone NP17 (Appendix 1). We therefore assign Zone ABZ14 to Zone NP17 (Fig. 6). Strontium isotope ratios from a sample with *Pl. tobleri* from Appleton, St Elizabeth, Jamaica (Robinson *et al.*, 2018) gave ages which are too young in stratigraphic terms suggesting diagenetic alteration.

ABZ15. *Orbitoina wrighti* Zone. From the LAD of *Pl. tobleri* to the FAD of *Heterostegina ocalana*. The reference section for the zone lies in the Swanswick Formation *s.l.* on the N-S Highway 2000 in the parish of St Ann, Jamaica. Nannofossil data from the Montpelier-New Market Belt indicate that ABZ15 ranges from Zone NP18 to the lower part of Zone NP19/20 (*sensu* Martini, 1971, non Speijer *et al.,* 2020; Fig. 6).

ABZ16. *Heterostegina ocalana* Zone. From the FAD of *H. ocalana* to the LAD of *H. ocalana*. The reference locality lies in the White Limestone at Dressikie, parish of St Mary, Jamaica. ABZ16 occurs in the type Swanswick (Robinson & Wright, 1993) and Somerset formations (Robinson, 1974) of the marginal facies of the Clarendon Block, as well as in deep-water turbidites in the Wag Water Belt (Robinson, 2004). Localities in the NW Wagwater Belt (ER176 from deep-water chalks of the White Limestone Group at Dressikie) that have yielded *H. ocalana* contain a nannoflora assignable to Zone NP21 (Robinson, 2004; Robinson *et al.*, 2018). In Cuba, Torres-Silva *et al.* (2017) suggested a range of *H. ocalana* from Zone NP17 to Zone NP19-20/CP15 (but the individual zones were not separated suggesting limited precision) and possibly Zone NP21 (CP16) and P18 (early Rupelian). These data do not seem to relate well to Jamaica and provisionally we suggest that ABZ16 ranges from Zone NP19/20 to lower Zone NP21 (Fig. 6). Strontium isotopes from the Claremont Formation (which we would attribute to ABZ16) gave ages of 35.05-35.95 Ma (Robinson *et al.*, 2018), which would indicate a level in lower Zone NP19-20.

Occurrences of what have been regarded as typical late Eocene LBF indicators (*e.g.*, orthophragmines, *H. ocalana* and *Fabularia verseyi*) in the Oligocene are likely due either to alteration of Sr-isotope values (giving an age that is too young) or due to reworking of the LBFs into the Oligocene (Robinson, 2004; Molina *et al.*, 2015; Robinson *et al.*, 2018; Torres-Silva *et al.*, 2017). The top of the zone is notable for the disappearance of many typical Eocene taxa including *H. ocalana*, *Fabularia verseyi*, *Coskinolina* cf. *douvillei*, *Pellatispirella matleyi* and *Butterliniana cubensis*.

5. Application to selected sections elsewhere in the American biogeographic province

Having established a zonation for the Eocene strata of Jamaica based on LBF, in this section we show how it can be used in selected areas of the American Bioprovince based on previous studies (that is, our interpretations of previously figured specimens) of LBF. Some areas are difficult to comment on, because of tectonic deformation and associated reworking of faunas. The Cuban arc underwent a collision with the North American Plate (Iturralde-Vinent *et al.*, 2016) in the middlate Eocene and there is extensive reworking of material; it is therefore difficult to work out successions in Cuba other than for the comments we have provided above. With further work, we beleave that the scheme can be used in Cuba, but will require extensive consideration of reworked material. A considerable amount of work has been undertaken in NE Brazil (*e.g.*, Mello e Sousa *et al.*, 2003), but is largely based on random sections of LBF in thin sections; as such it is difficult to apply the scheme there without a reinvestigation of the material available. Our regional correlation is shown in Fig. 7.

5.1. Florida. Extensive studies concern the Eocene LBF succession in Florida (*e.g.*, P.L. Applin & E.R. Applin, 1941; Cole, 1941, 1942, 1944, 1945; E.R. Applin & Jordan, 1945; Levin, 1957; Cole & E.R. Applin, 1964; Powell, 2010; Cotton *et al.*, 2018). We have reviewed the occurrences and illustrations in these works and present our reinterpretation of the biostratigraphy in Fig. 7.

The Oldsmar Formation consists of a lower unit of grey-brown dolostone and an upper unit of white to grey, interbedded layers of lime mudstone, wackestones, packstones and tan dolostones (Miller, 1986). The basal boundary is sharp. In Cedar Keys No. 2 well, *Linderina floridensis* occurs at 983-1068 ft. (= 300-326 m) and *Hel. gyralis* and *L. floridensis* occur at 1301-1308 ft (= 397-399 m) (Cole, 1942, p. 15), but no nummulitids were recorded from this well (although it is possible that nummulitids may occur in more open water environments that *Helicostegina*). Levin (1957) illustrated typical *Hel. gyralis* from the Oldsmar Formation. This suggests a correlation with upper ABZ6, or possibly lower ABZ7 (if nummulitids are absent due to facies control). However, the similar embryonic sizes of *H. gyralis* as given by Levin (1957) with specimens from upper ABZ6 suggests an assignment to upper ABZ6.

The Avon Park Formation of P.L. Applin & E.R. Applin (1944, p. 1686) includes the Lake City Formation of P.L. Applin & E.R. Applin (1944, p. 1693) (Miller, 1986). The formation consists of light-brown limestones and dolostones, and has an unconformable relationship with the underlying Oldsmar Formation (Miller, 1986). The best foraminiferal record from the Avon Park Formation comes from Hilliard Turpentine Company well W-366 (Cole, 1944, p. 33-34) where the following species and levels were indicated (species identifications updated): *Eolepidina antillea* (R = 5/6, Cole, 1944, Pl. 10, figs. 1-3, 5, 7) at a depth of 1340-1350 ft (= 408-411 m) (ABZ8); *Eo. subplana* (R = 4, Cole, 1944, Pl. 10, figs. 4, 6; Pl. 12, fig. 3) at a depth of 1300-1305 ft (= 396-398 m) (ABZ9); *Lep. ariana* (R = 2, Cole, 1944, Pl. 16, figs. 11-13) at a depth of 1065-1070 ft (= 324-326 m) (ABZ12) and *Orbitoina cedarkeyensis* Cole, 1944, p. 34) at a depth of 1005-1025 ft (= 306-312 m) (ABZ12 or ABZ13?). Above 1005 ft. (= 306 m), there is a change in fauna, with the upper part of the Avon Park Formation being characterised by conical agglutinated foraminifers including *Coskinolina*, *Fallotella* and *Cushmania* (Cole, 1944). Specimens of *Cushmania* from the Avon Park Formation (*e.g.*, Cole, 1944, Pl. 4, fig. 6) have a relatively large (400 µm) first chamber, and this morphology characterises ABZ13-ABZ15 in Jamaica. Thus the Avon Park Formation probably ranges from ABZ8 to at least ABZ13.

The Ocala Formation consists of white- to cream-coloured, highly fossiliferous wackestones, packstones and grainstones with a basal unconformity with the underlying Avon Park Formation (Miller, 1986). It yields a fauna characterised by *Lep. ocalana*, *Het. ocalana* and *Eu. chaperi* (Cole, 1941, 1942, 1944, 1945; Powell, 2010; Cotton, 2018). This assemblage indicates ABZ16.

5.2. Alabama. Robinson and Jiang (1996) provided biostratigraphic data on calcareous nannofossils and LBFs from the Bay Minette corehole and the section at Little Stave Creek in Alabama (Fig. 7). We recognize four depositional units, the upper three of which can be constrained by LBF. The appearance of *Operculinoides gravelli* indicates either ABZ7 or ABZ8, whereas the presence of *Eo. subplana* and *Eo. gardnerae* indicate ABZ9 and ABZ10, respectively. There is a hiatus representing ABZ11 and *Lep. ariana* indicates ABZ12. There is a further hiatus representing ABZ13-ABZ15 whereas the presence of *Lep. montgomeriensis* possibly suggests ABZ16. There is a general resemblance to the stratigraphy of Florida with similar hiatuses/unconformities.

5.3. Panama. Cole (1952) described the foraminifers of the Gatuncillo Formation from the Panama Canal Zone, and Woodring (1957) provided additional information on the samples. The samples of Cole (1952) indicate three zones: ABZ14 with *Plio. tobleri*; ABZ15 without either *Plio. tobleri* or *Heter. ocalana* (but some samples with *Eu. chaperi*); and ABZ16 with *Heter. ocalana* and *Eu. chaperi* (Fig. 7).

5.4. Mexico (state of Veracruz). The species recorded by Barker and Grimsdale (1936, 1937) and Barker (1939) allow the identification of some zones in the state of Veracruz, Mexico (Fig. 7). The association of *Hel. gyralis* with *Pseudolepidina trimera* and *Operc. jennyi* at Jenny Station No. 1573 (11 km southeast of Sabaneta, state of Veracruz, Mexico) indicates lower ABZ7, whereas the presence of *Hel. dimorpha* indicates upper ABZ7 or ABZ8. The presence of *Eu. guayabalensis* in association with *Operculinoides prenummulitiformis* and *Nummulites guayabalensis* (Barker, 1939, p. 325) also indicates ABZ7. The presence of *Eulinderina semiradiata* (= *Eolepidina antillea*) and *Eulinderina guayabalensis regularis* (= *Eu. regularis)* in association with *Tremastegina* would indicate a level around the ABZ7-ABZ8 boundary. *Polylepidina chiapasensis* var. *subplana* (= *Eo. subplana*) and *Polylepidina* '*chiapasensis*' (= *Eo. gardnerae*) indicate zones ABZ9 and ABZ10, respectively. Frost and Langenheim (1974) figured specimens of *Eo. gardnerae* as *Lepidocyclina (Polylepidina) antillea* from central Chiapas, Mexico, which would also indicate ABZ10.

5.5. Margarita Island, Venezuela. Brönnimann (1944), Butterlin (1970) and Caudri (1974) described Eocene LBF assemblages from the Punta Mosquito Formation of Margarita Island. Caudri (1974) figured the fauna in detail from three samples and these forms can be placed in the zonation scheme (Fig. 7). Sample B yielded *Eo. subplana* (= *Lepidocyclina (Polylepidina) antillea* of Caudri, 1974), *Orbitoina* sp., *Helicolepidina polygyralis* and *Operculinoides* spp. (Caudri, 1974, identifications updated) and can be placed in ABZ9. Sample A yielded *L. ariana*, *Orbitoina* spp. and *Operculinoides* spp. (Caudri, 1974) and can be assigned to ABZ12. Sample P.J.B.145 yielded *L. ariana*, *Orbitoina* spp., *Helicolepidina spiralis trinitatis* [= *nortoni* Vaughan], *Helicosteginopsis soldadensis*, *Caudriella ospinae* and *Operculinoides* spp. (Caudri, 1974, identifications updated) and can also be assigned to ABZ12.

5.6. Venezuela. Raadshooven (1951) described a series of LBF assemblages from Venezuela. The earliest Eocene assemblage from the Quebrada Grande Limestone (Baralt District, State of Zulia, western Venezuela) consisted of *Planorbitoinella nitida* (= *Lepidocyclina* sp. A of Raadshooven) which occurred with *Helic. gyralis* and *Operculinoides* cf. *oliveri* which suggests lower ABZ7 (Fig. 7). The San Juan Limestone (Baralt District, State of Zulia, western Venezuela) yields *Poly. ecuadorensis* in association with *Operculinoides* spp. (cited as *O. jennyi* by Raadshooven, 1951); this suggests upper ABZ7 (Fig. 7).

5.7. Saint Bartholomew (St. Barths). The Eocene succession in Saint Bartholomew has been described in many works (*e.g.*, Lewis & Robinson, 1976; Westercamp & Andreieff, 1983; Caron *et al.*, 2019; Cornée *et al.*, 2020) and details of the LBFs have been given in works such as Cushman (1919), Cole (1960), Robinson (1996) and Cornée *et al.* (2020). The succession consists of alternations of shallow-water limestones and volcaniclastic sedimentary rocks which have been intruded by various igneous plutons (Westercamp & Andreieff, 1983; Legendre *et al.*, 2018). The stratigraphy for the Eocene rocks has varied from paper to paper. Lewis and Robinson (1976) placed all the Eocene limestones in the Middle Eocene. Westercamp and Andreieff (1983) recognized six Eocene limestone horizons which they divided into a lower group (lower two limestones) and an upper group (upper four limestones), all of which were assigned to the Upper Lutetian. Caron *et al.* (2019) named the six limestone horizons from base to top: Flamands (1), Mangin (2), Cayes (3), Gouverneur (4) and Lurin (5-6); they assigned these to the upper Lutetian to Bartonian. In contrast, Cornée *et al.* (2020) divided the succession into three limestones: a Lower Limestone of Lutetian age, an Intermediate Limestone of late Bartonian/early-late Priabonian age, and an Upper Limestone of Priabonian age. The ages of the limestones as given by Cornée *et al.* (2020) were largely based on LBF identified in random thin sections to genus level, and judging by their illustrations, there are clearly some misidentifications of species and genera (*e.g.*, *Eoconuloides wellsi*, *Helicostegina*, *Heterostegina ocalana*). Detailed investigations of orientated sections of LBFs from two of the limestones have been given by Cole (1960) and Robinson (1996) and these can be placed within the zonal scheme presented here. The Flamands Limestone (1) of Caron *et al.* (2019) at Pointe Lézarde yields *Eolepidina antillea* (it is the type locality: Cole, 1960; Robinson, 1996), which allows assignment to ABZ8 (Fig. 7); whereas the Lurin Limestone (5-6) of Caron *et al.* (2019) yields *E. subplana* (Robinson, 1996) and can be assigned to ABZ9 (Fig. 7). Assuming that the LBFs are not reworked, this would suggest that the limestone sequence on Saint Bartholomew is solely of mid to mid-late Lutetian age (although higher levels could be represented in the upper part of the Lurin Limestone) and a study of orientated sections of LBF from other limestone horizons is needed. Miocene limestones occur above this interval but are not relevant to this work.

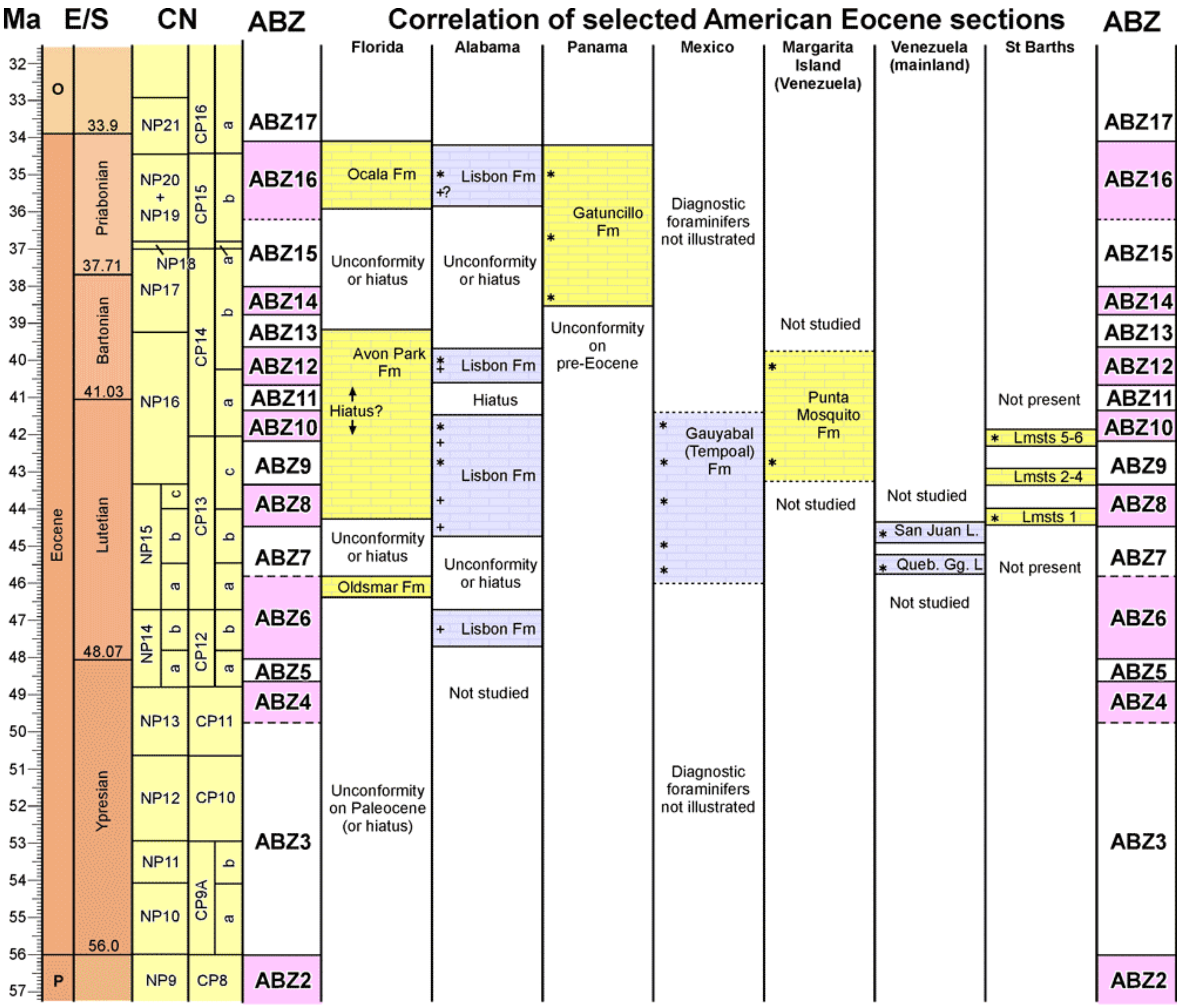


Figure 7: Our interpretation of representative sections in selected areas across the American biogeographical Province based on our zonal scheme presented here.

5.8. Trinidad. It is difficult to apply the zonation scheme to Trinidad because of the thin successions of Eocene rocks and the extensive reworking of specimens of LBFs. This is clearly seen in Soldado Rock (*e.g.*, CAUDRI, 1975, 1996) where there are extensive slump deposits and the reworking of older foraminifers into younger layers (KUGLER & CAUDRI, 1975). Ignoring the slump masses, the first appearances of specific foraminifers can be used to suggest some correlations for Soldado Rock. The presence of *Operculinoides* spp. in lower bed 3 suggests ABZ7 or younger, whereas the absence of typical Lutetian markers suggests that Bed 3 may be as young as Bartonian. The appearance of *Pliolepidina tobleri* in bed 7 would suggest a correlation with ABZ14. Because of the extensive reworking, we do not show Trinidad on Fig. 7.

5.9. Barbados. The Scotland District of Barbados also contains Eocene LBFs, but as with Trinidad there is extensive reworking. The Murphys Beds however yield *T. senni* in association with *H. minor* without *Operculinoides* spp. or *Nummulites* spp. (BRÖNNIMANN, 1950). This would suggest an assignment to either ABZ4 or ABZ6. Paleocene *Ranikothalia* occur throughout (CIZANCOURT, 1948; CAUDRI, 1972) indicating extensive reworking from the Paleocene. As a consequence, we do not show Barbados on Fig. 7.

6. Classification of LBFs and taxonomic notes

Previous classifications of the orbitoidiform foraminifers considered here can be found in ADAMS (1987), LOEBLICH and TAPPAN (1988), BUTTERLIN (1988), and BOUDAGHER-FADEL (2018), with the phylogeny suggested by BARKER and GRIMSDALE (1936) having been generally accepted in all subsequent works. With regard to the Lepidocyclininae, previous workers (*e.g.*, GRIMSDALE, 1959; VLERK, 1959; SIROTTI, 1983; BUTTERLIN, 1987) have suggested different clades. Our studies of the Asterigerinoidea ORBIGNY (forms surrounding *Amphistegina*, *Lepidocyclina* and their allies) clearly demonstrate that the current classification is polyphyletic, and also that the simple phylogenetic scheme presented by Barker and Grimsdale (1936) is too simplistic, ignores the different forms of test construction in the various groups, and thus should not be the basis for the classification of these foraminifers into families and subfamilies. Here, we introduce a revised classification (based on foraminiferal test morphology and our detailed stratigraphic occurrences) that we think provides a suitable monophyletic scheme and gives an appropriate classification rank to the various clades. We feel that the current classification of taxa into the Helicolepidininae and Lepidocyclininae is not appropriate and prefer to base families on clearly defined phylogenetic series regardless of whether orbitoidiform growth has not or has been achieved. We do not formally describe each genus or species (unless new), but provide synonyms, diagnostic criteria, and discussions that hopefully allow genera and species to be properly identified. We illustrate numerous specimens (some well preserved and some more poorly preserved) of each species so that there is no ambiguity in our specific interpretations. For ease of reference, we also list the bewildering array of synonyms at the generic level that have been previously introduced. The classification scheme adopted for the taxa we use in our zonation is laid out below.

6.1. Terminology

We follow standard guides on terminology for the classification of the foraminifers described here (*e.g.*, Adams, 1987; Hottinger, 2006). We discuss some of these terms in more detail below.

The terms used for the orientation of the tests of foraminifers are not uniform between different morphologies, and separate schemes are used for trochospiral and orbitoidiform taxa (Hottinger, 2006). In the Helicosteginidae fam. nov. the test is trochospiral, and in the early forms (*e.g.*, *Helicostegina wellsi*), one side of the test is elevated, and the other side of the test is flat or even concave (Fig. 8.1). In *Helicostegina wellsi*, the proloculus is situated close to the flat (or concave) side of the test (Fig. 8.1), which by definition makes this the 'spiral' or dorsal side of the test (Hottinger, 2006). In *H. wellsi* the subsidiary chamberlets are formed within the alar prolongations (or replace the septa forming the alar prolongations) on the 'umbilical' or ventral side of the test (Fig. 8.1). In later species of *Helicostegina* (*e.g.*, *H. gyralis, H. dimorpha*, *H. jeannemairae* sp. nov.) the ventral side of the test can be recognized by the layer of subsidiary chamberlets (Fig. 8.2-3). In forms with an orbitoidiform test, such as the Lepidocyclinidae, there is an equatorial layer with lateral chamberlets on both sides (Fig. 8.4). It is only in the earliest forms (*Eulinderina guayabalensis*) that the proloculus lies closer to one (dorsal) side of the test and there is a hint of low trochospiral coiling (Fig. 8.5); in later forms the dorsal and ventral sides of the test cannot be distinguished and an equatorial layer is overlain by two sets of lateral chamberlets (Fig. 8.4). Thus the subsidiary chamberlets in the Helicosteginidae are equivalent to one set of lateral chamberlets as developed in the Lepidocyclinidae. Thus the 'complete flange of equatorial chamberlets' described in *H. dimorpha* by Adams (1987, p. 294) represents a cut passing from the primary spire into the subsidiary layer of ventral chamberlets. In later species (*e.g.*, *H. jeannemairae* sp. nov.*, H. jamaicensis* sp. nov.) a true flange of equatorial chamberlets is developed from the primary spire and a subsidiary layer of ventral chamberlets (which have the same morphology as a true equatorial layer) is developed on the ventral side giving the flange a two-layered structure (Fig. 8.3).

Following Adams (1987, p. 289) we use the terms proloculus and deuteroloculus for the first two chambers in spiral forms (Asterigerinoidea, Nummulitidae) where the second chamber (deuteroloculus) has only one aperture or stolon (R = 3 or more; Fig. 8.6). We use the term protoconch and deuteroconch in forms where the deuteroconch has two (R = 2) apertures or stolons (Fig. 8.7). In many of these forms (whether they consist of a proloculus and deuteroloculus or a protoconch and a deuteroconch) the first two chambers frequently have a thicker and darker wall than the succeeding chambers and this represents the embryo (*e.g.*, Adams, 1987; Krüger *et al.*, 1997; Langer & Hottinger, 2000). We use the form of the embryo and subsequent growth as generic and specific characters. In axial sections either the first two chambers (Figs. 8.1-2, 8.5), or one of the first two chambers may be visible (Fig. 8.3-4).

We use the term chamber for successive growth stages of spiral foraminifers. In some forms, the alar prolongations of the chambers are divided up into smaller chamberlets on the ventral side of the test in trochospiral forms. In some trochospiral forms, the alar prolongations of the chambers on the ventral side of the test interfinger with short ventral chamberlets (*Amphistegina*, *Tremastegina*: Fig. 8.8); the term stellar chamberlets has been used for these short ventral chamberlets (Hottinger, 2006), but may not be appropriate and they may have had a separate origin. We tentatively use the term stellar chamberlet here pending further research on these forms. In other trochospiral forms (*e.g.*, *Helicostegina gyralis*), the alar prolongations on the ventral side of the test are divided up into a series of subsidiary chamberlets (Fig. 8.9) connected by a series of ventral stolons. In this case the lumina of the chambers with undivided dorsal alar prolongations can be seen interfingering with the subsidiary chamberlets on the ventral side of the test (*H. minor*, Fig. 8.9). In later forms (*H. jeannemairae*) the ventral layer of subsidiary

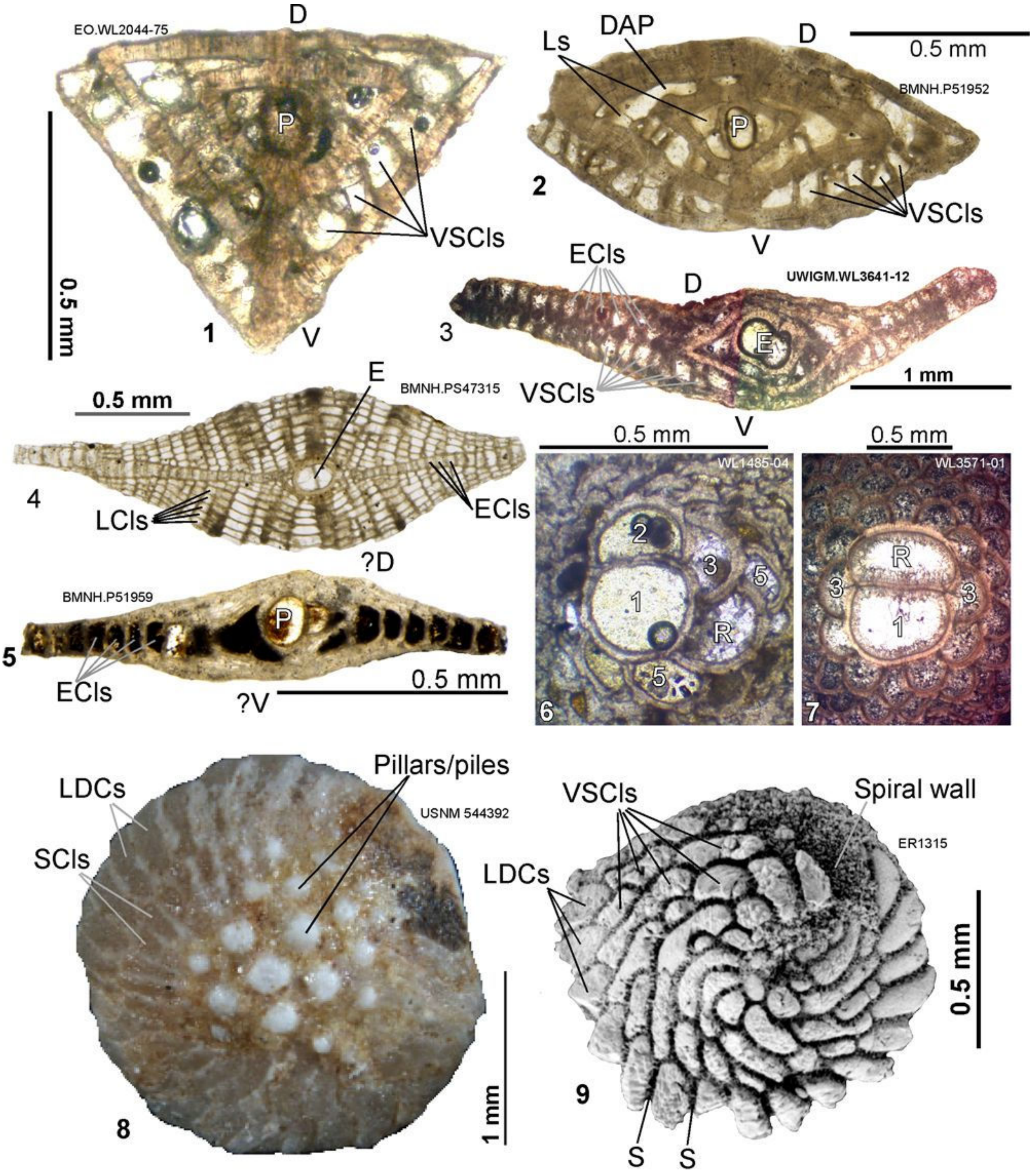


Figure 8: Terminology used in this paper. **1** *Helicostegina wellsi* (EO.WL2044-75) showing position of proloculus and ventral subsidiary chamberlets (axial section). **2** *Helicostegina gyralis* (BMNH. P51952) and **3** *Helicostegina jeannemairae* sp. nov. (UWIGM.WL3641-12) showing ventral layers of subsidiary chamberlets (axial sections). **4** *Lepidocyclina yurnagunensis morganopsis* (BMNH PS47315) showing equatorial layer with lateral chamberlets (axial section). **5** *Eulinderina guayabalensis* (BMNH. P51959) showing proloculus closer to one side (?dorsal) than the other (axial section) and a lack of lateral chamberlets. **6** *Eulinderina subplana* (UWIGM. WL1485-04) showing embryo consisting of proloculus and deuteroloculus with the deuteroloculus having one budding chamber (3), equatorial section. **7** *Lepidocyclina ariana* (UWIGM.WL3571-01) showing embryo with protoconch and deuteroconch with the deuteroconch having two budding chambers (R) and symmetrical spires of peri-embryonic chambers, equatorial section. **8** *Tremastegina lopeztrigoi* (USNM 544392) showing stellar chamberlets and piles/pillars, ventral exterior view. **9** *Helicostegina minor* (ER1315), decortized specimen showing lumina of dorsal chambers extending onto ventral side, septa between chambers, ventral subsidiary chamberlets, and the spiral wall between whorls, ventral view.Key to symbols: 1 - protoconch or proloculus; 2 – deuteroloculus or deuteroconch; 3, 4, 5 - subsequent chambers/chamberlets. D - dorsal; DAP - dorsal alar projections; E - embryo; ECls - equatorial chamberlets; LCls - lateral chamberlets; LDCs - lumina of dorsal chambers; Ls - lumina; P - protoconch /proloculus or deuteroloculus/deuteroconch; R - first chamber with a retrovert aperture; S - septa; V – ventral; VSCls - ventral subsidiary chamberlets.

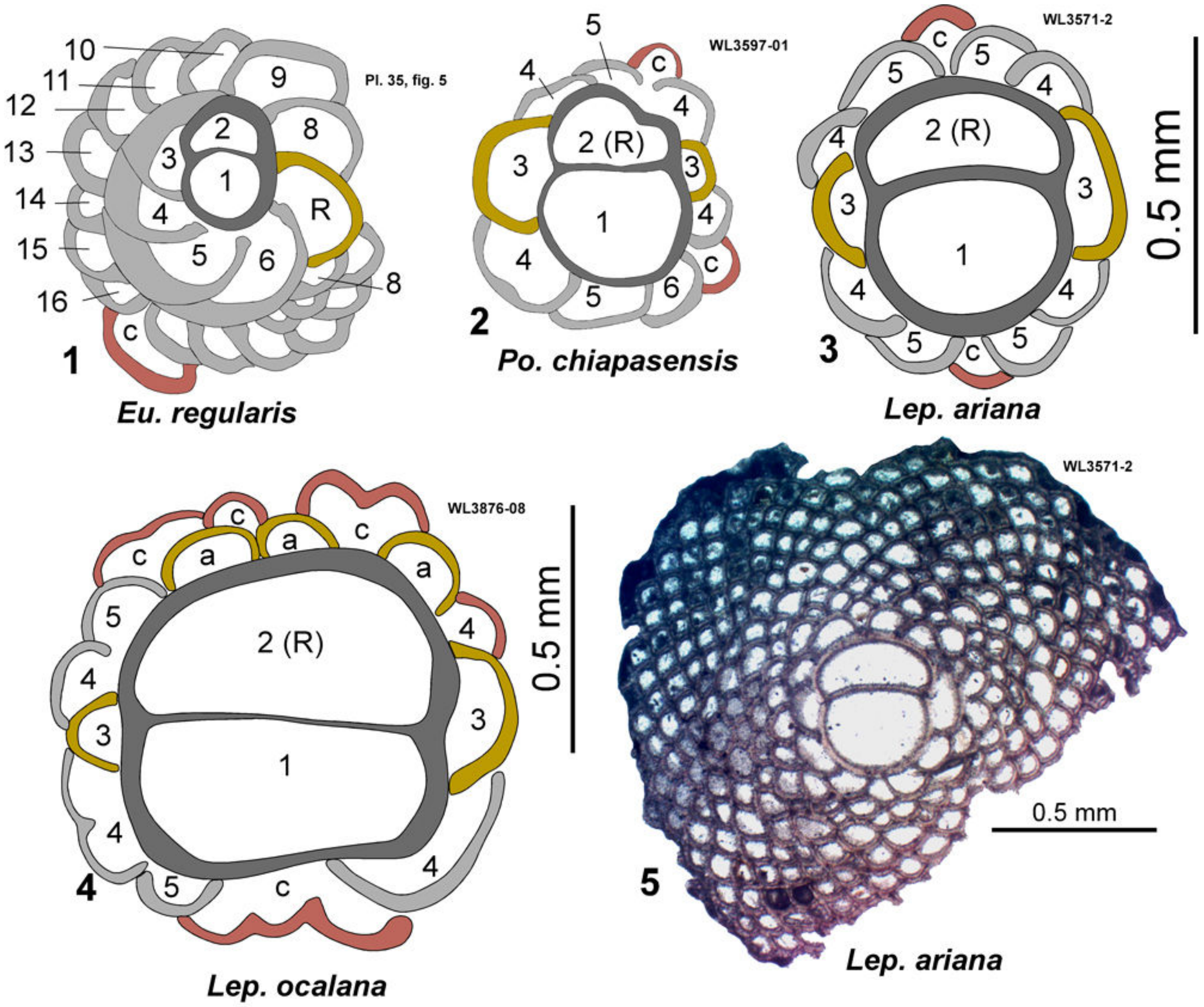


Figure 9: Forms of equatorial chambers and chamberlets. **1-4**, line drawings showing equatorial chambers. **1**, Proloculus (1) and deuteroloculus (2) followed by a short spire of equatorial chambers ending in a chamber with a retrovert aperture (R) from which two spires (spire and counterspire) of equatorial chambers develop and meet in a closing chamber (c). **2**, Form with a protoconch and deuteroconch and two Principal Auxiliary Chambers (PACs) with four asymmetrical spires meeting in two closing chambers (c). **3**, Form with a protoconch and deuteroconch and two Principal Auxiliary Chambers (PACs) with four symmetrical spires meeting in two closing chambers (c). **4**, Form with four adauxiliary chamberlets and multiple closing chambers. **5**, Form with equatorial chamber arrangement as in 3, showing equatorial chamberlets developing from the equatorial chambers.

chamberlets passes into a ventral sheet of chamberlets which mimics the growth in the equatorial layer of orbitoidiform foraminifers (Fig. 8.3). In contrast, the equatorial layer of orbitoidiform foraminifers has lateral chamberlets on both sides (Fig. 8.4) of the equatorial layer which are separated by irregular or regular walls and connected by diagonal stolons (HOTTINGER, 2006).

The equatorial layer in more primitive members of many megalospheric forms of various lineages starts with a proloculus and a deuteroloculus followed by a primary spire of equatorial chambers (Fig. 9.1). In many forms, the primary spire persists to the edge of the test, but in others the spire terminates in a chamber (R) with two apertures (Fig. 9.1) from which a spiral and a counterspiral of equatorial chambers encircle either the embryo (of two chambers) or the earlier chambers of the initial spire (following the embryo) and terminate in a closing chamber (Fig. 9.1). Each chamber in these two spires has two apertures which gives rise to equatorial chamberlets and initiates orbitoidiform growth. In many lineages, the length of the primary spire shows a progressive reduction over time (nepionic acceleration); this may give rise to one PAC (in which case a proloculus and deuteroloculus are still present and R = 3) or two PACs (in which a protoconch and deuteroconch are present and R = 2; Fig. 9.2). Once an embryo and two PACs are developed, either three of four unequal spires of peri-embryonic chambers encircle the embryo, with two closing chambers; Fig. 9.2). In more primitive forms the three or four spirals are asymmetrical (Fig. 9.2), but over time four symmetrical spirals of peri-embryonic chambers en-

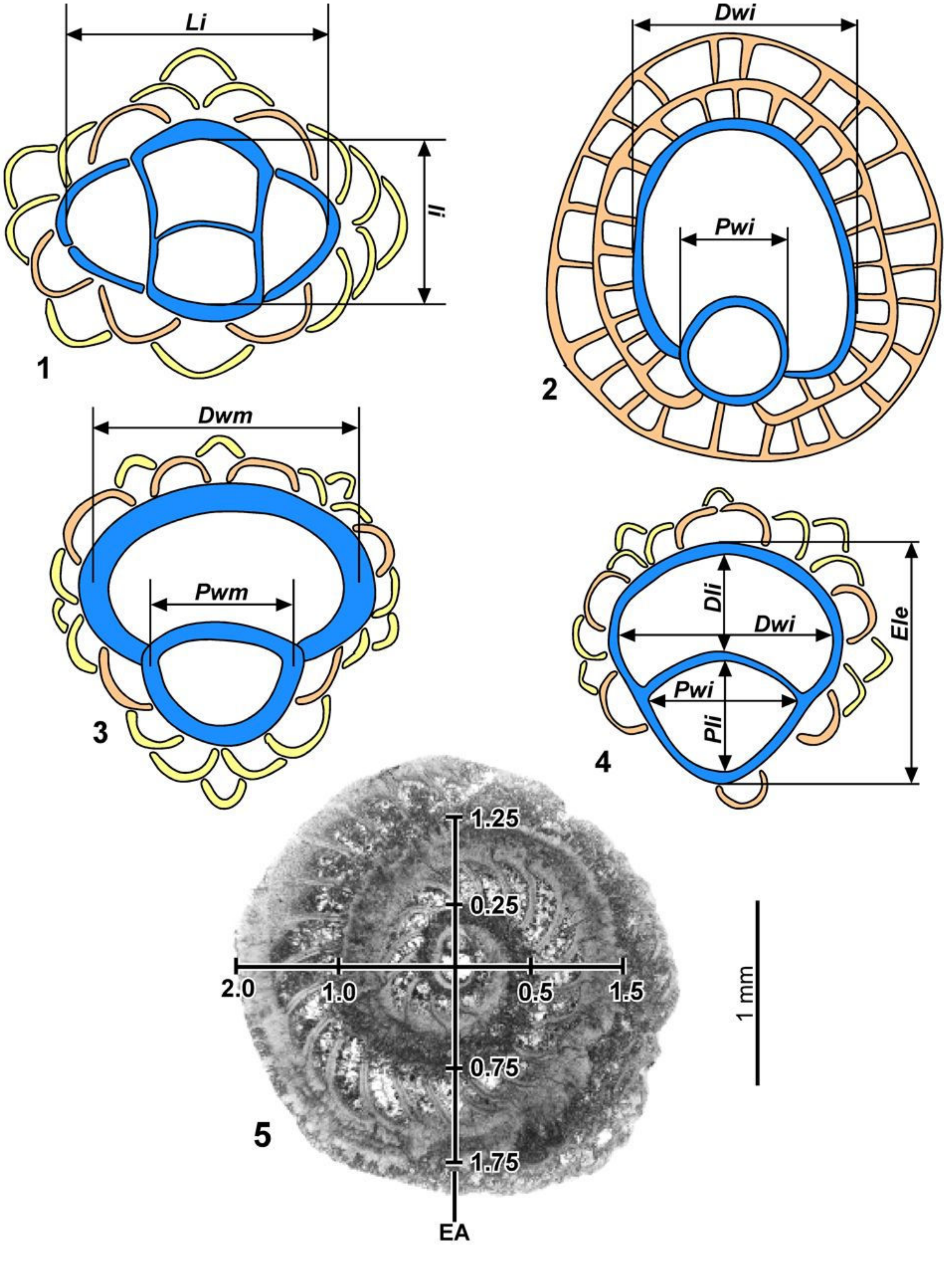


Figure 10: Measurements and coiling diagrams for selected LBFs. Note that either the internal dimensions (i), external dimensions (e) or middle of the wall (m) are used in different schemes. **1**, measurement for Cretaceous *Orbitoides* (after Hinte, 1965; Gorsel, 1978). **2**, measurements for Tethys orthophragmines (after Less, 1987). **3**, Measurements for Tethys lepidocyclinids (after Vlerk, 1959; Drooger, 1993). **4**, measurements for American lepidocyclinids (after various authors). Note that different measurements are used for different groups in different biogeographic provinces. For the Americas, we use the external length of the embryo (Ele) and the internal width of the proloculus/protoconch (Pwi). **5**, measurements for construction of a coiling diagram: primary axis is the embryonic axis (EA), with measurements of length (from centre of proloculus) to edge of spiral wall being made at 90° intervals (as shown); coiling diagrams are produced by plotting length versus whorl and the gradient of the linear regression (with intercept not set to the origin) gives the coiling parameter.

circle the embryo (Fig. 9.3). Subsequently, some forms develop adauxiliary chambers (Fig. 9.4) which are connected to the protoconch and/or the deuteroconch by stolons; in these forms short spirals and multiple closing chambers are developed. This progressive evolution of the equatorial layer is repeated in many lineages and this gives rise to homeomorphs which are not phylogenetically related. We use other criteria to separate these different clades.

The size of the embryo has commonly been used in separating species in the Americas (*e.g.*, COLE, 1952; BARKER & GRIMSDALE, 1936; COLLETTI *et al.*, 2019). However, the size of the embryo has both phylogenetic significance and environmental significance, with variations due to salinity, temperature, and water depth (*e.g.*, NIGAM & RAO, 1987; BRYAN, 1995; YU *et al.*, 2016). Given the variation in the size of the embryo in populations of the same species from different environments, the size of the embryo, in itself, is not diagnostic for species identification (we show examples of this in our work here). Notwithstanding this, the size of the embryo helps in distinguishing between different lineages (*e.g.*, *Lepidocyclina* and *Orbitoina*) and needs to be taken into consideration (with other characters).

Equatorial chamberlets in an orbitoidiform growth plan are developed from the primary spiral(s) of chambers or from the peri-embryonic equatorial chambers (Fig. 9.5). Their morphology is dependent on shape (*i.e.*, how the chambers interlock), the radial distance versus the concentric distance of the connecting walls, and the position of the connecting stolons between radially adjacent equatorial chamberlets. The form of equatorial chamberlets in American lepidocyclinids has been investigated by HOHENEGGER and TORRES SILVA (2020), but we do not consider this in detail in this work. We illustrate the equatorial chamberlets in the figures of the species that follow.

Lateral chamberlets (seen in axial sections) may form regular stacks (tiers) or alternate. They may be separated by thin walls, thick walls or piles (pillars). The surface of the test may be smooth, have irregular anastomosing patterns representing the walls between the lateral chamberlets, or have piles (pillars or pustules). We illustrate the form of the lateral chamberlets in the figures for each taxon below. In some forms (*e.g.*, *Tremastegina*, *Helicostegina*), small pustules may follow the septa on the dorsal and/or ventral side/s of the test. In some forms, the ventral side of the test may be divided into chamberlets or stellar chamberlets (Fig. 8.8).

Various measurements have been made on the embryos of LBF. This has varied both by geographical region (*e.g.*, Tethys versus the Americas) and by group. For instance, in Cretaceous *Orbitoides* (Fig. 10.1) the length and width of the nucleoconch excluding the thickness of the walls has been measured (*e.g.*, HINTE, 1965; GORSEL, 1978). For orthophragmines (Fig. 10.2) the thickness of the wall has been included in the measurements of the width of the protoconch and the deuteroconch (*e.g.*, LESS, 1987). In contrast, for Tethys lepidocyclinids (Fig. 10.3) the width of the protoconch and deuteroconch (including half the thickness of the walls) has been used (*e.g.*, VLERK, 1959; DROOGER, 1993). Subsequent work has tended to follow a particular scheme for a particular group so as to allow comparisons (*e.g.*, MITCHELL, 2006; LESS *et al.*, 2018; ÖZCAN *et al.*, 2018, 2021a). For American lepidocyclinids and their allies, different measurements have been made. These are typically the internal widths (Pwi and Dwi) and internal lengths (Pli and Dli) of the protoconch/proloculus and deuteroconch/deuterolocus (*i.e.*, excluding the wall) and the length and width of the embryo (including the wall: Ele, Ewe). Some workers have only given parameters for the embryo, Ele and sometimes Ewe (*e.g.*, GORTER & VLERK, 1932; GRAVEL, 1933; VAUGHAN, 1933; COLE & PONTON, 1934; RITTEN & VERMUNT, 1932; RUTTEN, 1935; EAMES *et al.*, 1962; CAUDRI, 1996; SERRA-KIEL *et al.*, 2007); some workers have only given lengths (Pli, Dli) or widths (Pwi, Dwi) of the proloculus/protoconch and sometimes deuteroloculus/deuteroconch (*e.g.*, FROST & LANGENHEIM, 1974; ROBINSON & JIANG, 1995); and some workers both (*e.g.*, BERRY, 1930, 1932; BARKER, 1932, 1934; BARKER & GRIMSDALE, 1936; COLE & BERMUDEZ, 1944; COLE & VAUGHAN, 1945; COLE, 1952; BUTTERLIN, 1961; COLE, 1963; EAMES *et al.*, 1968; COLLETTI *et al.*, 2019). In the Tethys the terms height and width have been used, whereas in the Americas the terms length and width have been used. In order to compare our results with those that have been made before in the Americas, we provide details of the width of the protoconch/proloculus (Pwi) and the length of the embryo (Ele) herein. These measurements are shown in Fig. 10.4. In the Eocene taxa we are dealing with, the proloculus/protoconch and deuterolocus/deuteroconch are generally of similar sizes; we therefore do not provide parameters for Pli, Dli nor Dwi at the present time. To compare the tightness of coiling in the Helicosteginidae, we also construct coiling diagrams (*e.g.*, ROBINSON, 1993) using measurements every 90° (Fig. 10.5).

6.2. Species concepts

Species concepts in American LBF have varied greatly among various specialists using orientated equatorial sections, with some accepting very broad species definitions (*e.g.*, COLE, 1963; FROST & LANGENHEIM, 1974; ROBINSON & WRIGHT, 1993), while others have narrow species definitions (COLE, 1956, 1958a, 1958b; ROBINSON & JIANG, 1995, ROBINSON, 1996, 1997). This is partly due to the material available for study, with random sections in rock samples being much more difficult to identify than isolated specimens from which orientated thin sections can be cut. It may also be due to the reworking of specimens where

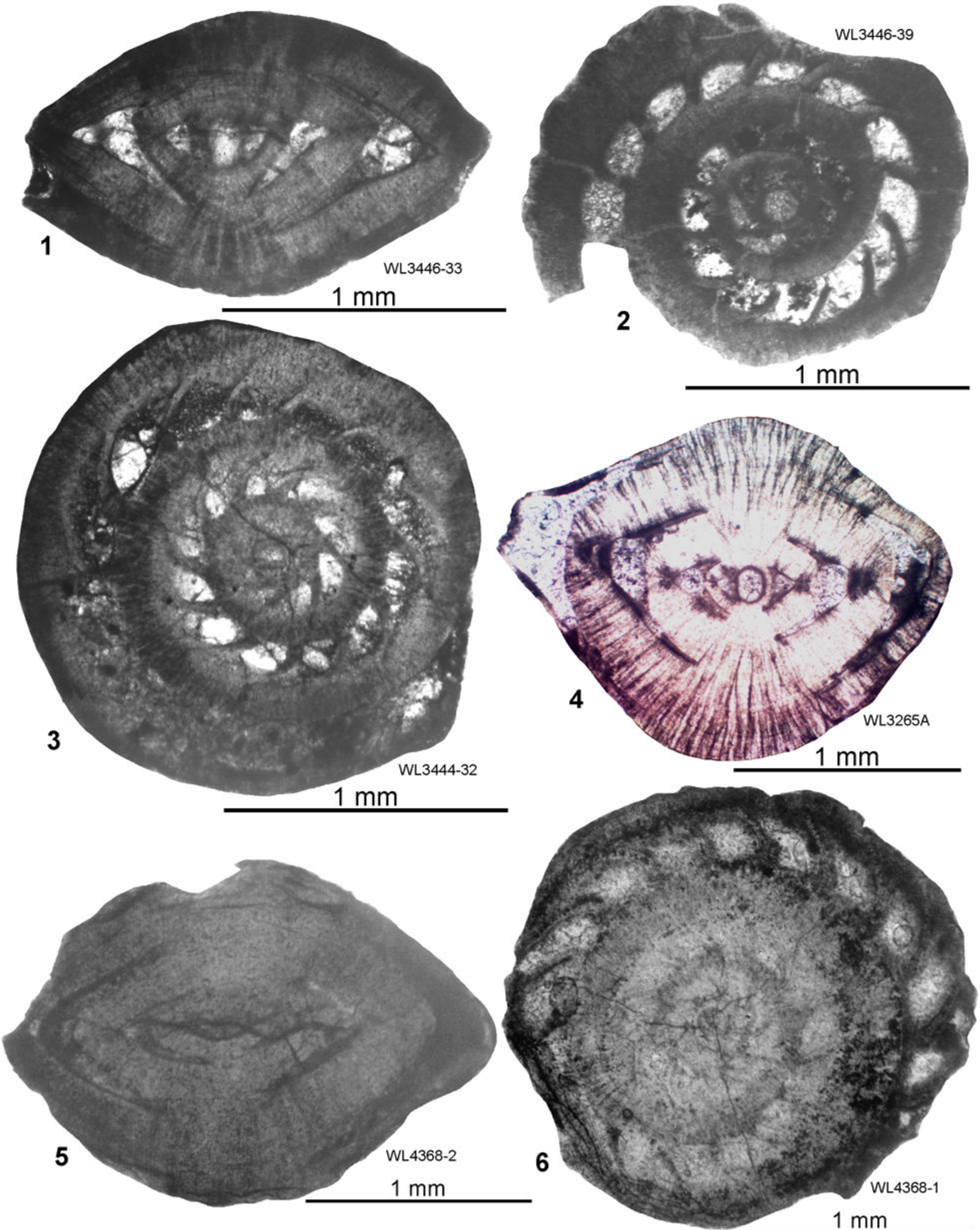


Figure 11: *Butterliniana cubensis* (Palmer, 1934). **1**, axial section (UWIGM.WL3446-33); **2**, orientated equatorial section (UWIGM.WL3446-39); **3**, equatorial section (UWIGM.WL3444-32): Chapelton Formation (ABZ11), Albert Town. **4** (UWIGM.WL3265A), random axial section, type Swanswick Formation (ABZ16), Swanswick House, Trelawny. **5**, off-centre, axial section (UWIGM.WL4368-2); **6**, equatorial section (UWIGM.WL4368-1), turbidite bed in chalk (ABZ11), Windsor Castle, Portland, Jamaica.

populations from different stratigraphic levels have been mixed together (*e.g.*, COLE, 1963; CAUDRI, 1975, 1996). In order to achieve a high-resolution biostratigraphy, multiple isolated specimens are clearly preferable, because this allows detailed measurements of features of the test to be made. We have found that there is generally a uniformity in equatorial sections and 4 or 5 specimens generally allow species to be identified, but (many) more specimens are desirable.

There are also the differences between a typological approach and a statistical approach to be considered. This can be illustrated by considering the evolutionary development within *Eolepidina* in specimens from populations used in this study. Consider, for instance a typological approach to a set of specimens using the criterion R. A 'population' might include specimens with R = 5, R = 4, and R = 3, which, under a typological approach, might be assigned to *Eo. antillea* and *Eo. subplana*, and *Eo. gardnerae*, respectively. Under a statistical approach, the mean value of R can be calculated, which, with values for R defined for each species) would allow a population to be placed in a single species (so in the previous population if the mean R was 4.2, it would allow the population to be assigned to *Eo. subplana*). Our samples, albeit often with only a limited number of specimens, calibrated using nannofossils, demonstrate that mean values of R are very useful biostratigraphy, and we define limits for R for different species in this paper.

In the following sections, we describe the various families, genera, and species of LBF that we use in the zonation scheme. We illustrate each species with numerous specimens (some well preserved, others more poorly preserved) so that our species concepts can be used by other workers.

Superfamily ASTERIGERINOIDEA ORBIGNY, 1839

Family AMPHISTEGINIDAE CUSHMAN, 1927

Remarks. LOEBLICH and TAPPAN (1988) included only *Amphistegina* in the family Amphisteginidae. We place the genus *Butterliniana* gen. nov. also in this family, but further work may indicate that it belongs elsewhere.

Genus *Amphistegina* ORBIGNY, 1826

Type species. *Amphistegina quoyii* ORBIGNY, 1826 (by monotypy: LOEBLICH & TAPPAN, 1988, p. 610) from the Recent of the island of Rawack, Papua province, Indonesia.

Remarks. Species such as *Amphistegina lopeztrigoi* Palmer and *Nummulites parvula* CUSHMAN have previously been placed in *Amphistegina*; in this work we place these taxa in other/new genera. CAUDRI's (1975) species *grimsdalei* (and associated forms), from the Eocene of Trinidad might be an *Amphistegina*, but this needs more work to confirm and is beyond the scope of this paper.

Genus *Butterliniana* MITCHELL, E. ROBINSON & ÖZCAN gen. nov.

Type species. *Amphistegina cubensis* PALMER, 1934, from the Eocene of Cuba.

Diagnosis. Low trochospiral coil, embryo consists of a proloculus and deuteroloculus followed by a spiral arrangement of chambers; stellar chamberlets absent; stolons between chambers without countersepta.

Origin of name. Named after Jacques BUTTERLIN for his work on the foraminifers of the Caribbean region.

Discussion. Carefully prepared thin sections cut perpendicular to the axis on the ventral side (although invariable close to the thick wall of the test and difficult to illustrate) show that the septa divide a short distance from the umbo, but typical stellar chamberlets, as seen in *Amphistegina* are not present. *Butterliniana* differs from *Amphistegina* in lacking stellar chamberlets, and also in having simple stolons between chambers without the development of countersepta. We retain *Butterliniana* in the Amphisteginidae for the present but recognize that the lack of stellar chamberlets might require placement in a new family in the future. This can only be determined once studies of well-preserved, early forms of the Amphisteginidae have been completed.

Butterliniana cubensis (PALMER, 1934)

(Figs. 11 - 12)

Previous descriptions. PALMER, 1934, p. 256-257, Figs. 15-16, Pl. 15, fig. 2; BUTTERLIN, 1970, p. 293, Pl. 3, figs. 5-6; ROBINSON & WRIGHT, 1993, p. 309, Figs. 18.3-5.

Remarks. CUSHMAN (1919) figured four specimens as *Nummulites parvula* (his Pl. 4, figs. 3-6) from St. Bartholomew which are preserved in the Smithsonian. The Smithsonian catalogue records his Pl. 4, fig. 3 (USNM.MO.328183) as holotype and the other specimens (his Pl. 4, figs. 4-6: USNM.PAL27143, PAL.27143 [number duplicated], and PAL.321801) as paratypes. CUSHMAN (1919, p. 51) clearly stated that his Pl. 4, fig. 3 was the type specimen, and that the other three specimens may not represent the same species; as such these should not be considered part of the type series or as paratypes. The species '*parvula*' should therefore only be interpreted based on the holotype. The holotype is a natural, approximately equatorial section in which no indication of the original ornament of the test is visible. It has a diameter of 1.75 mm (as measured from the plate) and shows 5 whorls, with maybe 20 chambers in the final whorl.

COLE (1958a, p. 201, Pl. 25, figs. 17-19; 1969, p. 80, Pl. 16, figs. 1, 3, 5-7, 10-12; Pl. 17, fig. 5) interpreted '*parvula*' based on CUSHMAN's (1919) Pl. 4, fig. 3, 6, probably fig. 4, but not fig. 5. He interpreted '*parvula*' as a senior synonym of *Amphistegina lopeztrigoi* PALMER, 1934. Exterior features of *A. lopeztrigoi* were given by PALMER

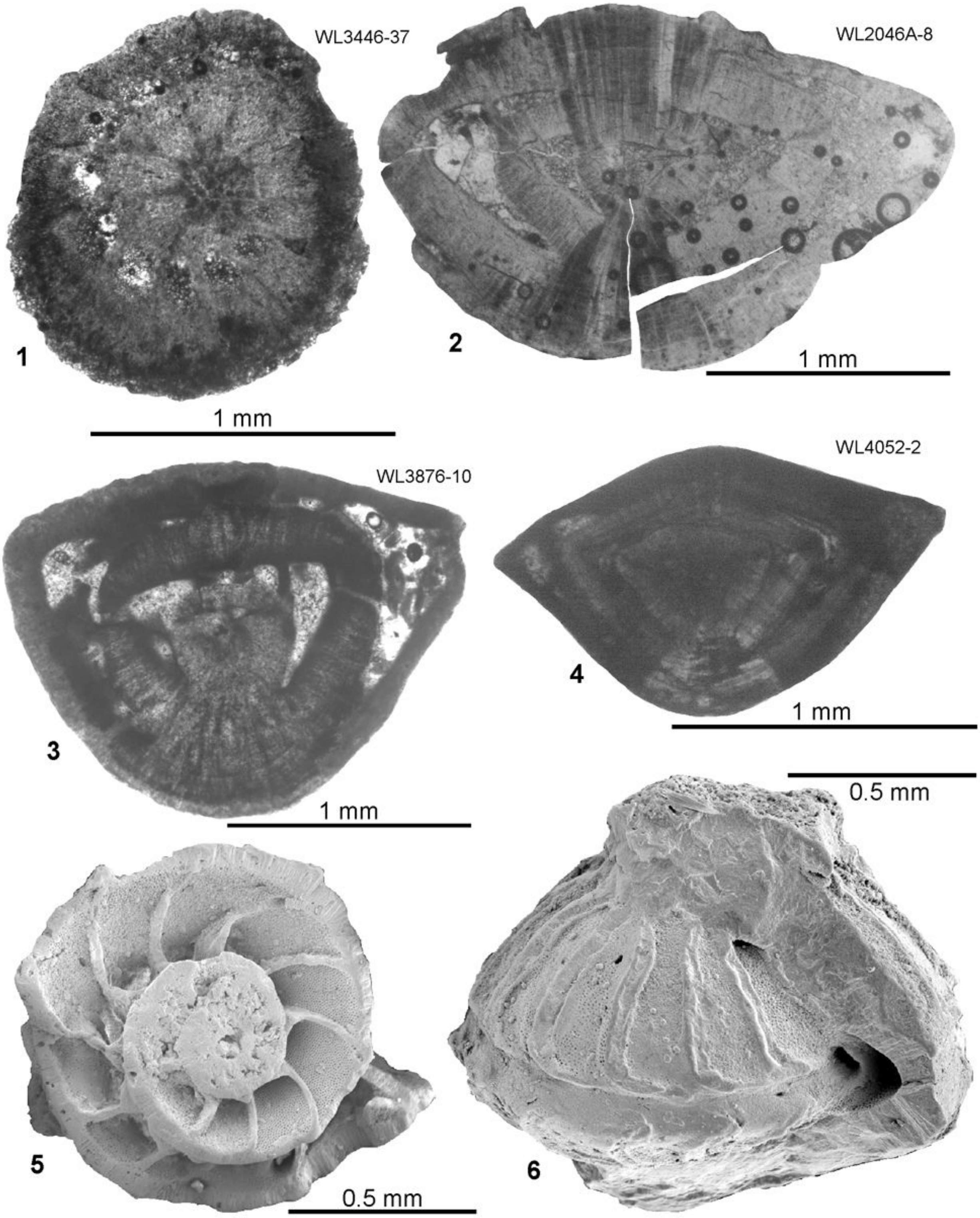


Figure 12: *Butterliniana cubensis* (Palmer, 1934). **1**, section cut parallel to the equatorial plane on the spiral (ventral side) of the test (UWIGM.WL3446-37) showing diverging septa but no stellar chamberlets, Chapelton Formation (ABZ11), Albert Town, Trelawny, Jamaica. **2**, axial section (UWIGM.WL2046A-8), Chapelton Formation (ABZ9), Lilyfield, St Ann, Jamaica. **3**, axial section (UWIGM.WL3876-10), Swanswick (*s.l.*) Formation (ABZ15), N-S Highway 2000, St Ann, Jamaica. **4**, axial section (UWIGM.WL4052-2), Guys Hill Formation (ABZ4), Rio Sambre Gorge, St Mary, Jamaica. **5-6**, SEM photomicrographs, close to type locality of *Nummulites parvula* Cushman, St Bartholomew (ABZ8); **5**, view of chambers on ventral side of test, **6**, view of ventral aspect of test (in opposite view to other specimens because of the light direction in the SEM) showing indications of diverging septa between chambers.

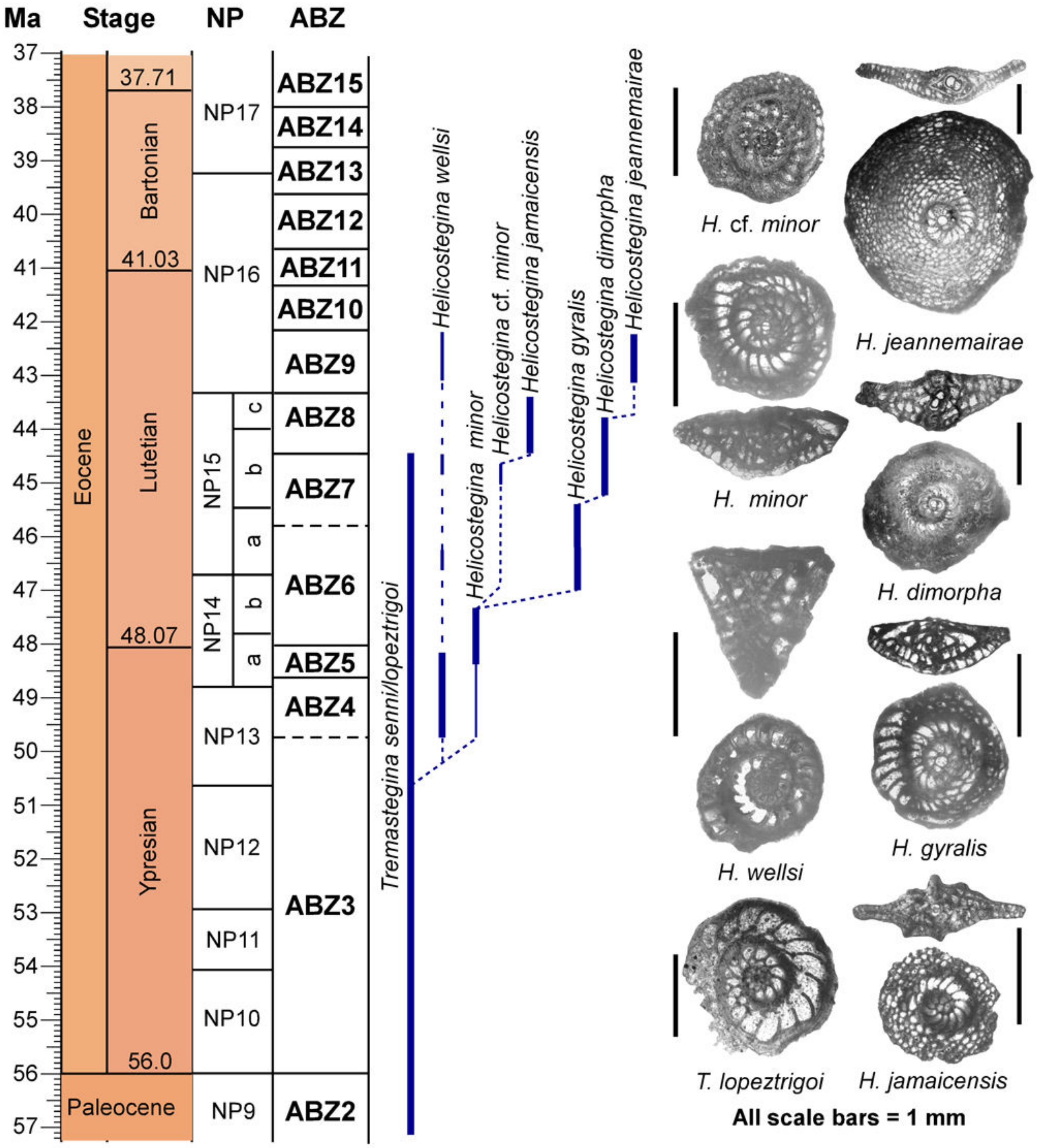


Figure 13: Evolutionary development of the family Helicosteginidae through the Ypresian and Lutetian based on the occurrences of species in Jamaica.

(1934) and interior features of topotype material were provided by Cole and Gravell (1952). Cole's (1958a) Pl. 25, figs. 17-18, show thick-tested forms in axial section with small chambers which are similar to Cushman's (1919) Pl. 4, fig. 5; whereas his Pl. 25, fig. 19 (and Cole, 1969, Pl. 12) shows an equatorial section with 4¼ whorls, which appears to show forwardly orientated (away from the protoconch) septal necks (countersepta) and 17 chambers in the final whorl. Cole (1958a, 1969) does not provide information on the external ornament of specimens, but he included Cushman's (1919) Pl. 4, fig. 6, in synonymy, and this form clearly lacks pustules and is smooth.

A second interpretation of Cushman's (1919) *Nummulites parvula* has followed Butterlin (1970), p. 294, Pl. 3, figs. 5-6 (*e.g.*, Robinson & Wright, 1993, p. 309, Figs. 18.3-5; Serra-Kiel *et al.*, 2007, p. 369, Pl. 2, figs. 11-12, 15). This interpretation effectively includes Cushman's (1919), Pl. 4, fig. 5, and Cole (1958a), Pl. 25, figs. 17-18.

This form was named *Amphistegina cubensis* by Palmer (1934), p. 256-257, Figs. 15-16, Pl. 15, fig. 2.

Loeblich and Tappan (1988, p. 611) placed Cushman's Pl. 4, figs. 3, 6 (but not 5), in synonymy with *'Amphistegina' lopeztrigoi* Palmer, 1934. Clearly Cushman's, 1919, Pl. 4, fig. 3, is not related to what we name here as *Butterliniana*, but we are unable to directly assign this specimen to *lopeztrigoi* because of its very weathered nature.

It is clear that an interpretation of Cushman's (1919) species *Nummulites parvula* is made difficult because the name-bearing type is so poorly preserved. The holotype might be close to *Amphistegina lopeztrigoi* as maintained by Cole (1958a, 1969), but would appear to lack ornament (as judged from other illustrated sections that might be attributed to that species) and it is difficult to interpret as that species. Similarly, one of Cushman's (1919) figured specimens (his Pl. 4, fig. 5) is equivalent to the two axial sections illustrated by Cole (1958a, Pl. 25, figs. 17-18) and was named *Amphistegina cubensis* by Palmer (1934). The name *parvula* is therefore surrounded by nomenclature issues that make it an ambiguous species of debatable affinity. It seems the best course of action would be to prepare a submission to the ICZN for the suppression of the species *parvula* in the combination *Nummulites parvula* Cushman and that *Amphistegina lopeztrigoi* Palmer and *Amphistegina cubensis* Palmer should be placed on the list of accepted names. A case will be prepared for this. We use the specific name '*cubensis*' for this species here.

Butterliniana cubensis is a distinctive long-ranging species appearing in the late Ypresian and apparently becoming extinct near, or at, the top of the Eocene. Specimens vary from forms which are relatively symmetrical in axial section (*e.g.*, Cushman, 1919, Pl. 4, fig, 5; Butterlin, 1970, Pl. 3, figs. 5-6; Cole, 1958a, Pl. 25, figs. 17-18; Robinson & Wright, 1993, Figs. 18.3-5; Serra-Kiel *et al.*, 2007, Pl. 2, figs. 11-12, 15) to forms that are strongly asymmetrical (*e.g.*, Palmer, 1934, Pl. 15, fig. 2). Asymmetrical forms are present at some levels in the mid and late Eocene in Jamaica, but without an analysis of populations it is not possible to determine if more than one species might be recognizable at this time. The number of chambers in the final whorl also varies significantly; without the study of populations it is not possible to determine if this is due to natural variation or might be stratigraphically significant.

Family HELICOSTEGINIDAE

Mitchell, E. Robinson & Özcan fam. nov.

Diagnosis. The family is characterised by involute to secondarily orbitoidiform taxa which have an early stage of trochospiral coiling. There is a progressive development from multiple stolons into a spiral sheet of subsidiary chamberlets on the ventral side in early forms. The development of chamberlets in the peripheral primary spire may lead to the development of an equatorial layer and in some forms a retrovert chamber may develop leading to orbitoidiform growth. In some forms the spiral sheet of equatorial chambers may form a second 'orbitoidiform' layer composed of orbitoidiform chambers on the ventral side of the equatorial layer.

Table 15: Measurements (in µm) of the lengths of the first two chambers (embryo) including the chamber walls (Ele) for species of *Tremastegina* and *Helicostegina* from Jamaica (WL numbers) and reported values (1) and our measurements from figures (2) from other locations.

Taxon	Zone	Min	Mean	Max	SD	N	Source
Tremastegina lopeztrigoi	ABZ7	215	-	230	-	-	[1] Barker & Grimsdale, 1936
Helicostegina wellsi	ABZ4	-	140	-	-	1	Unnamed lmst (WL3324)
H. wellsi	ABZ6	-	100	-	-	-	[1] Cole & Bermudez, 1944
H. wellsi	ABZ6	78	101	135	25.54	4	[2] Cole & Gravell, 1952
H. minor	ABZ4	114	128.7	146	16.17	3	Richmond Fm (WL4052)
H. minor	ABZ6	135	150	181	14.97	11	Stettin Fm (WL3667 & others)
H. gyralis	ABZ6	148	200	256	40.97	8	Helicostegina beds (WL3520)
H. gyralis	ABZ6	312	334	355	30.4	2	Palmetto Grove Fm (WL1705)
H. gyralis	ABZ6	-	235	-	-	1	[2] Florida, Levin, 1957
H. gyralis	ABZ6	200	316	455	111.9	5	[2] Cole & Gravell, 1952
H. gyralis	ABZ7	185	-	240	-	-	[1] Barker & Grimsdale, 1936
H. gyralis	ABZ7	253	275	297	31.11	2	Swanswick House (WL3275)
H. dimorpha	ABZ7	246	308.6	431	61.65	7	Preston Hill Fm (WL3309)
H. dimorpha	ABZ7	-	260	-	-	-	[1] Barker & Grimsdale, 1936
h. dimorpha	ABZ8	336	350	363	19.1	2	Preston Hill Fm (WL2100)
H. cf. *minor*	ABZ7	135	167.5	210	32.79	4	Preston Hill Fm (WL2098)
H. jamaicensis	ABZ8	135	165.6	190	20.38	9	Preston Hill Fm (WL2047)
H. jamaicensis	ABZ8	175	176	176	0.7	2	Preston Hill Fm (WL2086)
H. jamaicensis	ABZ8	188	189	189	0.7	2	Preston Hill Fm (WL2048)
N. jeannemairae	ABZ9	278	340.4	400	46.4	10	Rock Spring (WL3641)

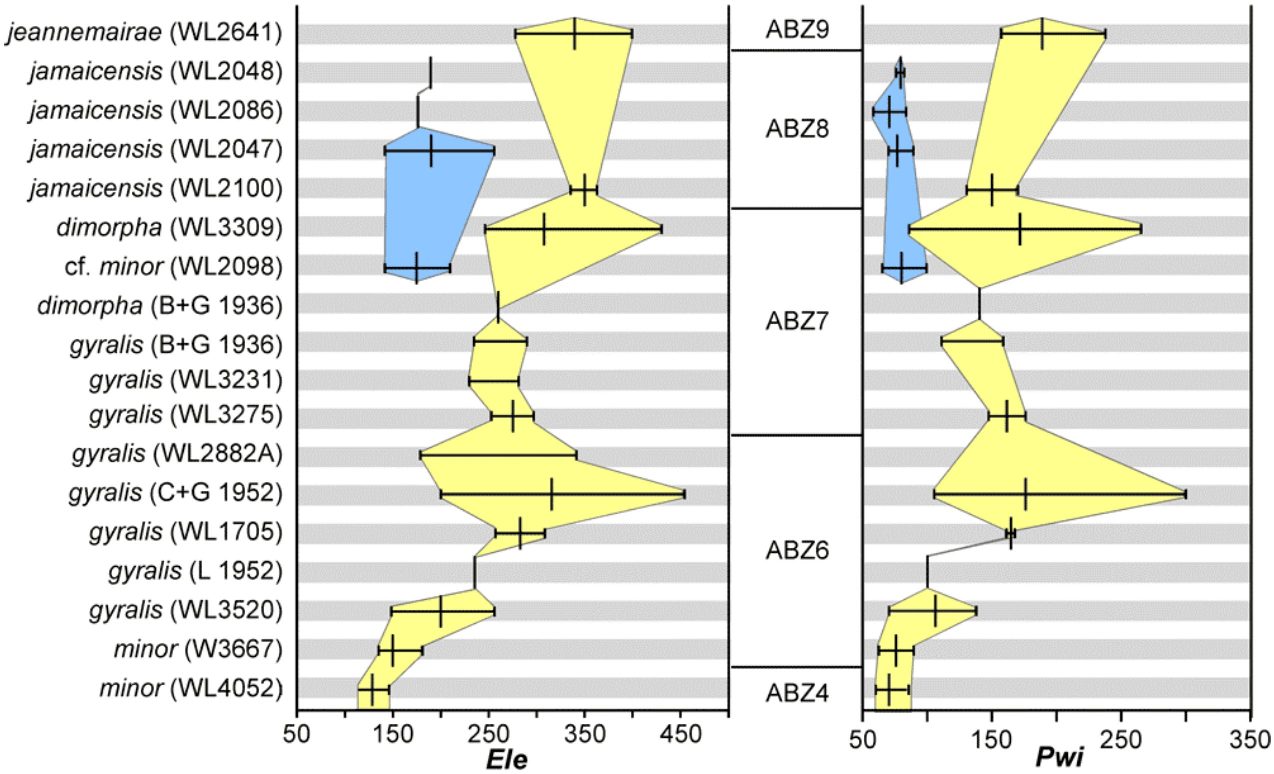


Figure 14: Length of the embryo (Ele) in Helicosteginidae including published material (B&G, 1936 = Barker & Grimsdale, 1936; C&G = Cole & Gravell, 1952) and populations from Jamaica (WL numbers).

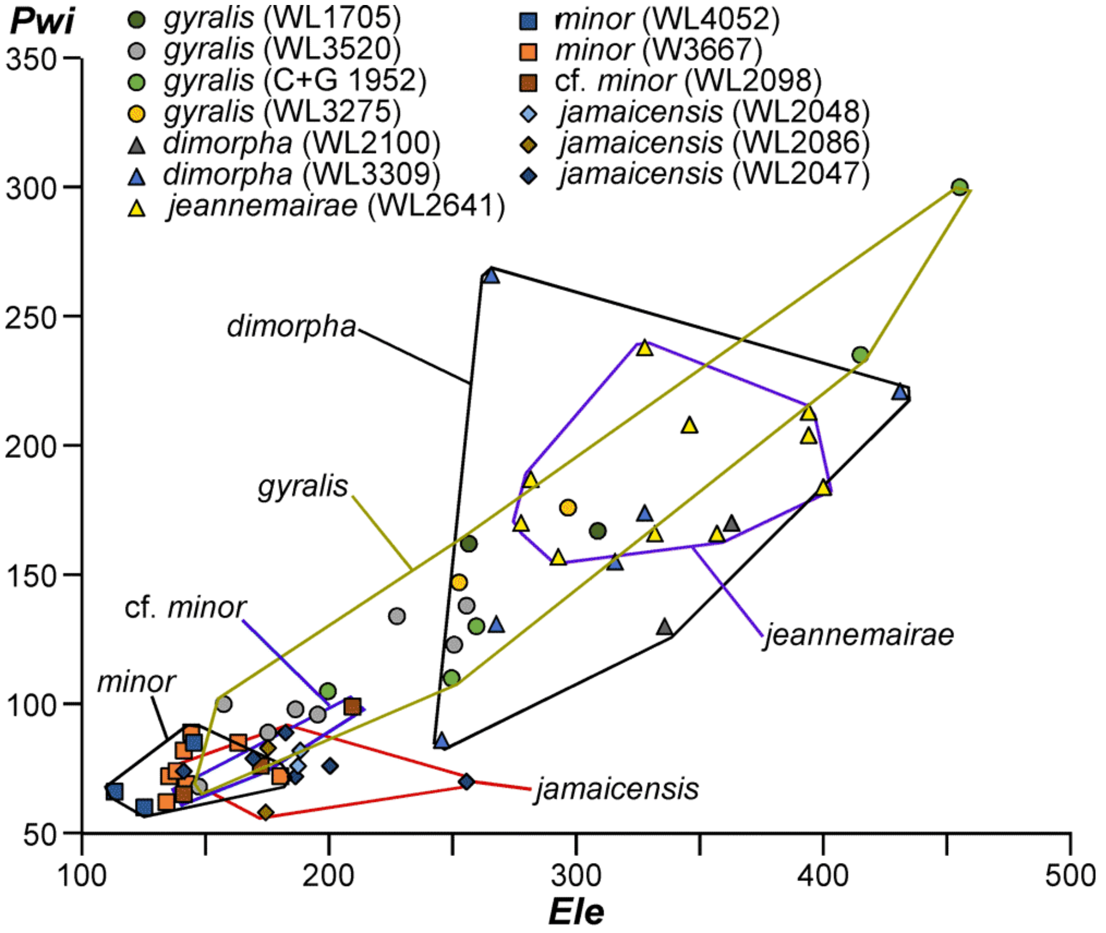


Figure 15: Scatter plot of width of protoconch (Pwi in µm) versus length of embryo (Ele in µm) for selected populations of *Helicostegina* from Jamaica.

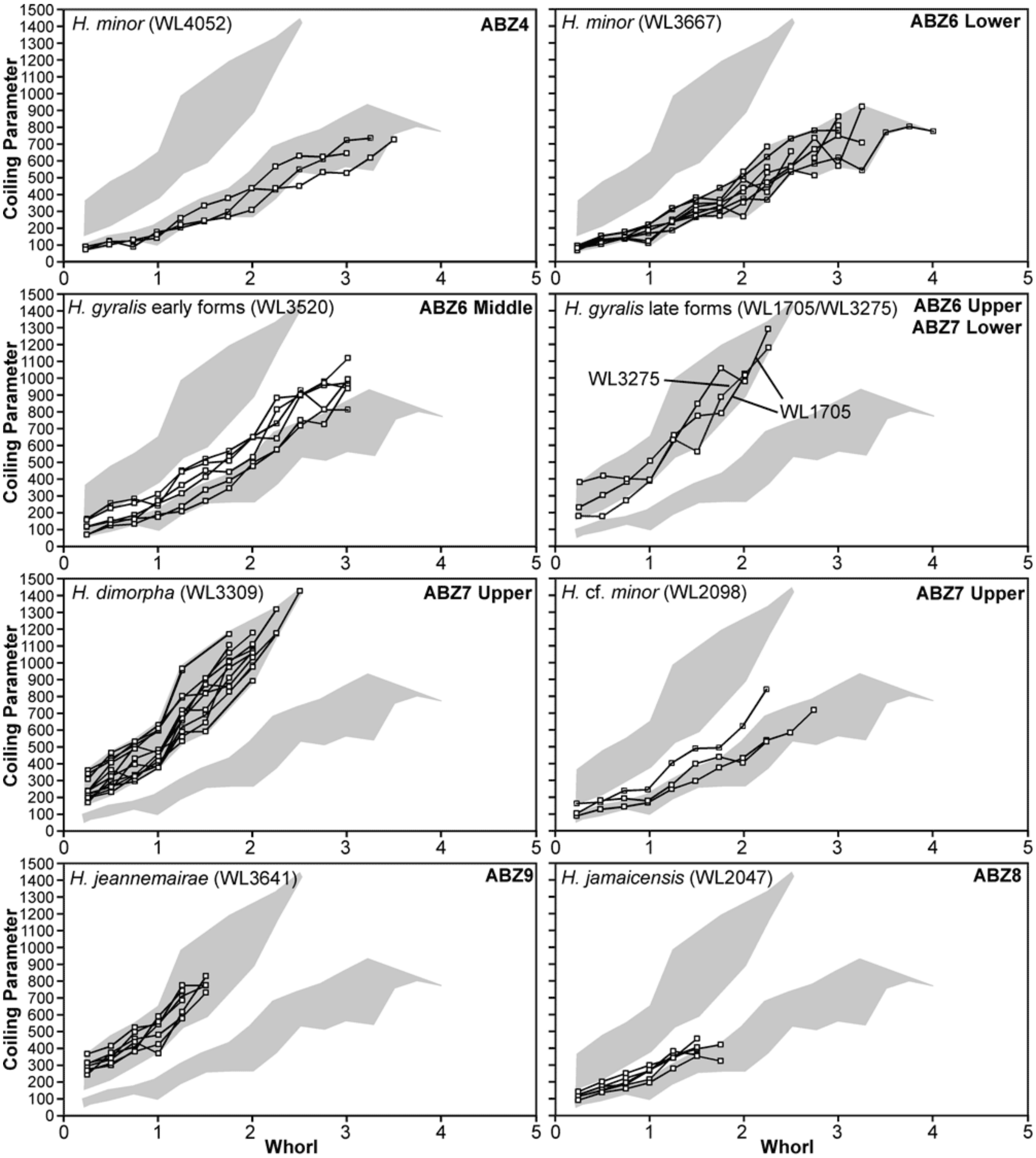


Figure 16: Coiling diagrams (coiling parameter versus whorls) for selected species and populations of the Helicosteginidae from Jamaica. Grey areas are the fields for *Helicostegina minor* (sample WL3667) and *H. dimorpha* (samples WL3309/WL2098).

Genera included. *Tremastegina* BRÖNNIMANN, 1950; *Helicostegina* BARKER & GRIMSDALE, 1936.

Remarks. This family shows the development of advanced forms which either show low trochospiral growth with an equatorial layer or orbitoidiform growth with the ancestral form being *Tremastegina*. Below, we synonymise *Eoconuloides* with *Helicostegina*, and this leaves the genus *Boreloides* (type species *Boreloides cubensis* COLE & BERMÚDEZ, 1947) as the only genus in the family Boreloididae REISS, 1963, a family which we regard as of uncertain affinity at the present time. Further research on *Boreloides* is needed to determine its affinity.

Table 15 shows the length (including the walls) of the first two chambers (embryo consisting of a proloculus and a deuteroloculus; Ele) for different species belonging to the family. Table 16 shows the width (excluding the walls) of the first chamber (proloculus; Pwi) for different species belonging to the family. Figure 13 tracks the evolutionary development of the family. Figure 14 shows the size of the embryo and protoconch in selected species of *Helicostegina*. Figure 15 shows a scatter plot of protoconch width versus embryo length, and Fig. 16 shows coiling diagrams for selected species of *Helicostegina*.

Table 16: Measurements (in µm) of the width of the first chamber (proloculus) excluding the chamber walls (Pwi) for species of *Tremastegina* and *Helicostegina* from Jamaica (WL numbers) and reported values ([1]) and our measurements from figures ([2]) from other locations.

Taxon	Zone	Min	Mean	Max	SD	N	Source
Tremastegina lopeztrigoi	ABZ7	115	-	160	-	-	[1] Barker & Grimsdale, 1936
Helicostegina wellsi	ABZ4	-	27	-	-	1	Unnamed Imst (WL3324)
H. wellsi	ABZ6	40	-	60	-	-	[1] Cole & Bermudez, 1944
H. wellsi	ABZ6	30	39	45	6.68	4	[2] Cole & Gravell, 1952
H. minor	ABZ4	60	70	85	13.05	3	Richmond Fm (WL4052)
H. minor	ABZ6	62	76	89	8.99	8	Stettin Fm (WL3667 & others)
H. gyralis	ABZ6	68	106	138	23.99	8	Helicostegina beds (WL3520)
H. gyralis	ABZ6	162	165	167	3.5	2	Palmetto Grove Fm (WL1705)
H. gyralis	ABZ6	-	100	-	-	-	[2] Florida, Levin, 1957
H. gyralis	ABZ6	105	176	300	87.13	5	[2] Cole & Gravell, 1952
H. gyralis	ABZ7	110	-	160	-	-	[1] Barker & Grimsdale, 1936
H. gyralis	ABZ7	147	162	176	20.51	2	Swanswick House (WL3275)
H. dimorpha	ABZ7	86	172	266	64.20	6	Preston Hill Fm (WL3309)
H. dimorpha	ABZ7	-	140	-	-	-	[1] Barker & Grimsdale, 1936
H. dimorpha	ABZ8	130	150	170	28.3	2	Preston Hill Fm (WL2100)
H. jamaicensis	ABZ8	58	71	83	17.7	2	Preston Hill Fm (WL2086)
H. jamaicensis	ABZ8	76	79	82	4.2	2	Preston Hill Fm (WL2048)
H. cf. *minor*	ABZ7	65	80	99	17.3	3	Preston Hill Fm (WL2098)
H. jamaicensis	ABZ8	70	77	89	6.8	6	Preston Hill Fm (WL2047)
N. jeannemairae	ABZ9	157	189	238	25.89	10	Rock Spring (WL3641)

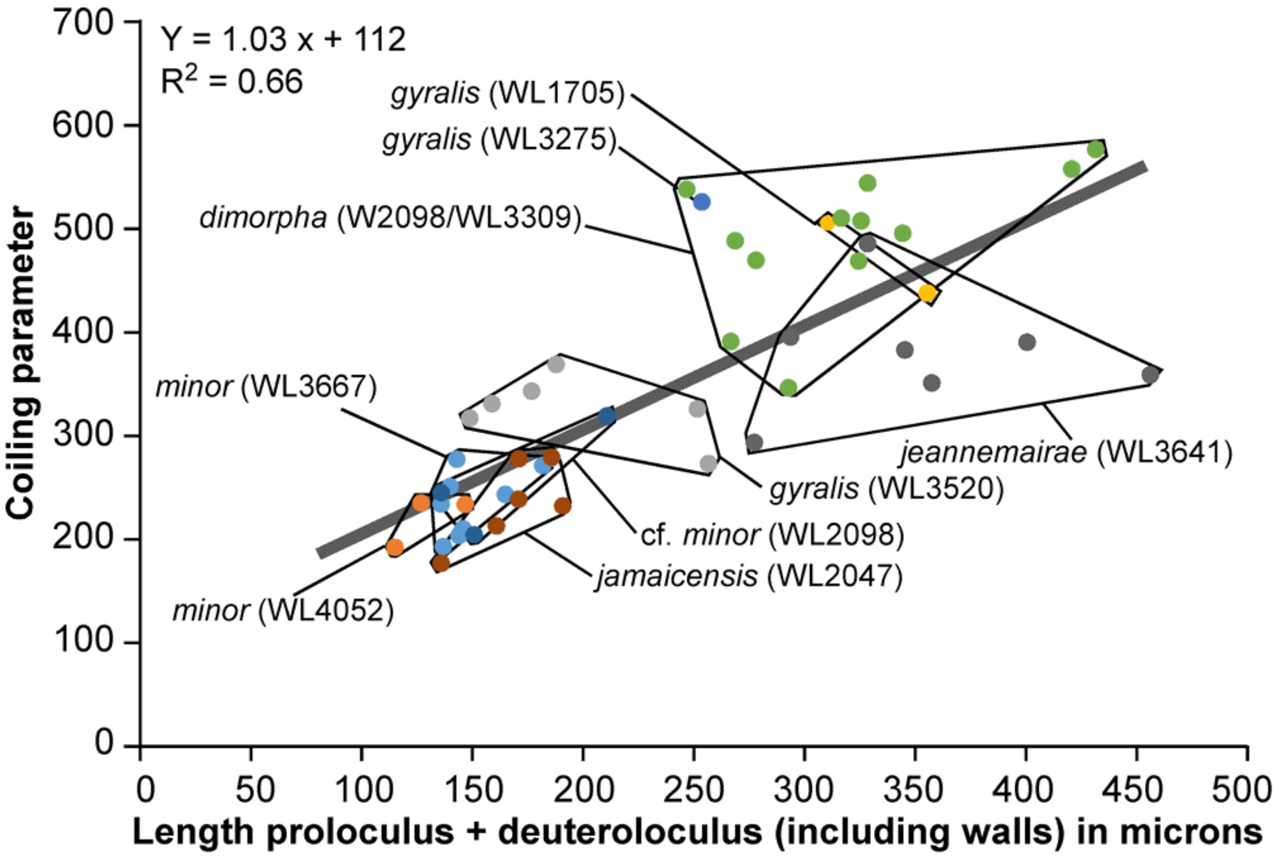


Figure 17: Coiling parameter plotted against length of embryo (proloculus + deuteroloculus including walls) for selected species of *Helicostegina*. Coiling becomes looser (larger coiling parameter values) as the length of the first two chambers increases. The regression line relates to all data points.

Genus *Tremastegina* Brönnimann, 1950

Type species. *Amphistegina senni* Cushman (in Vaughan, 1945) from the Eocene of the Murphys Beds, Upper Scotland Group, Barbados.

Diagnosis. The genus is characterised by 'stellar' chamberlets on the ventral side in combination with forwardly (away from the protoconch) directed septal necks (counter septa) around the stolons between dorsal chambers. The 'stellar' chamberlets are connected to each other by a series of basal stolons, with the most peripheral stolon(s) connecting to the dorsal chamber (Fig. 18).

Remarks. *Amphistegina* differs from *Tremastegina* in having backwardly (towards the protoconch directed septal necks: O'Herne, 1974), whereas in *Tremastegina* the septal necks (counter septa) point away from the protoconch (Barker & Grimsdale, 1936; Fig. 13). These septal necks reflect the condition seen in other members of the Helicosteginidae fam. nov., but *Tremastegina* lacks the spiral sheet of subsidiary chamberlets developed on the ventral side in *Helicostegina*. *Tremastegina* is further distinguished from *Amphistegina* by the presence of the basal stolons, which we regard as the first step in the development of the spiral sheet of chamberlets seen in *Helicostegina*. We therefore regard *Tremastegina* as a primitive member of the Helicosteginidae. We provisionally recognize *Tremastegina senni* (Cushman in Vaughan, 1945) and *T. lopeztrigoi* (Palmer, 1934) as separate species and discuss this below.

Tremastegina senni
(Cushman in Vaughan, 1945)

(Fig. 18)

Previous descriptions. Cushman in Vaughan, 1945, p. 49, Pl. 19, figs. 1-4; Brönnimann, 1950, p. 257-265, Figs. 1-7.

Recognition. *Tremastegina senni* is a relatively small species of *Tremastegina* (typically less than 1 mm in diameter) with a small embryo.

Remarks. Cushman (in Vaughan, 1945, p. 49) stated that the holotype of *A. senni* came from Senn station S. 34B, but in the plate descriptions (Vaughan, 1945, Pl. 19, figs. 1-4) all the specimens were stated to come from Senn station S. 34C. Brönnimann (1950, p. 255) stated that the holotype did come from Senn station S. 34C, and that the statement by Cushman (in Vaughan, 1945, p. 49) was an error (this was probably communicated to Brönnimann by Senn who sent him material of the species to study from station S. 34C in 1946: Brönnimann, 1950, p. 255). Therefore, Brönnimann's (1950) descriptions refer to topotype material of *T. senni*.

T. senni was originally compared to *T. lopeztrigoi* by Senn (1940) who referred to the species as *Amphistegina* cf. *lopeztrigoi* following a personal communication from Vaughan (Senn, 1940, p. 1550). *T. senni* is, however, significantly smaller (about half the size) than *T. lopeztrigoi*, although this may be partly due to the loss of the final whorl in many specimens (Brönnimann, 1950, p. 259). Cole and Gravell (1952) regarded size of relatively little importance and synonymised *'A'. senni* with *'A'. lopeztrigoi*. Brönnimann (1950, p. 263) gives the diameter of the first chamber as 34 to 58 µm in *'A.' senni*. This compares to the internal size of the first chamber in *T. lopeztrigoi* of 140-160 µm with walls from 10-30 µm thick (Barker & Grimsdale, 1936, p. 236). The two species may therefore be distinct.

Vaughan (1945) used the presence of *'A'. senni* to argue for a middle Eocene age for that part of the Scotland Group in Barbados based on the range of *'A'. lopeztrigoi* in Mexico (Barker & Grimsdale, 1936) and Florida (Cole, 1942, 1944). Both Caudri (1972) and Jones (2009) also considered that *T. senni* was part of the Middle Eocene fauna. However, *Tremastegina* has a relatively long range first appearing in the late Paleocene (Robinson & Wright, 1993) and extending up to ABZ7 in Jamaica. As noted by Cizancourt (1948) and Brönnimann (1950), the LBFs from the Scotland Group of Barbados have been strongly abraded; Brönnimann (1950, p. 259) stated that most of the specimens of *T. senni* had either lost their outer whorl or had it significantly worn away showing the interior structure. Furthermore, *Ranikothalia* occurs in the same deposits as *T. senni* in Barbados, and the former species is considered reworked from the late Paleocene (Caudri, 1972). Small specimens that could be attributed to *T. senni* occur in the late Paleocene Nonsuch Limestone of Jamaica (Robinson & Wright, 1993) adding potential support that *T. senni* may be an older species. There could be a progressive size increase (as well as increase in the size of the proloculus) from the late Paleocene to the mid Lutetian, which may make sequential populations of *Tremastegina* useful for biostratigraphy. However, until a section is found where the evolution of *Tremastegina* can be determined, and the variation in the size of the early chambers can be measured, it is impossible to determine if *T. senni* is a Paleocene, Ypresian or early Lutetian species.

Tremastegina lopeztrigoi
(Palmer, 1934)

(Fig. 19)

Previous descriptions. Palmer (1934), p. 255, Pl. 15, figs. 6, 8; Barker & Grimsdale, 1936, p. 233, Pl. 30, figs. 1-2; Pl. 32, figs. 1-3; Pl. 34, fig. 1; Pl. 38, fig. 3; Robinson & Wright, 1993, p. 311, Figs. 19.6-9; Hottinger, 2006, Figs. 33E-G.

Recognition. *Tremastegina lopeztrigoi* is a relatively large species of *Tremastegina* (typically more than 1 mm in diameter) with a large embryo.

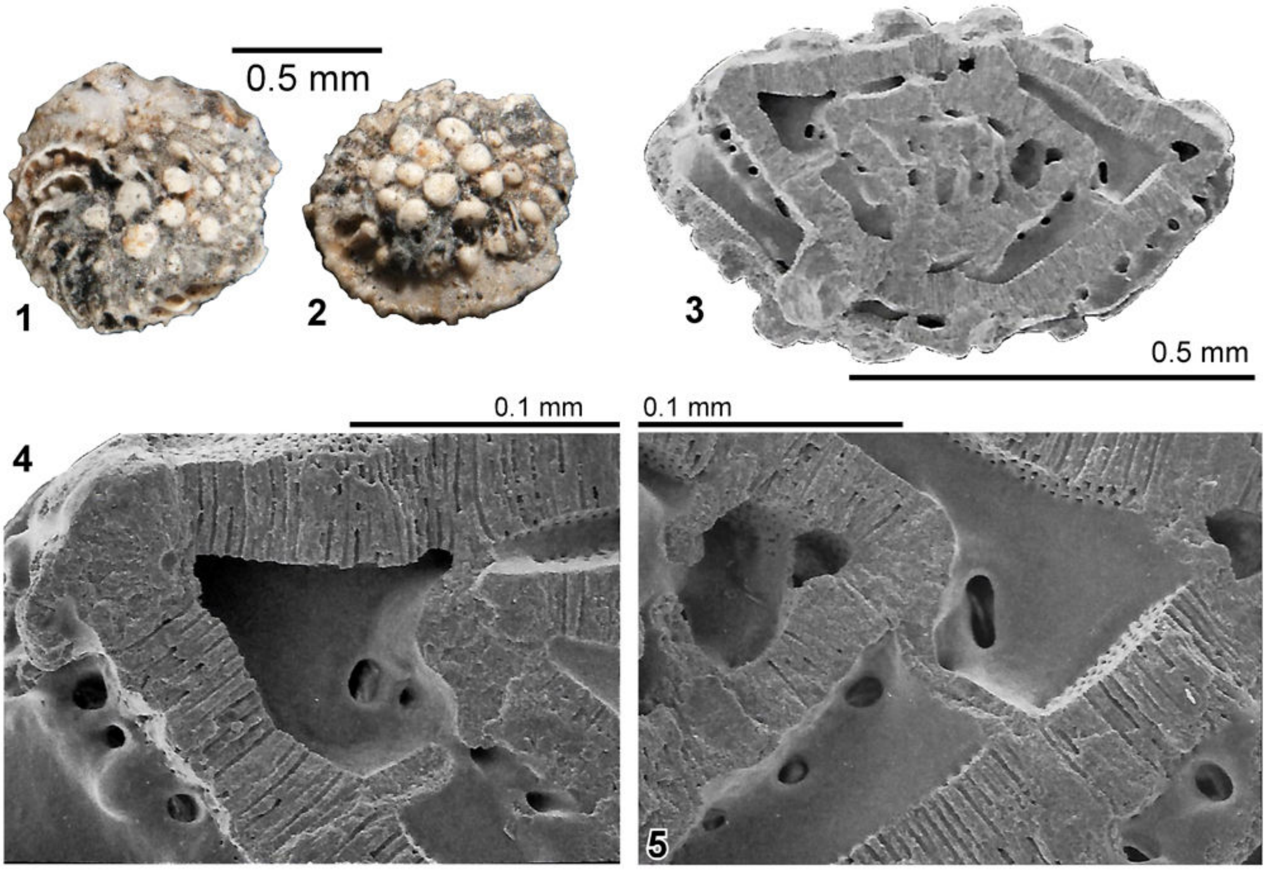


Figure 18: *Tremastegina senni* (Cushman in Vaughan, 1919). **1-2** (USNM.MO.625411), holotype (**1**, ventral; **2**, dorsal), Senn locality S.34C, Murphys Beds, Upper Scotland Group, Barbados (image from Smithsonian websire, used by permission). **3-5** (USNM.0001), Senn locality 34C, Murphys Beds, Upper Scotland Group, Barbados. Note that there are one or two stolons connecting the 'dorsal' chambers (which are separated from the ventral, stellar chamberlets by a stolon with counter septum) and a string of stolons connecting the ventral stellar chamberlets. Also note the finely perforate test.

Remarks. Cushman (1919) erected *Nummulites parvula* which Cole (1969) regarded as a senior synonym of *A. lopeztrigoi*. As discussed above, we regard the holotype of *N. parvula* as indeterminate and suggest suppression of the specific name. *T. lopeztrigoi* ranges at least from the mid early Eocene to the mid Lutetian (ABZ7) in Jamaica. It is the nominate taxon for ABZ3, which represents a low-diversity interval for LBFs other than for dictyoconids and orthophragmines.

Genus *Helicostegina*

Barker & Grimsdale, 1936

Synonyms. *Helicolepidinoides* Tan, 1936 (type species *Helicostegina gyralis* Barker & Grimsdale, 1936) [junior synonym]; *Eoconuloides* Cole & Bermúdez, 1944 (type species *Eoconuloides wellsi* Cole & Bermúdez, 1944) [junior synonym].

Diagnosis. A lenticular to conical helicosteginid with an involute test throughout growth; the primary spire extends to the edge of the test; the alar prolongations on the dorsal side are separated by radial septa; the alar prolongations on the ventral side are represented by strongly spiral septa that merge into the spiral sheet of subsidiary chamberlets in early species, but are not recognizable in later species. The subsidiary chamberlets on the ventral side are separated by arcuate (in the direction of spiral growth) chamberlet walls. The youngest forms show the arcuate septa of the subsidiary chamberlets directed in the direction of growth, whereas in later species they show a radial (orbitoidiform) arrangement.

Remarks. Barker and Grimsdale (1936, p. 234) clearly described the morphology of this genus; their description states "Test multichambered, the earliest chambers coiled in an involute trochoid spire, the chambers of the later coils subdividing ventrally into two or more subsidiary chambers or chamberlets" and "In … *H. gyralis* the chamberlets are restricted to the ventral region of the test, upon which they form a continuous layer but in … [*H. dimorpha*] this layer of chamberlets extends peripherally as a more or less undulating compressed flange one cell thick, almost surrounding the early spiral portion which forms eccentric umbones on the dorsal and ventral surfaces of the test." The latter statement is a little misleading (as shown by Barker & Grimsdale, 1936, Pl. 32, figs. 6-7) where a narrow double-layered (in part) flange is developed, with one layer corresponding to the ventral sheet of subsidiary chamberlets and the other corresponding to

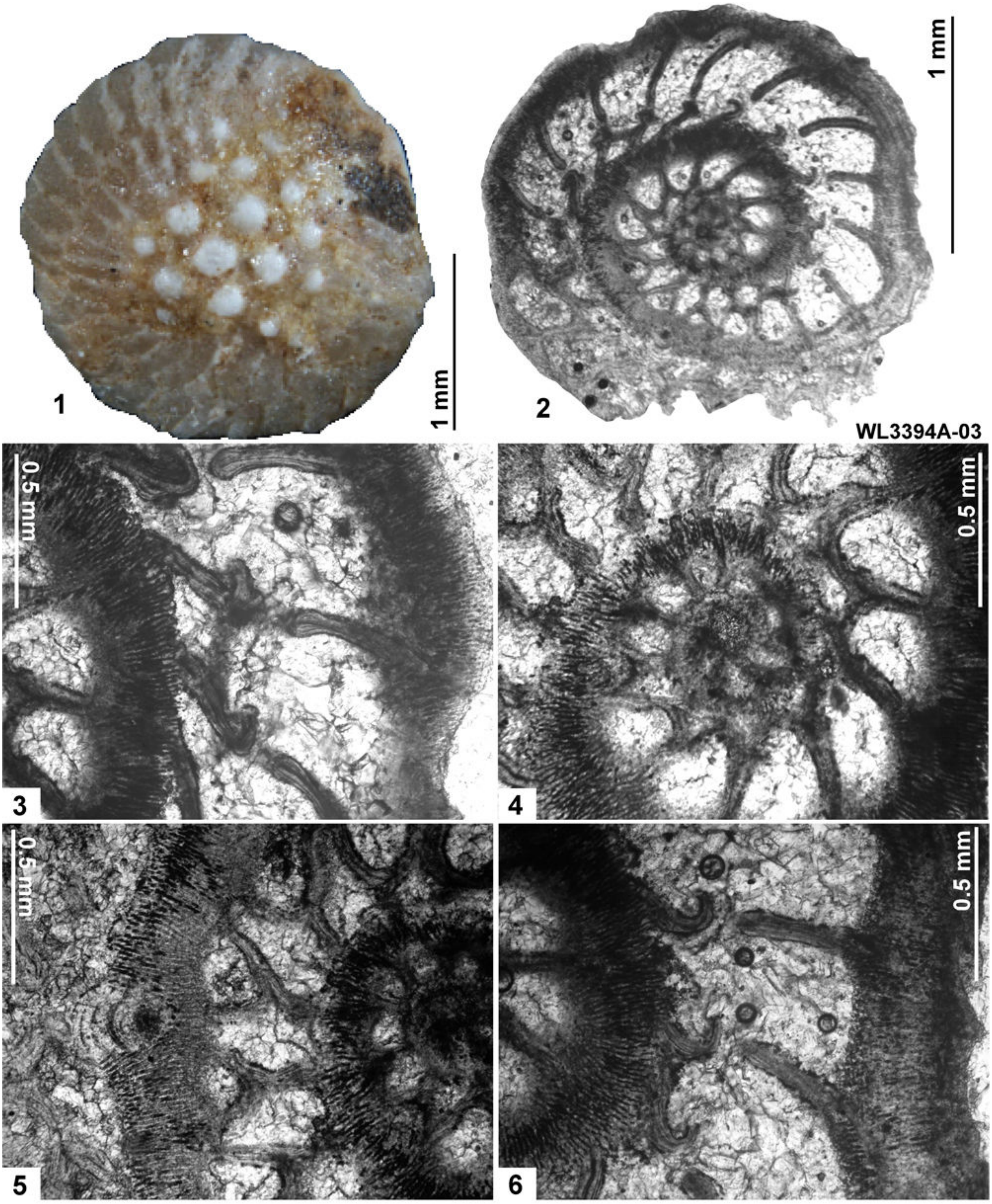


Figure 19: *Tremastegina lopeztrigoi* (Palmer). **1**, exterior of cotype (USNM.MO.544392), showing stellar chamberlets, Cuba (image from Smithsonian websire, used by permission). 2-6, slightly off-centred (on the ventral side) section parallel to the equatorial plane (WL3394A-03), Richmond Formation, Langley, St Mary, Jamaica. **2**, showing complete test. **3**, detail showing counter septa directed away from the proloculus. **4**, detail showing stellar chamberlets developed on the ventral side. **5**, detail showing stellar chamberlets developed on the ventral side and part of a pile. **6**, detail showing counter septa directed away from the proloculus. Note the finely perforate test in 3-6.

the alar prolongations on the dorsal side of the test or to the primary spire or equatorial chambers. Certainly in more derived forms (*e.g.*, *H. jeannemairae* sp. nov.) this would appear to be developed from the primary spire of equatorial chambers.

The relationships between *Helicostegina dimorpha* and *H. gyralis* have always been difficult to determine because of the figures of *H. dimorpha* given by Barker and Grimsdale (1936); yet all specimens of *H. dimorpha* came from Jenny station No. 1592, and all specimens of *H. gyralis* came from Jenny station No. 1573. Axial sections of *H. dimorpha* (Barker & Grimsdale, 1936, Pl. 32, figs. 6-7) show forms in which a thickened wall extends to the margin of the shell, and which contain a few peripheral subsidiary chamberlets in the outer whorl. Yet equatorial sections (Barker & Grimsdale, 1936, Pl. 34, figs. 7, 9) seem to show a relatively short spire and a 'wide flange' of orbitoidiform chambers. However, if straight lines are drawn on the axial sections corresponding to the equatorial plane, the trochospiral coiling of the test means that the equatorial sections will not pass through the spire across the whole of the section, but will also include the peripheral ventral portions of the test with subsidiary chamberlets. This is confirmed from numerous sections of Jamaican specimens, which have identical axial sections, but in relatively symmetrical tests (*i.e.*, very low trochospiral coiling) the complete spire can be seen in equatorial section.

Adams (1987) maintained *H. gyralis* and *H. dimorpha* as separate species, but stated (p. 294) that "Cole (1960) considered that *H. gyralis* should be placed in synonymy with *H. dimorpha* …", but that "These were not, however, from the same sample or locality, and while it is true that temporal gradation between these species may occur, two individuals seen in median section do not constitute proof, neither does their synonymy warrant the possible loss of important biostratigraphical information." Yet, Adams himself figured specimens from the type locality of *H. dimorpha* (Jenny station No. 1592) as both *H. dimorpha* (Adams, 1987, Pl. 1, figs. 1-3) and *H. gyralis* (Adams, 1987, Pl. 1, figs. 4-8), and a specimen from the type locality of *H. gyralis* (Jenny station No. 1573) as *H. gyralis* (Adams, 1987, Pl. 1, fig. 9), thus confusing the issue.

Furthermore, Adams (1987) description of the genus *Helicostegina* states that the equatorial layer passes into an orbitoidiform layer with a chamber having a retrovert aperture. This is quite a different interpretation to the description given by Barker and Grimsdale (1936) who clearly stated that the lateral chambers on the ventral side of the test are divided into subsidiary chamberlets. We agree with the interpretation of Barker and Grimsdale (1936) and illustrate material herein that demonstrates this without ambiguity. Adams (1987) erroneous interpretation of the structure of *H. dimorpha* led him to place forms that had been separated as *Helicolepidina* (*e.g.*, *H. spiralis*) within *Helicostegina*. However, the test construction in *Helicolepidina* is completely different to that of *Helicostegina*, and the two genera cannot be closely related.

Tan (1936) established the genus *Helicolepidinoides* for *H. gyralis*. Tan (1936), however, failed to realise that the difference between *H. dimorpha* and *H. gyralis* is due to the equatorial sections cut through a trochospiral test, and this is clearly indicated by the axial sections of *H. dimorpha* as illustrated by Barker and Grimsdale (1936) as well as by the topotype material illustrated by Adams (1987, Pl. 1, figs. 1-8). Since there is no major constructional difference between *H. dimorpha* and *H. gyralis* (other that the extension of the chamberlets into chamber lumina), and particularly since random sections are difficult to identify as either *H. gyralis* or *H. dimorpha*, there is no need for the genus *Helicolepidinoides* as pointed out by Adams (1987). We therefore synonymise *Helicolepidinoides* with *Helicostegina* herein.

Eoconuloides wellsi shows a similar test construction to *H. gyralis* and only differs in a stronger trochospiral coiling giving rise to a conical test; we therefore synonymise *Eoconuloides* with *Helicostegina* here. Cole and Bermudez (1944, p. 340) stated that *Eoconuloides wellsi* lacked the ventral subsidiary chamberlets seen in *Helicostegina*, yet they are clearly present in the holotype as figured here (Fig. 20.3). We do not regard the conical shape as of generic significance, particularly as microspheric specimens of *Helicostegina minor* sp. nov. show a weakly conical test. We therefore transfer *E. wellsi* to the genus *Helicostegina*, and synonymise *Eoconuloides* with *Helicostegina* herein.

The two more derived species of *Helicostegina*, *H. jamaicensis* sp. nov. and *H. jeannemairae* sp. nov., develop orbitoidiform growth in the equatorial layer. While this could be a justification for the establishment of new genera, they are clearly the terminations of two separate lineages. For the present, we feel it is best to leave these two terminal species within *Helicostegina*, particularly as the trochospiral coiling makes it difficult to distinguish orbitoidiform growth from spiral growth when a spiral layer of subsidiary chamberlets is present. We distinguish species here based on three criteria: the tightness of the coiling, the size of the embryo, and the distribution of subsidiary chamberlets.

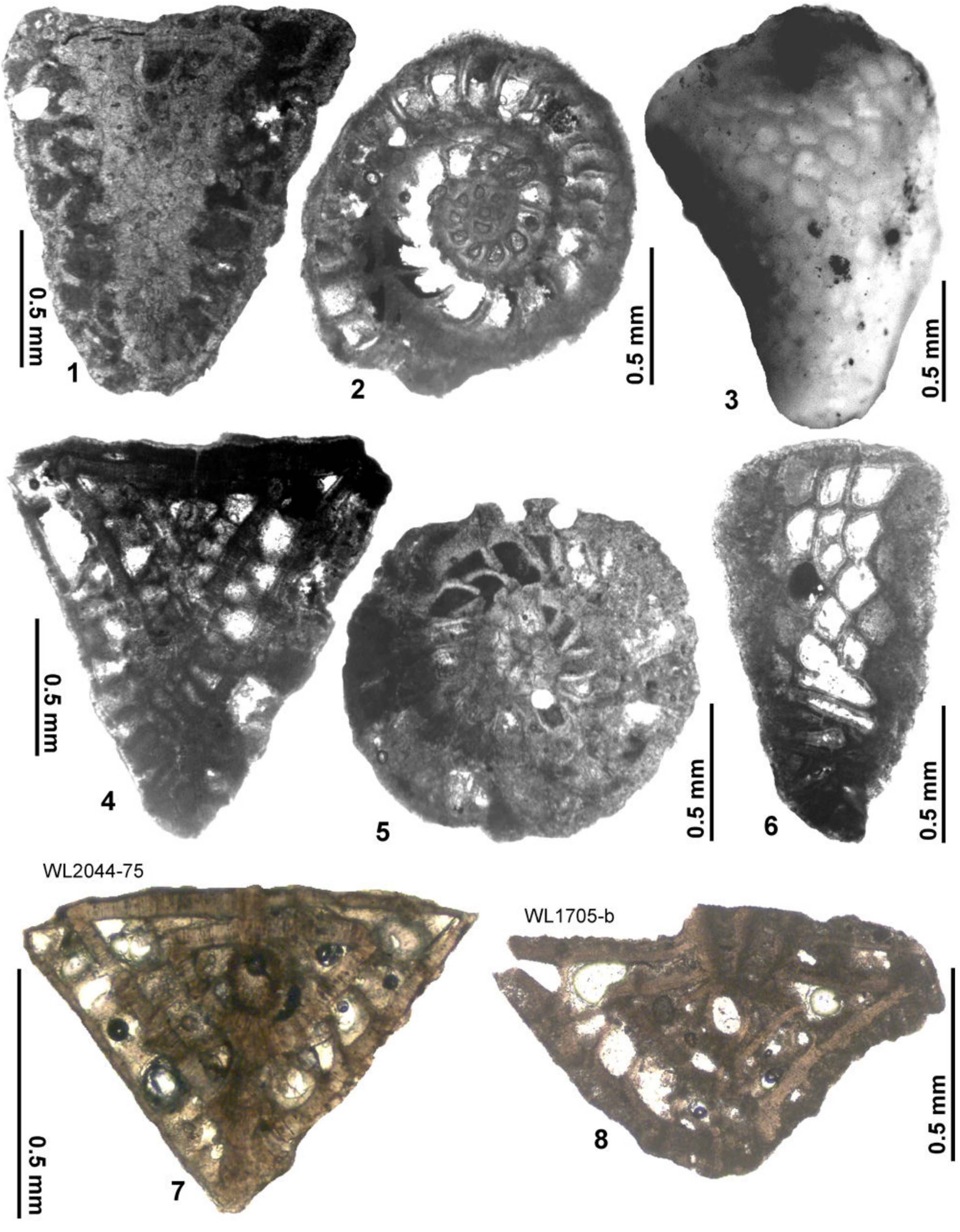


Figure 20: *Helicostegina wellsi* (Cole & Bermudez). **1**, off-centre axial section (WL3324-16) showing typical conical form and chamberlets of the spiral sheet. **2**, equatorial section through proloculus and primary spire of a megalospheric specimen (WL3324-8), note that chamberlets of the spiral sheet are not seen at this level. **3**, holotype (USNM PAL 338960), exterior view, photographed under water to show chamberlets of the spiral sheet. **4**, axial section (WL3324-7). **5**, equatorial section below (*i.e.*, on ventral side of) the nucleoconch (WL3324-18) showing well-developed chamberlets. **6**, tangential section parallel to side of test (WL3324-17) showing chamberlets developed in the spiral sheet. **7** (EO.WL2044-75), axial section, relatively low conical form with a weakly convex dorsal surface, Chapelton Formation, Lilyfield, St Ann. **8** (EO.WL1705-b), axial section, very low, conical specimen. **1-2** and **4-6**, unnamed limestone above the Pembroke Hall Formation and below the Richmond Formation (ABZ4), Darlands, parish of St Mary, Jamaica (ABZ4). **3**, road cut on road from Managuaco to Nazareno, Habana Province, Cuba (monospecific assemblage tentatively attributed to ABZ4 or ABZ6 here). **7**, Chapelton Formation (ABZ9), Lilyfield, St Ann, Jamaica. **8**, Palmetto Grove Formation (ABZ6), near Gayle, St Mary, Jamaica.

Helicostegina wellsi
(Cole & Bermúdez, 1944)
(Fig. 20)

Previous descriptions and figures. Cole & Bermúdez, 1944, p. 341-342, Pl. 1, figs. 4-10; Cole & Gravell, 1952, p. 713, Pl. 92, figs. 1-10; Robinson & Wright, 1993, p. 311, Pl. 18.1-2, Pl. 19.1-5.

Recognition. The species is easily recognized because of its strongly conical form with the ventral side being highly expanded to form a tall pointed conical umbo and the dorsal side being gently convex, flat, or even gently concave. The ventral surface of the test is covered by small papillae, which are difficult to see in poorly preserved specimens. There are about 3½ whorls in megalospheric specimens, and the final whorl has about 20 or 21 chambers. The embryo (the first two chambers - proloculus and deuteroloculus) is relatively small with a length (including the walls) of 100 to 255 µm.

Synonyms. *Amphistegina elliotti* Cushman & Stainforth, 1946 [junior synonym].

Remarks. *Helicostegina wellsi* has a test constructed in exactly the same way as *H. gyralis* and *H. minor* sp. nov. and they often occur in the same samples; the only difference is that *H. wellsi* is conical with a flat, weakly concave or very weakly convex dorsal side, whereas *H. gyralis* is lenticular. *H. wellsi* is a highly distinctive form which ranges from forms in which the axial height is slightly greater than the diameter to forms in which the axial height is twice that of the diameter. The relative height of the test may have some biostratigraphic significance, but this has yet to be worked out. *H. wellsi* is easily recognizable, although specimens may be rather small and missed if too coarse a sieve is used in sample preparation. The species can be recognized in the field with a hand lens. *Amphistegina elliotti* Cushman & Stainforth (1946) has the same morphology (their Pl. 20, fig. 5 shows the alar prolongations on the dorsal side, whereas their Pl. 20, fig. 6 shows the ventral layer of subsidiary chamberlets), and falls within the range of variation of *H. wellsi*. The ornamentation of *H. wellsi* consists of small papillae scattered across the whole surface of the test; this contrasts with the central crown of large pustules in *H. gyralis* (although early examples of *H. minor* from ABZ4 have an ornament closer to *H. wellsi*).

We use *H. wellsi* as the nominate taxon for ABZ4. *H. wellsi* has its peak abundance in ABZ4 and lower ABZ5 in Jamaica, but also occurs in very small numbers in the upper part of ABZ6 and in zones ABZ8 and ABZ9. The association of *H. wellsi* with *H. gyralis* (cited as *Eoconuloides senni*) and *Operculinoides* sp. in Calyx wells 50 and 50A in Trinidad (Caudri, 1996, Fig. 7) suggests assignment to ABZ7. Reworked(?) specimens also occur in the Upper Scotland Group in Barbados according to Brönnimann (1950, p. 264).

Kalia and Banerjee (1995) recorded '*Eoconuloides*' *wellsi* from India. They recorded associated planktic foraminifers as indicating zone P12 and P14 (equivalent to ABZ9 to ABZ11), which is a partly younger age range than the range of *H. wellsi* in the Caribbean as indicated here (ABZ4 to ABZ9). We identify their Pl. 1, figs. 5 and 10 as *Asterigerina* sp., whereas other specimens are typical *Nummulites*. We doubt the occurrence of *H. wellsi* in India.

Helicostegina minor
Mitchell, E. Robinson & Özcan, sp. nov.
(Figs. 21 - 26)

1945 *Amphistegina senni* Cushman in Vaughan, in part?

1993 *Helicostegina gyralis* Barker & Grimsdale; Robinson, Pl. 5, figs. 11, 13.

1993 *Helicostegina gyralis* Barker & Grimsdale; Robinson & Wright, p. 313-314, Fig. 18.6-8.

1993 *Eoconuloides lopeztrigoi* (Palmer); Robinson & Wright, in part, p. 311, Fig. 19.7 only.

Diagnosis. A species of *Helicostegina* with a very small proloculus followed by a smaller deuteroloculus and then a primary spiral that extends to the margin of the test; tightly coiled. Alar prolongations radial on the dorsal side and undivided; alar prolongations on the ventral side are spiral with more-or-less continuous walls and subdivided into arcuate subsidiary chamberlets.

Origin name. 'Minor' after its small proloculus.

Type specimens. Holotype: UWIGM.WL3667-5; Paratypes: UWIGM.WL3667-8, UWIGM.WL 3667-7, UWIGM.WL3667-6, UWIGM.WL3667-4, UWIGM.WL3667-9; all from sample WL3667, Stettin Formation (ABZ6), Stettin, Trelawny, Jamaica.

Description. Microspheric forms have a diameter of up to 2.0 mm, megalospheric forms have a diameter of up to 1.6 mm. The ornament consists of a central crown of pustules with small pustules along the septa. Microspheric forms have a very small proloculus, with about five whorls; there are 33 chambers in the final whorl. Megalospheric specimens have the first two chambers (proloculus and deuteroloculus) with a length of 114-181 um (including the walls), with means of 129 um (sample WL4052) and 150 um (sample WL3667). The internal width of the proloculus (Pwi) ranges from 60-89 µm (Table 16). The first two chambers are followed by 3½ to 4½ whorls, with 27 to 31 chambers in the final whorl. Chambers on the dorsal side undivided with simple arcuate septa; dorsal chambers visible from ventral side (where they form the marginal series of chambers). Septa on the ventral side of the test can be traced through the subsidiary chamberlets and are strongly spirally arranged. Alar prolongations of chambers on the ventral side divided into subsidiary chamberlets, with arcuate walls, and extending up to the spire of

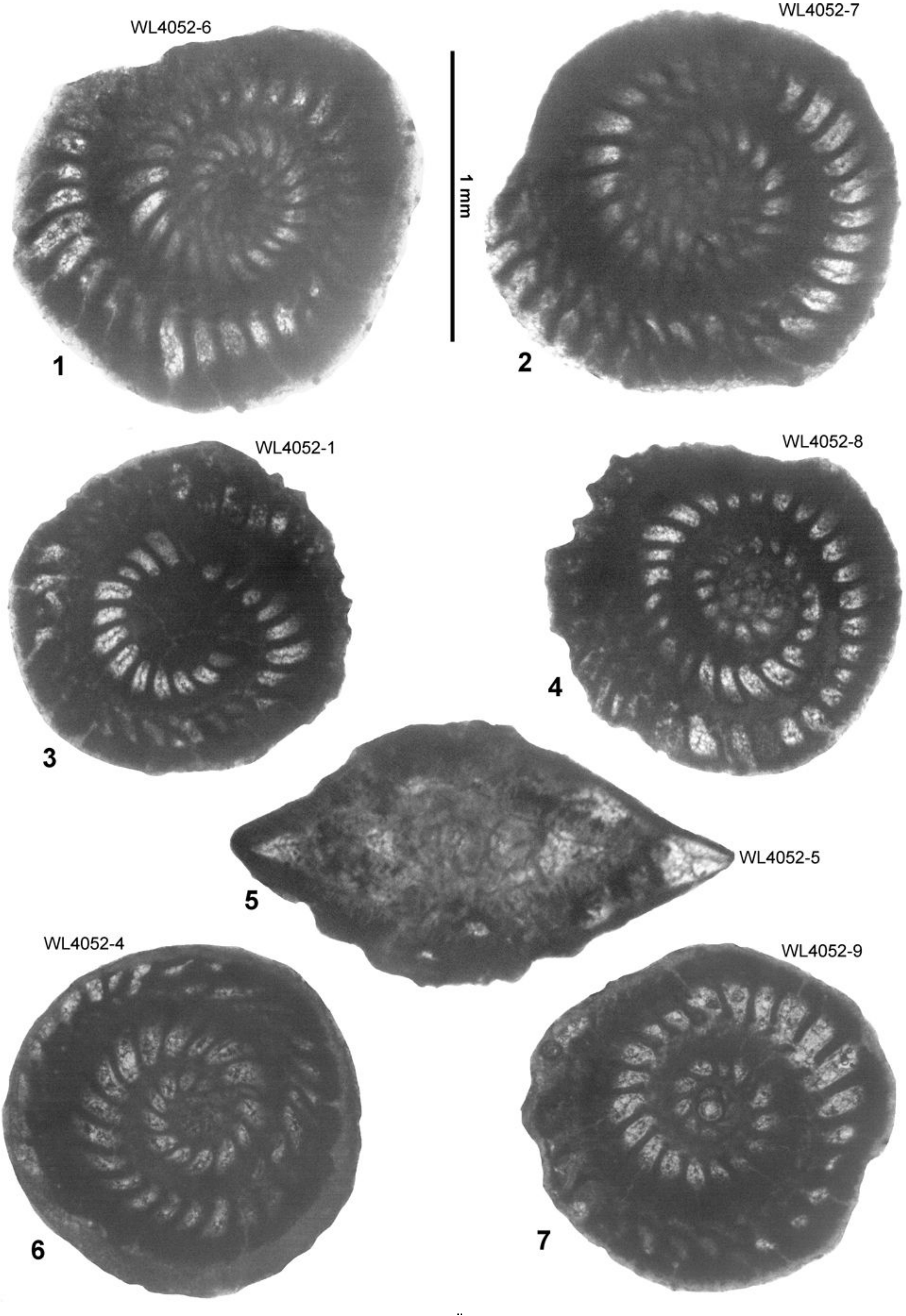


Figure 21: *Helicostegina minor* Mitchell, E. Robinson & Özcan sp. nov., megalospheric specimens. **1** (UWIGM. WL4052-6), **2** (UWIGM.WL4052-7), **3** (UWIGM.WL4052-1), **4** (UWIGM.WL4052-8), **6** (UWIGM.WL4052-4), **7** (UWIGM. WL4052-9): equatorial sections. **5** (UWIGM.WL4052-5): axial section. Sample WL4052 (ABZ4), Richmond Formation, Rio Sambre Gorge, St Mary, Jamaica.

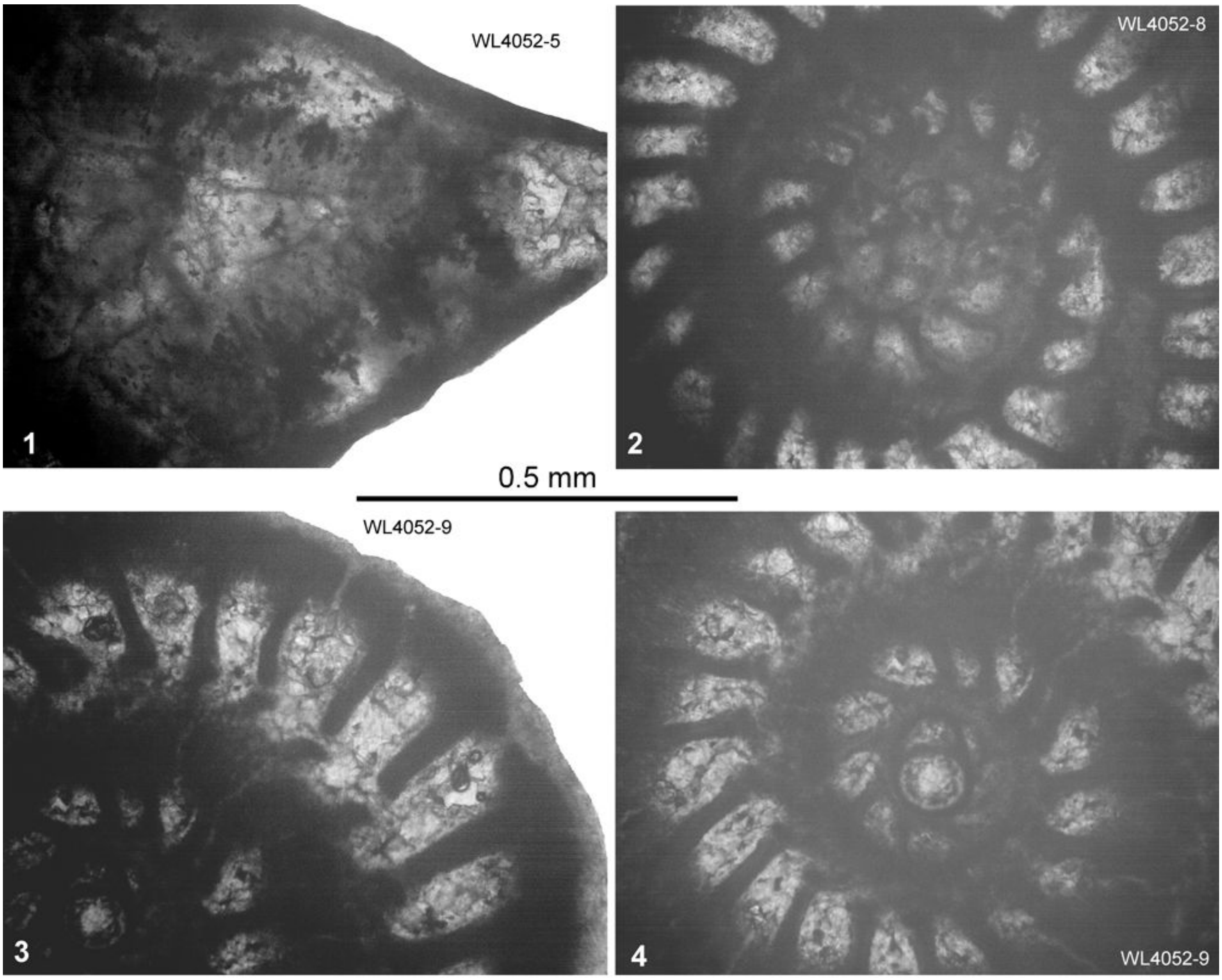


Figure 22: *Helicostegina minor* MITCHELL, E. ROBINSON & ÖZCAN sp. nov., megalospheric specimens. **1** (UWIGM. WL4052-5): detail of axial section. **2** (UWIGM.WL4052-8), **3-4** (UWIGM.WL4052-9): details of equatorial sections. Sample WL4052 (ABZ4), Richmond Formation, Rio Sambre Gorge, St Mary, Jamaica.

the previous whorl. Axial sections range from relatively symmetrical to asymmetrical forms. Septa on the dorsal side are only occasionally visible in orientated axial sections, so that most of the alar prolongations on the dorsal side of the test are 'open.' In axial section, the walls of the ventral chamberlets are closely spaced and fill the alar prolongations on the ventral side of the test.

Remarks. *H. minor* can be distinguished from *T. lopeztrigoi* by the presence of subsidiary chamberlets in or replacing the alar prolongations on the ventral side, which extend up to the keel of the primary spire of the previous whorl. The well-marked septa forming the alar prolongations are retained on the ventral side such that a spiral pattern is quite obvious. This is lost in later species where a true spiral sheet of subsidiary chamberlets is developed which have a more typical orbitoidiform arrangement of the chamberlets. *H. minor* differs from *H. wellsi* by the presence of large tubercles on the surface of the test that are concentrated at the centre (crown) and the fine series of papillae that mark the courses of the septa across the flanks of the test on the dorsal side.

Helicostegina minor ranges from ABZ4 to ABZ6. It is replaced in the upper part of ABZ6 by *H. gyralis*. The species is recorded from Jamaica (ROBINSON & WRIGHT, 1993, herein) and Barbados (Fig. 26.3).

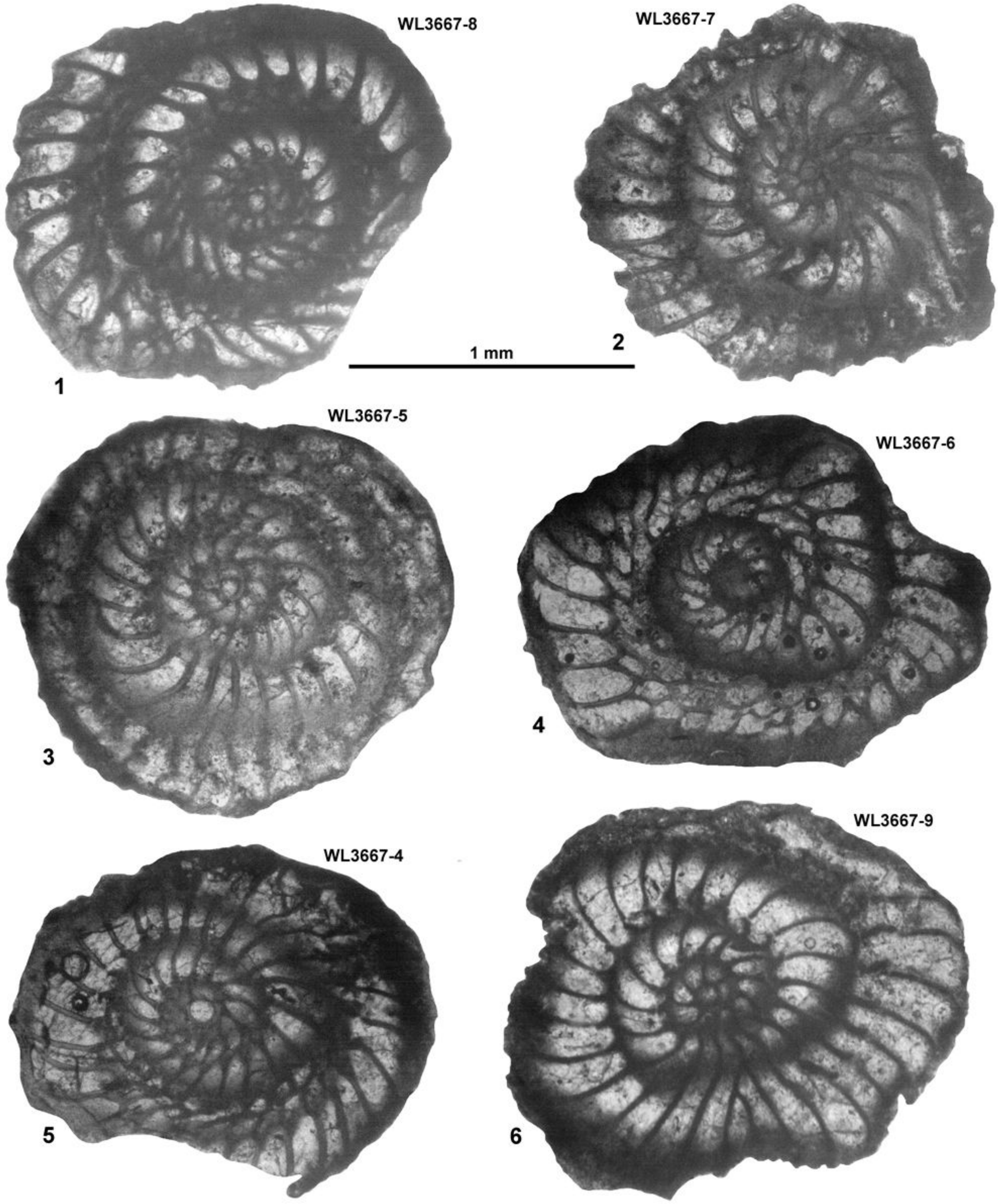


Figure 23: *Helicostegina minor* Mitchell, E. Robinson & Özcan sp. nov., megalospheric specimens. **1** (UWIGM. WL3667-8), paratype; **2** (UWIGM.WL3667-7), paratype; **3** (UWIGM.WL3667-5), holotype; **4** (UWIGM.WL3667-6), paratype; **5** (UWIGM.WL3667-4), paratype; **6** (UWIGM.WL3667-9) paratype: equatorial sections. Sample WL3667, Stettin Formation (ABZ6), Stettin, Trelawny, Jamaica.

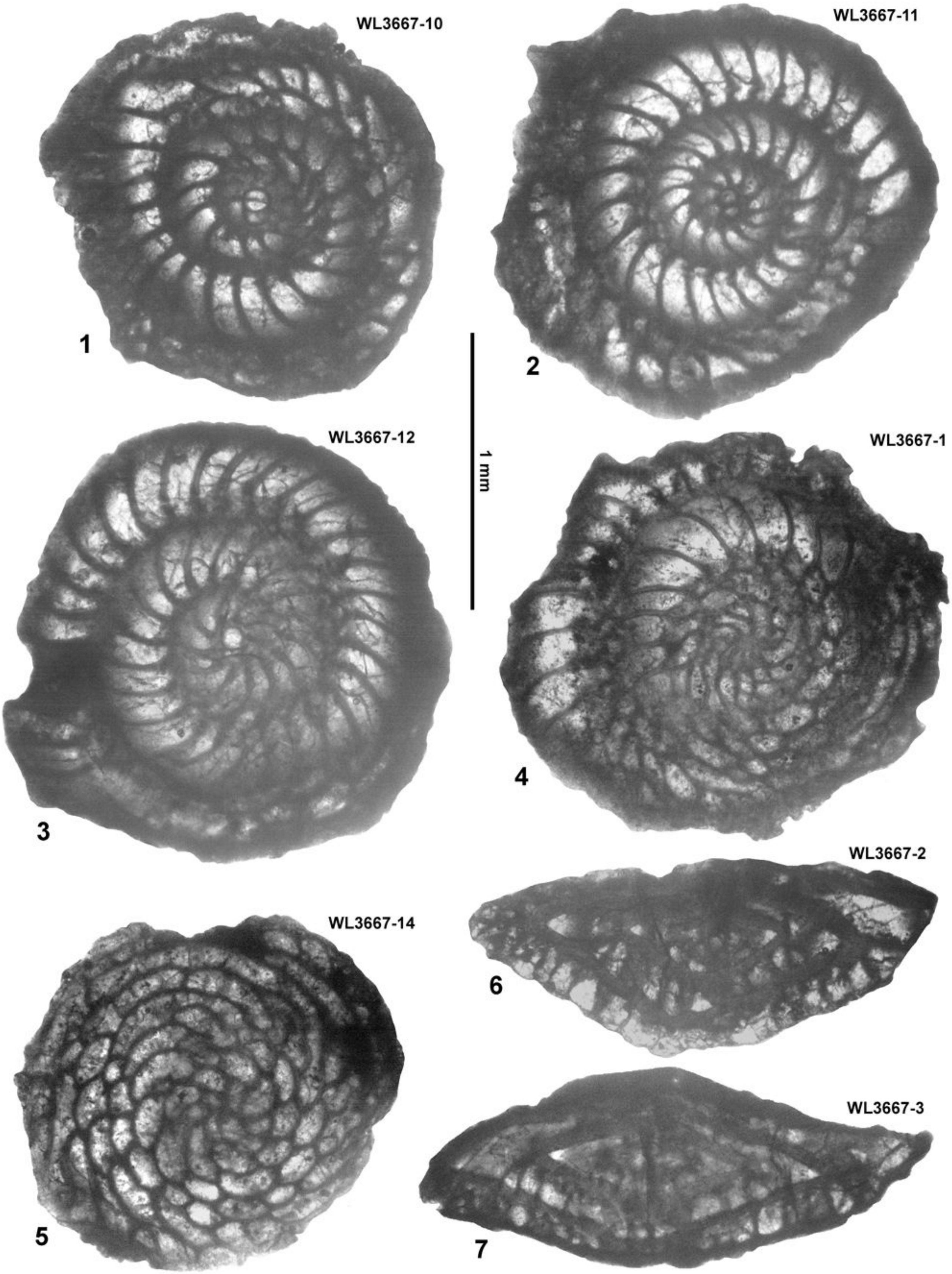


Figure 24: *Helicostegina minor* MITCHELL, E. ROBINSON & ÖZCAN sp. nov., megalospheric specimens. **1** (UWIGM.WL3667-10), **2** (UWIGM.WL3667-11), **3** (UWIGM.WL3667-12): equatorial sections. **4** (UWIGM.WL3667-1), **5** (UWIGM.WL3667-14): sections cut through the spiral sheet of subsidiary chamberlets. **6** (UWIGM.WL3667-2), **7** (UWIGM.WL3667-3): axial sections. Sample WL3667, Stettin Formation (ABZ6), Stettin, Trelawny, Jamaica.

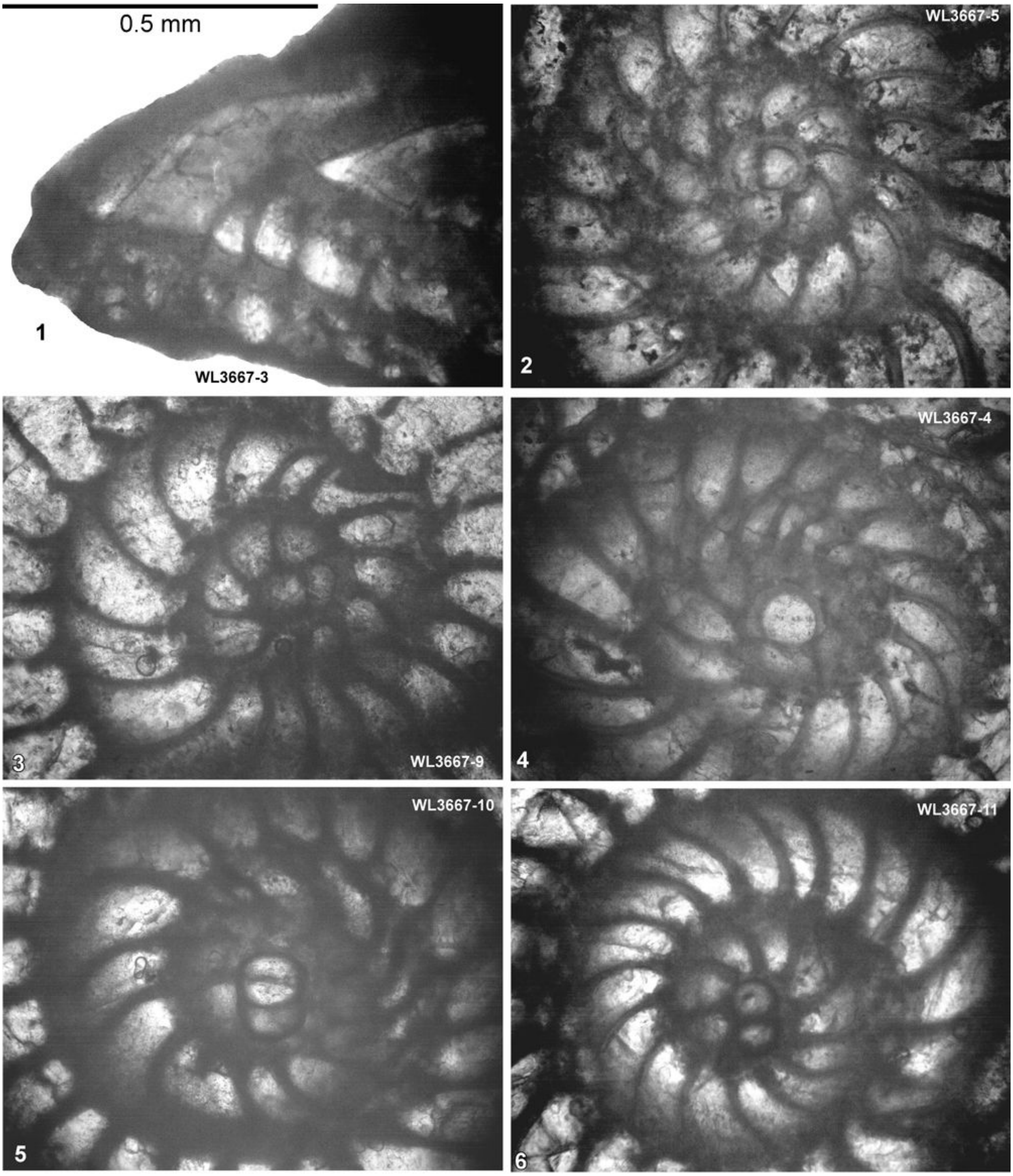


Figure 25: *Helicostegina minor* MITCHELL, E. ROBINSON & ÖZCAN sp. nov., megalospheric specimens. **1** (UWIGM. WL3667-3): detail of axial section. **2** (UWIGM.WL3667-5), **3** (UWIGM.WL3667-9), **4** (UWIGM.WL3667-4), **5** (UWIGM.WL3667-10), **6** (UWIGM.WL3667-11): details of equatorial sections. Sample WL3667, Stettin Formation (ABZ6), Stettin, Trelawny, Jamaica.

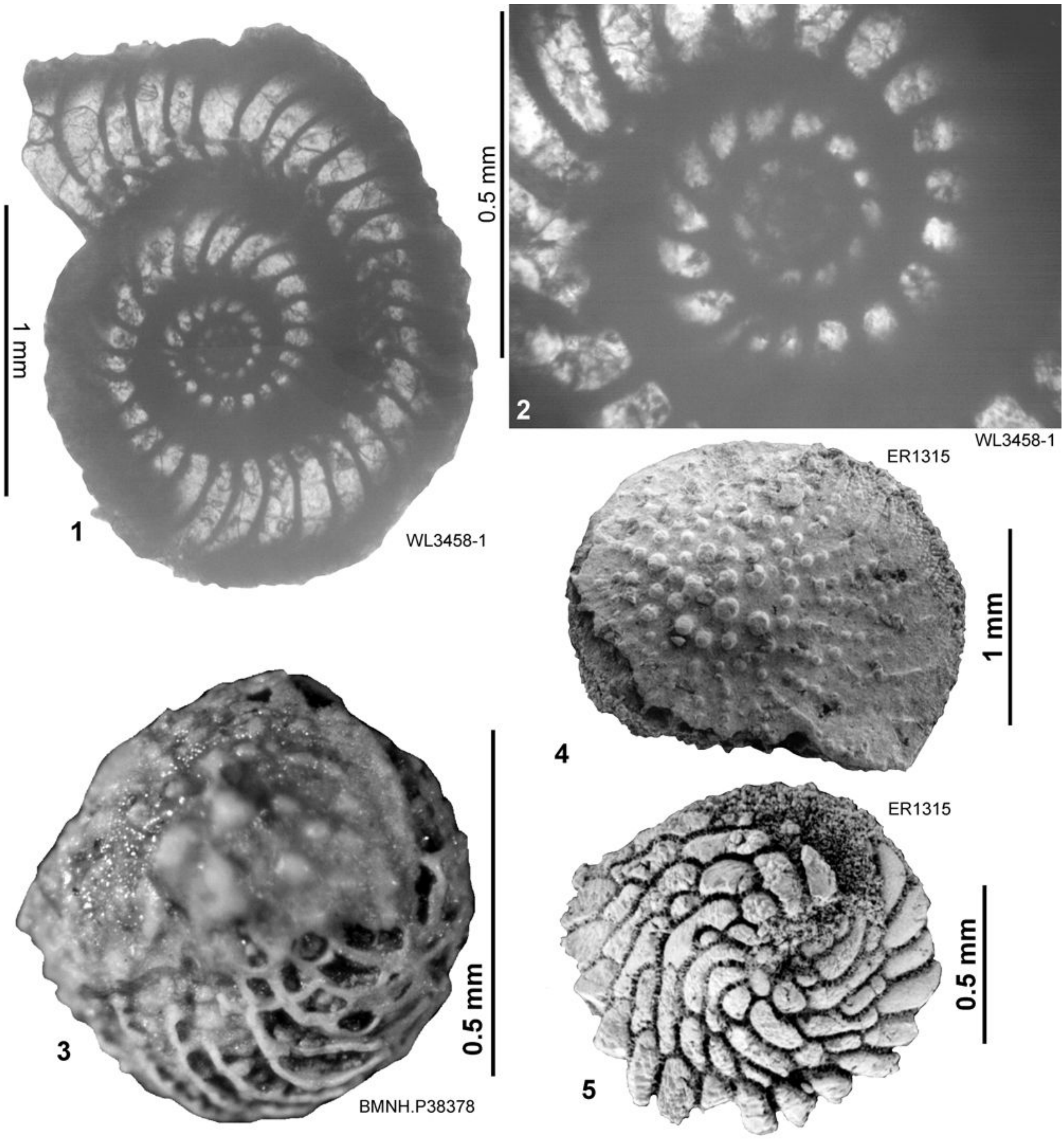


Figure 26: *Helicostegina minor* MITCHELL, E. ROBINSON & ÖZCAN sp. nov. **1-2** (UWIGM.WL3458-1), microspheric form, equatorial section, Stettin Formation (ABZ6), Coleyville, Jamaica. **3** (BMNH.P38378), exterior view (ventral side), partially eroded to show chamberlets, Murphys' Beds, Scotland Formation, Barbados. **4** (ER1315), SEM, dorsal side showing crown of pustules and smaller pustules extending along septa, Stettin Formation (ABZ6), Stettin, Jamaica. **5** (ER1315), exterior view (ventral side) of decortitized specimen showing ventral sheet of subsidiary chamberlets, Stettin Formation (ABZ6), Stettin, Jamaica.

Helicostegina cf. *minor* MITCHELL, E. ROBINSON & ÖZCAN, sp. nov.

(Fig. 27)

Remarks. Four specimens from middle ABZ7 show an equatorial section with a small proloculus and small deuteroloculus combined with a spiral wall that extends to the margin of the test. We do not have an axial section so cannot determine if they have an incipient double layer, and we attribute these specimens to *Helicostegina* cf. *minor* sp. nov. Further material will need to be collected to determine whether this species should be retained in *H. minor* sp. nov. or placed in a new species transitional between *H. minor* sp. nov. and *H. jamaicaensis* sp. nov.

Figure 27: *Helicostegina* cf. *minor* Mitchell, E. Robinson & Özcan sp. nov. megalospheric specimens. **1** (EO.WL 2098-117), **2** (EO.WL2098-118), **3** (EO.WL2098-119): equatorial sections. Preston Hill Formation (ABZ7), Farm Turn, St Mary, Jamaica.

Helicostegina gyralis
Barker & Grimsdale, 1936
(Figs. 28 - 33)

Previous descriptions and figures. Barker & Grimsdale, 1936, p. 236-237, Pl. 30, figs. 3-5; Pl. 32, figs. 4-5; Pl. 34, figs. 2-6; Pl. 37, fig. 6; Cole & Gravell, 1952, p. 713, Pl. 92, figs. 11-21.

Recognition. *Helicostegina gyralis* is a lenticular species, but shows a low trochospiral coil such that in many specimens it is difficult to cut true equatorial sections, and the sections often pass from the primary spire in the centre of the test into part of the spiral sheet of subsidiary chamberlets. Barker and Grimsdale (1936, p. 236) stated that the first two chambers have a length of 185-240 µm and there are about 25-30 chambers in the 'final whorl'. Measurements of populations from Jamaica are given in Tables 15 and 16. The dorsal surface of the test is ornamented with coarse piles (pillars) on the central area of the test with finer papillae aligned along the septa separating the alar prolongations/chambers. Axial sections of most specimens lack chamberlets at the periphery of the test, although a few specimens (*e.g.*, Barker & Grimsdale, 1936, Pl. 32, fig. 4: reproduced in Fig. 28.4 here) show a few chamberlets at the periphery, but not the clear double row of chamberlets seen in *H. dimorpha*.

Remarks. *H. gyralis* can be distinguished from *T. lopeztrigoi* by the presence of a spiral sheet of subsidiary chamberlets on the ventral side. These can be seen during section preparation even if the resulting equatorial section apparently shows none (which is the case in rela-

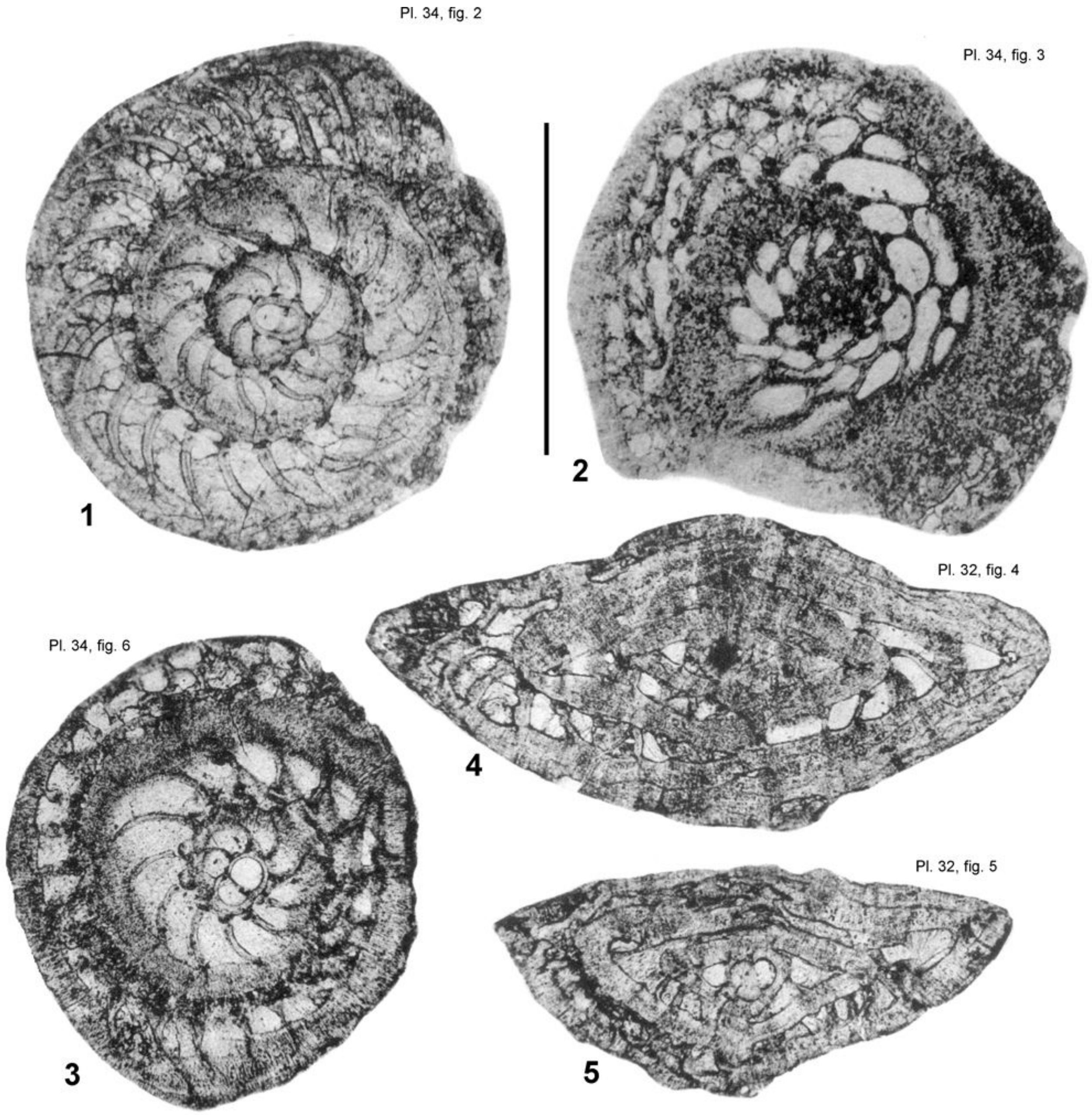


Figure 28: Reproduction of the original illustrations of *Helicostegina gyralis* from Barker & Grimsdale (1936). **1** (Pl. 34, fig. 2), equatorial section. **2** (Pl. 34, fig. 3) section cut on ventral side of the equatorial plane showing ventral sheet of chamberlets. **3** (Pl. 34, fig. 6), equatorial section. **4** (Pl. 32, fig. 4) axial section. 5 (Pl. 32, fig. 5) axial section. Note that in 4 the ventral chamberlets extend into the periphery of the test, whereas in 5 they do not. Guayabal Formation, Jenny Section No. 1573, 11 km southeast of Sabaneta, state of Veracruz, Mexico. Scale bar = 1 mm.

tively symmetrical specimens). *H. gyralis* differs from *H. minor* in having a larger embryo and in being less tightly coiled. *H. gyralis* differs from *H. wellsi* by its shape, and by the presence of large tubercles on the surface of the test that are concentrated at the test's centre and the fine series of papillae that mark the courses of the septa across the flanks of the test on the dorsal side.

The two populations of *H. gyralis* (upper ABZ6 and lower ABZ7) from Jamaica plot in different areas on Coiling Parameter vs. Embryo Length diagrams (Fig. 17). Since we have not measured the Coiling Parameter on specimens of the type population of *H. gyralis* from Mexico, and since the coiling parameter is highly dependent on reproduction of figures at the correct scale in publications (unless a scale bar is present), we do not separate the Jamaican populations at the present time. Pwi of specimens from upper ABZ6 is smaller than for lower ABZ7 (Table 16, Fig. 14), and the specimen of *H. gyralis* from Florida figured by Levin (1957) falls within the range of the upper ABZ6 population from Jamaica; this may be of stratigraphic significance and populations from Florida need to be measured to determine this.

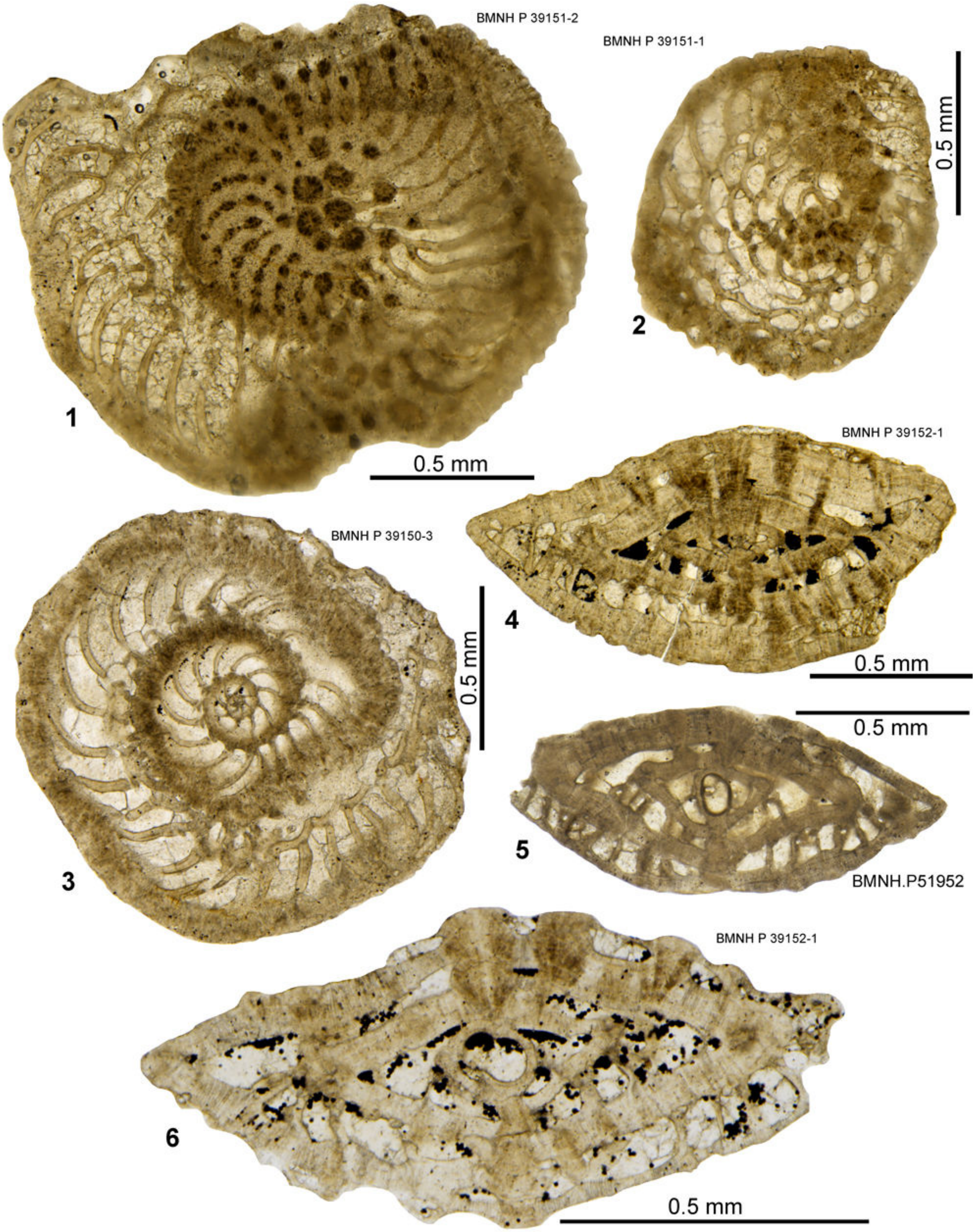


Figure 29: *Helicostegina gyralis* Barker & Grimsdale 1936. Topotypes. **1** (BMNH.P.39151-2), section cut on the dorsal side of the equatorial layer showing the pillars. **2** (BMNH.P.39151-1), equatorial section. **3** (BMNH. P.39150-3), equatorial section. **4** (BMNH.P.39152-1), axial section. **5** (BMNH.P.39152), axial section. **6** (BMNH.P.39152-1), axial section. All from Eleven km SE of Sabaneta, State of Veracruz (Collection of Dr. H. Jenny, No. 1573), Mexico. Note that the lumina of the chambers do not contain subsidiary chamberlets in 5 and 6, but do in 4.

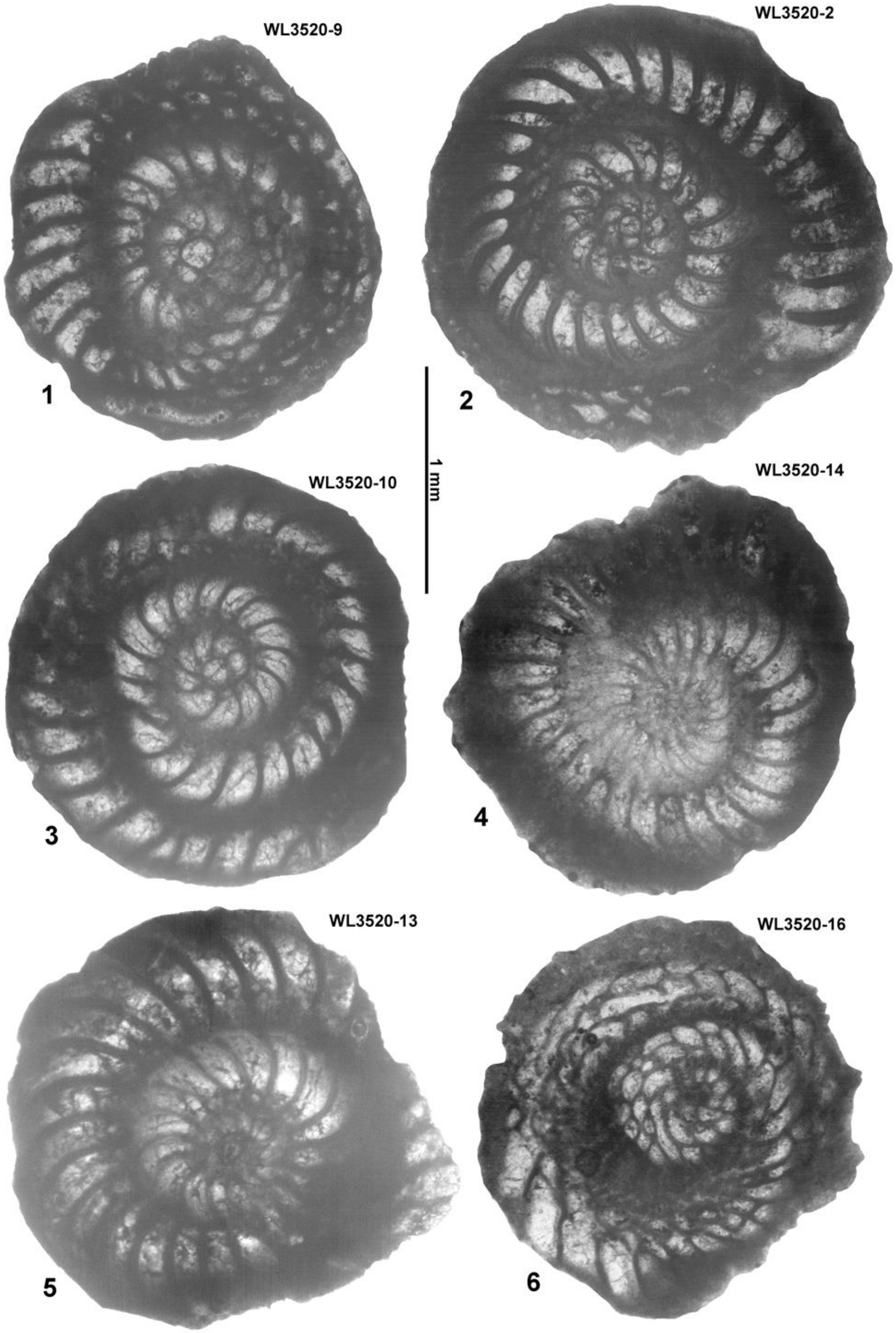


Figure 30: *Helicostegina gyralis* Barker & Grimsdale, 1936. **1** (UWIGM.WL3520-9), equatorial section. **2** (UWIGM.-WL3520-2), equatorial section. **3** (UWIGM.WL3520-10), equatorial section. **4** (UWIGM.WL3520-14), equatorial section. **5** (UWIGM.WL3520-13), equatorial section. **6** (UWIGM.WL3520-16), section parallel to the equatorial plane passing through the ventral sheet of subsidiary chamberlets. 'Helicostegina-beds' (upper ABZ6), road from Springfield to Mount Horeb, parish of St James, Jamaica.

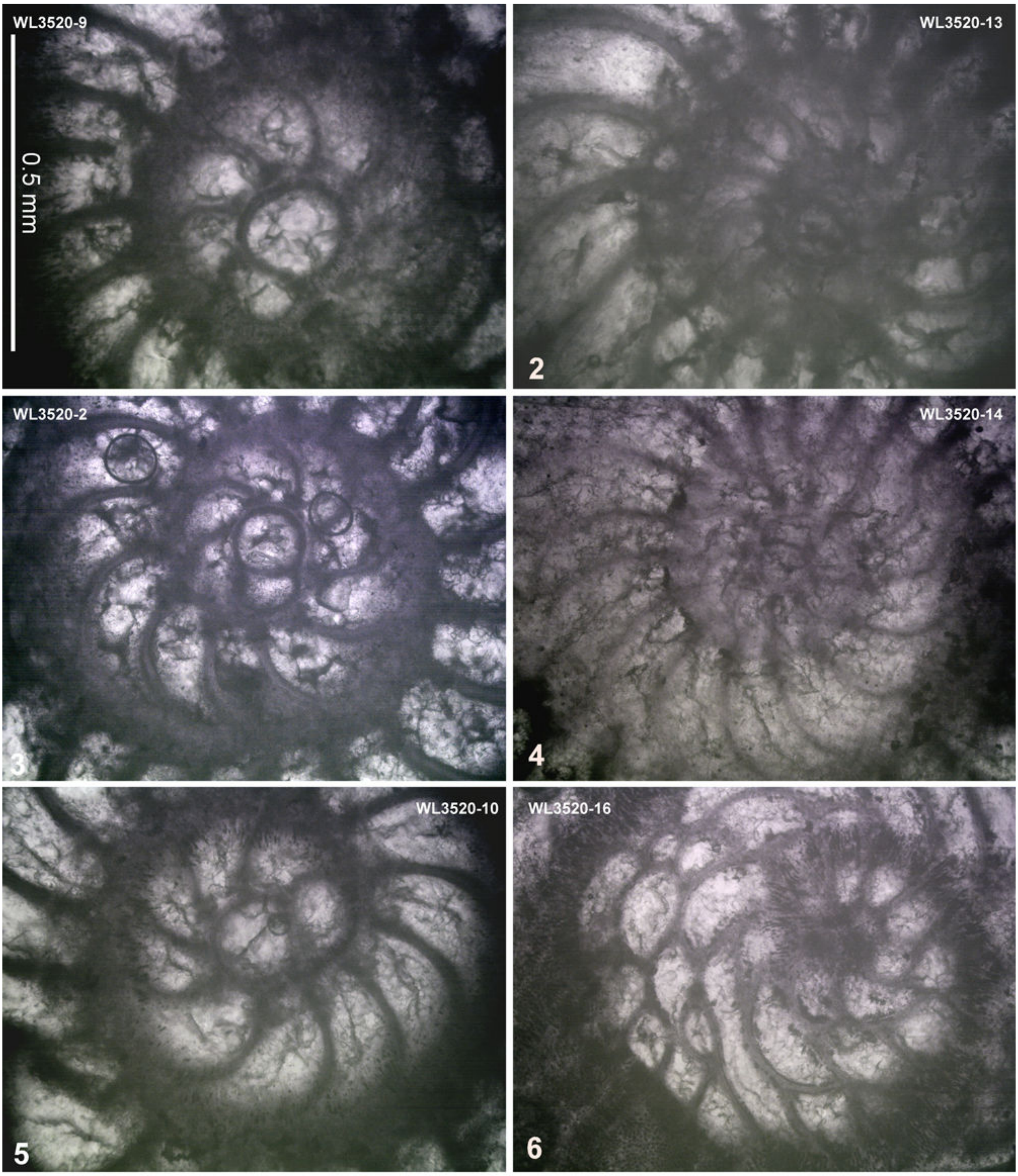


Figure 31: *Helicostegina gyralis* Barker & Grimsdale, 1936. Details of embryos. **1** (UWIGM.WL3520-9), equatorial section. **2** (UWIGM.WL3520-13), equatorial section. **3** (UWIGM.WL3520-2), equatorial section. **4** (UWIGM.WL3520-14), equatorial section. **5** (UWIGM.WL3520-10), equatorial section. **6** (UWIGM.WL3520-16), section parallel to the equatorial plane passing through the ventral sheet of subsidiary chamberlets. 'Helicostegina-beds' (ABZ6), road from Springfield to Mount Horeb, parish of St James, Jamaica.

H. gyralis ranges through the middle of ABZ6 to the lower part of ABZ7 in Jamaica. The type locality of *H. gyralis* is Jenny Station No. 1573 (11 km southeast of Sabaneta, state of Veracruz, Mexico: Barker & Grimsdale, 1936); this locality has also yielded *Pseudolepidina trimera* (Barker & Grimsdale, 1937) and *Operculinoides jennyi* (Barker, 1939) and can therefore be assigned to lower ABZ7. *H. gyralis* is widely distributed across the American region being reported in Mexico (Barker & Grimsdale, 1936), Florida (Cole, 1942; Levin, 1957), probably Venezuela (Raadshooven, 1951), Cuba (Cole & Bermudez, 1944; Cole & Gravel, 1952) and Jamaica (herein). Previous records from the Stettin Formation of Jamaica (*e.g.*, Robinson, 1993; Robinson & Wright, 1993) are here placed in *Helicostegina minor* sp. nov.

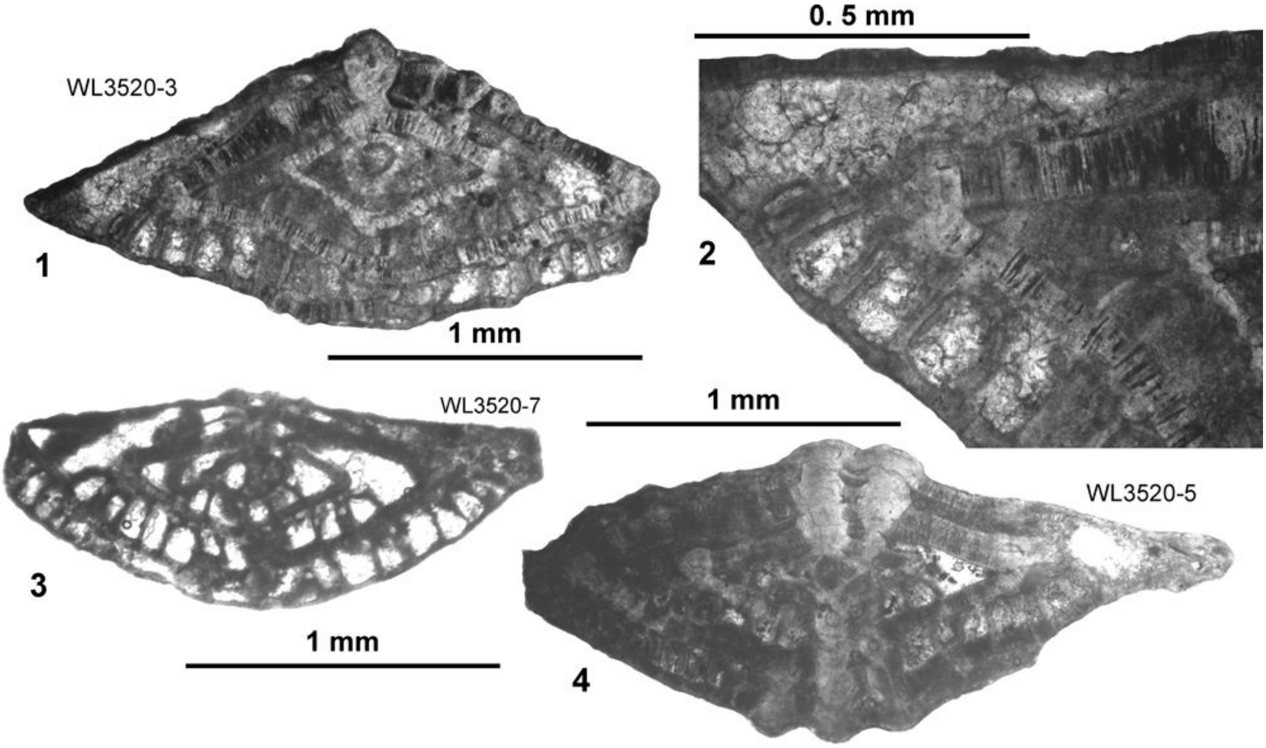


Figure 32: *Helicostegina gyralis* Barker & Grimsdale, 1936. **1-2** (UWIGM.WL3520-3), axial section. **3** (UWIGM. WL3520-7), axial section. **4** (UWIGM.WL3520-5), axial section. Note that the subsidiary chamberlets on the ventral side only extend to the periphery of the previous whorl. 'Helicostegina-beds' (ABZ6), road from Springfield to Mount Horeb, parish of St James, Jamaica.

Helicostegina dimorpha
Barker & Grimsdale, 1936
(Figs. 34 - 37)

Previous descriptions and figures. Barker & Grimsdale. 1936, p. 235, Pl. 30, fig. 6; Pl. 32, figs. 6-7; Pl. 33, fig. 9; Pl. 34, figs. 7, 9; Pl. 37, fig. 3.

Recognition. According to Barker and Grimsdale (1936), the spire of *H. dimorpha* has a length of 18 to 21 chambers, inclusive of the proloculus. However, because of the trochospiral coiling it is probable that this is only the part of the spire that is cut in the section and in reality the spire is longer extending to the margin of the test. This is confirmed by Adams' (1987) Pl. 1, fig. 2, a topotype, which shows the spiral wall extending to the periphery of the test. Barker and Grimsdale (1936, p. 236) reported that the first two chambers (proloculus and deuteroloculus) had a length of 240 µm. There is no orbitoidiform layer and the apparent presence of one is due to equatorial sections cutting the spiral sheet of subsidiary chamberlets because of the trochospiral coiling of the test. Axial sections show the presence of subsidiary chamberlets in the peripheral area of the dorsal chambers, although the primary septa of the spire continue to the margin of the test.

Remarks. The type material of Barker and Grimsdale (1936) is confusing because the two equatorial sections pass from the primary spire into the spiral sheet of subsidiary chamberlets and this makes it look like the primary spire passes into an orbitoidiform layer. This is clearly not the case in the two axial sections that are presented (Barker & Grimsdale, 1936, Pl. 32, figs. 6-7, reproduced here in Fig. 35.3-4). Adams (1987) illustrated topotype material that shows that the primary spire extends to the margin of the test, yet even he talked about an orbitoidal layer. *H. dimorpha* occurs in upper ABZ7 (samples WL2098 and WL3309/WL3309A) and lower ABZ8 (sample WL2100) in Jamaica.

Helicostegina dimorpha has only been found in the middle and upper parts of ABZ7 and lower ABZ8 in Jamaica, where it is locally common. It is distinguished from *H. gyralis* by the acquisition of subsidiary chamberlets in the periphery of the chamber which, with the equatorial chamberlets, produces an incipient double layer.

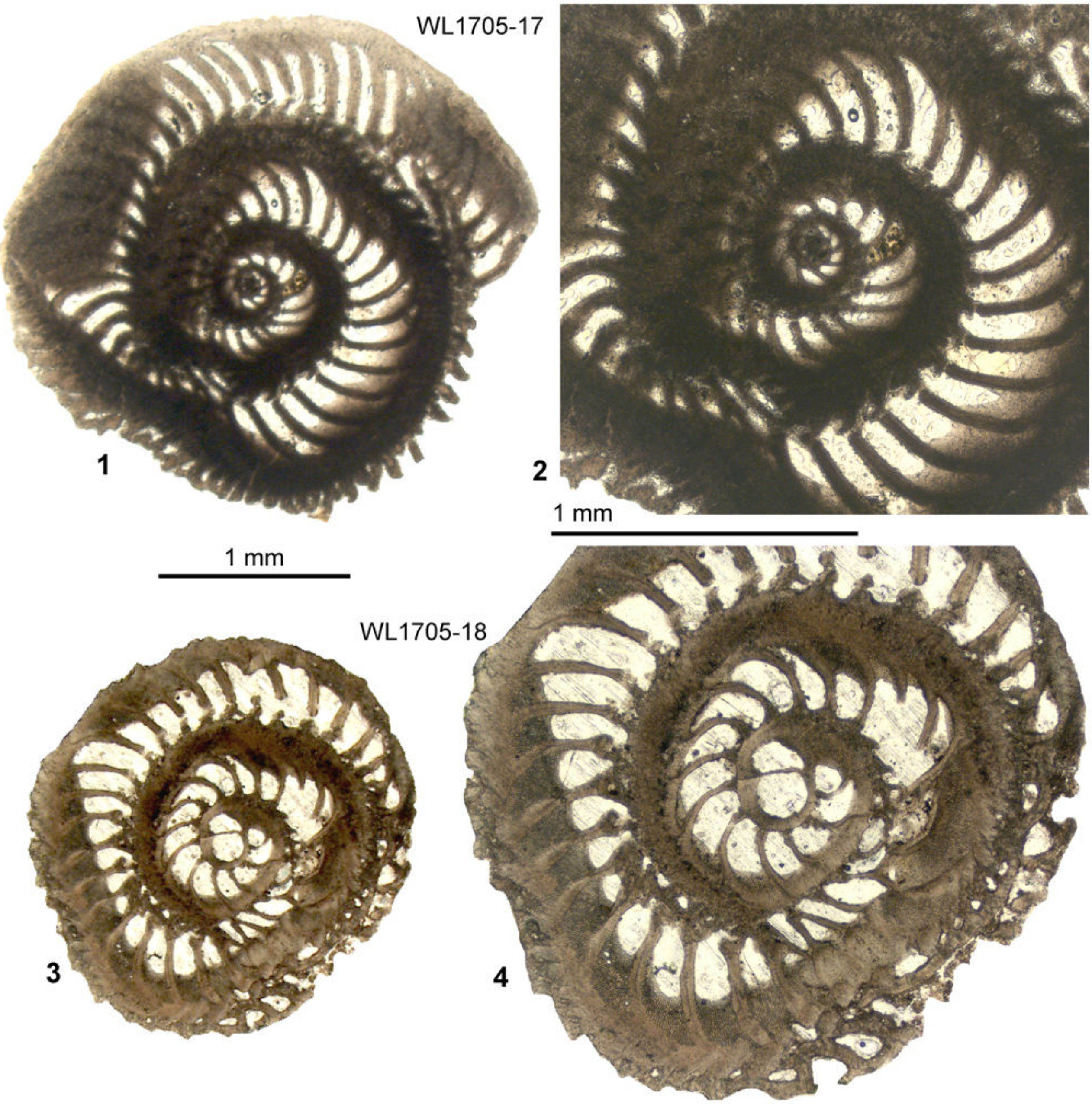


Figure 33: *Helicostegina gyralis* Barker & Grimsdale, 1936. **1-2** (EO.WL1705-17), microspheric specimen, equatorial section. **3-4** (EO.WL1705-18), megalospheric specimen, equatorial section. Upper Palmetto Grove Formation (sample WL1705), upper ABZ6, near Gayle, St Mary, Jamaica.

Helicostegina jamaicensis

Mitchell, E. Robinson & Özcan, sp. nov.

(Figs. 38 - 40)

Diagnosis*.* A species of *Helicostegina* with a small embryo (proloculus and deuteroloculus), a thickened spiral wall which terminates before the margin of the test, and with two layers (equatorial, and ventral sheet of subsidiary chamberlets) in the flange. Low lateral chambers present during adult growth.

Type specimens*.* Holotype: EO.WL2047-51; Paratypes: EO.WL2047-21, EO.WL2047-22, EO.WL2047-23, EO.WL2047-26, EO.WL2047-4, EO.WL2047-41, EO.WL2047-53, EO.WL2047-57, EO.WL2047-57, UWIGM.WL3532C-07, UWIGM.WL 3532C-08. Samples WL2047 and WL3532C (both from the same level), Preston Hill Formation, Lilyfield, St Ann, Jamaica.

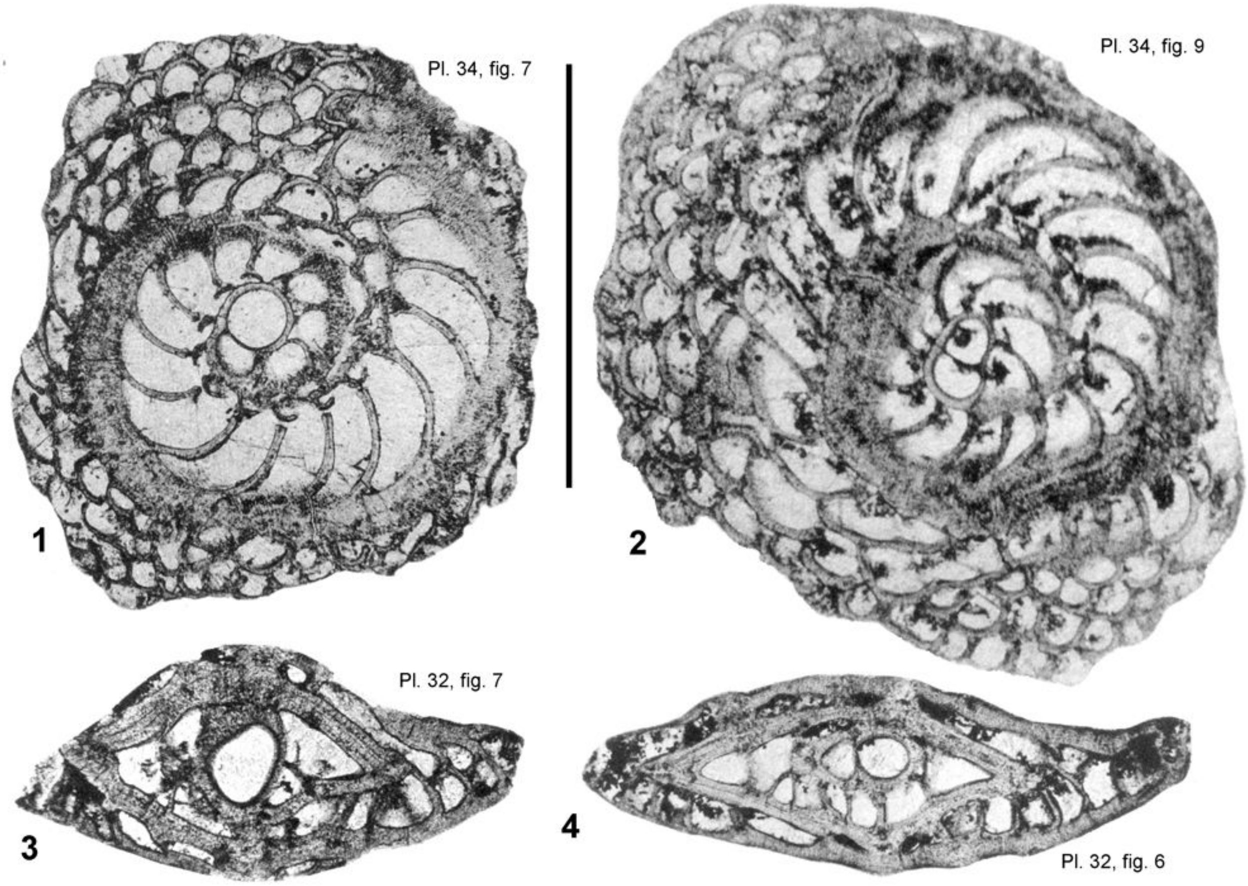


Figure 34: Reproduction of illustrations of *Helicostegina dimorpha* BARKER & GRIMSDALE, 1936 (Pls. 32 and 34). **1-2**, equatorial sections. **3-4**, axial sections. Nine km SE of Sabaneta, Veracruz, Mexico. Scale bar 1 mm.

Description. Only megalospheric specimens seen. Megalospheric specimens are up to 1.5 mm in diameter and 0.8 mm thick. The surface is covered with regularly arranged piles (pillars). The equatorial layer consists of the embryo and a primary spire of 17-20 chambers (including the proloculus and deuteroloculus) occupying 1½ to 1¾ whorls. The length of the embryo (Ele) ranges from 135 to 190 µm (including the walls). The primary spire has a thickened wall which does not extend to the margin of the test. The last chamber in the primary spire has two apertures and gives rise to orbitoidiform growth of the equatorial layer. In axial sections the alar prolongations of the spiral chambers on the dorsal side are not divided into chamberlets. The ventral side of the test is divided into subsidiary chamberlets, and this extends as a layer parallel to the equatorial layer giving the test a double flanged appearance. 'Lateral' chamberlets (*i.e.*, additional layers of dorsal and ventral chamberlets) are added in the adult stage, but do not extend onto the flange which just has a thickened wall.

Remarks. The species is distinguished from *H. gyralis* and *H. dimorpha* by its small embryo, and in the spiral wall not reaching the margin of the test. It is distinguished from *H. minor* sp. nov. and *H.* cf. *minor* sp. nov. by the fact that the spiral wall does not reach the edge of the test whereas in the latter forms the spiral wall extends to the margin of the test; thus orbitoidiform growth is neither achieved in *H. minor* sp. nov. nor in *H.* cf. *minor* sp. nov., but is in *H. jamaicensis* sp. nov.

Distribution. Only recorded from ABZ8, upper Lutetian, along the deep-water facies of the Preston Hill Formation, Lilyfield, St Ann, northern Jamaica.

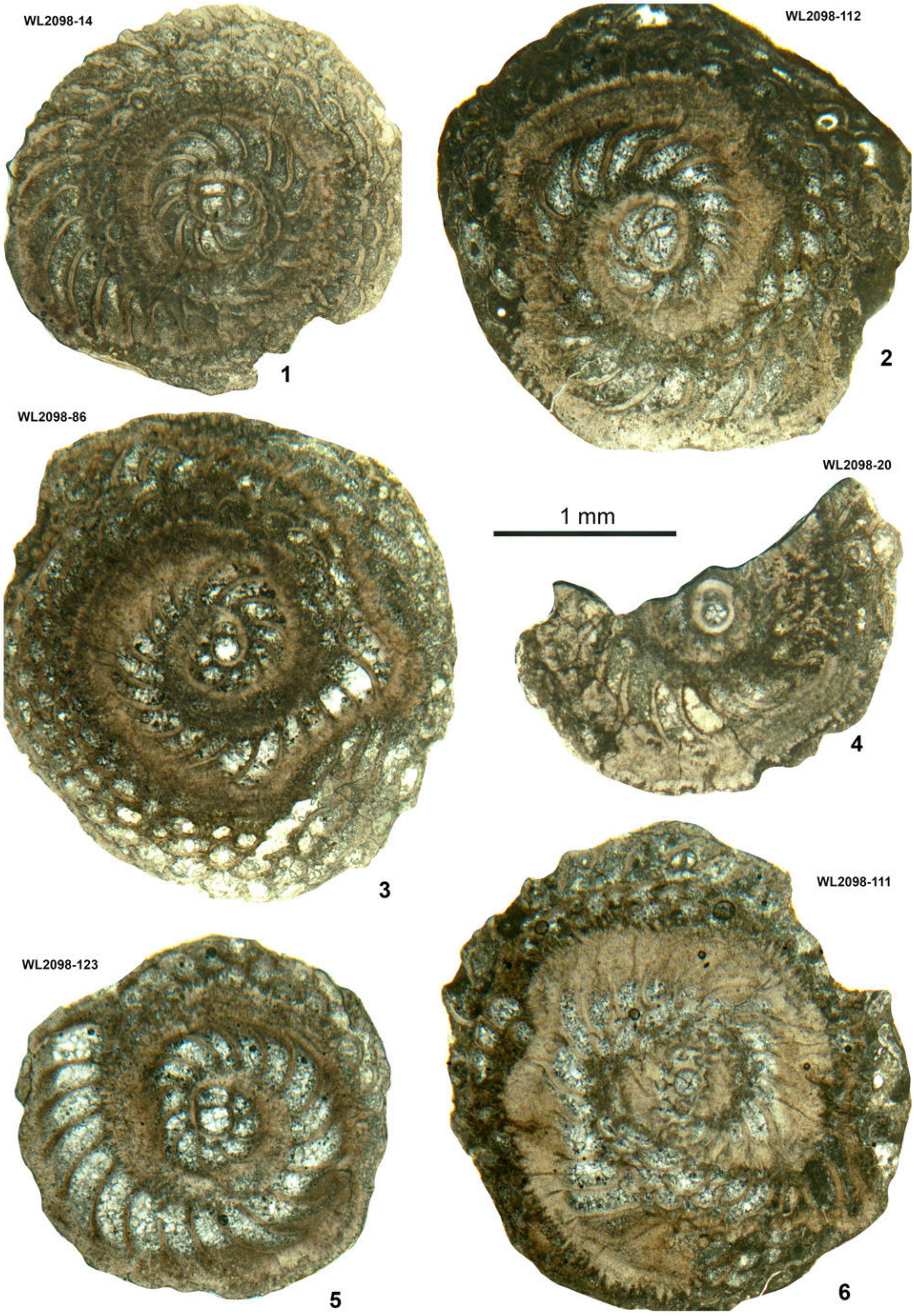


Figure 35: *Helicostegina dimorpha* BARKER & GRIMSDALE, 1936. **1** (EO.WL2098-14), **2** (EO.WL2098-112), **3** (EO.WL-2098-86), **4** (EO.WL2098-20), **5** (EO.WL2098-123), **6** (EO.WL2098-111): equatorial sections. Sample WL2098 (ABZ7), Farm Turn, St Mary, Jamaica.

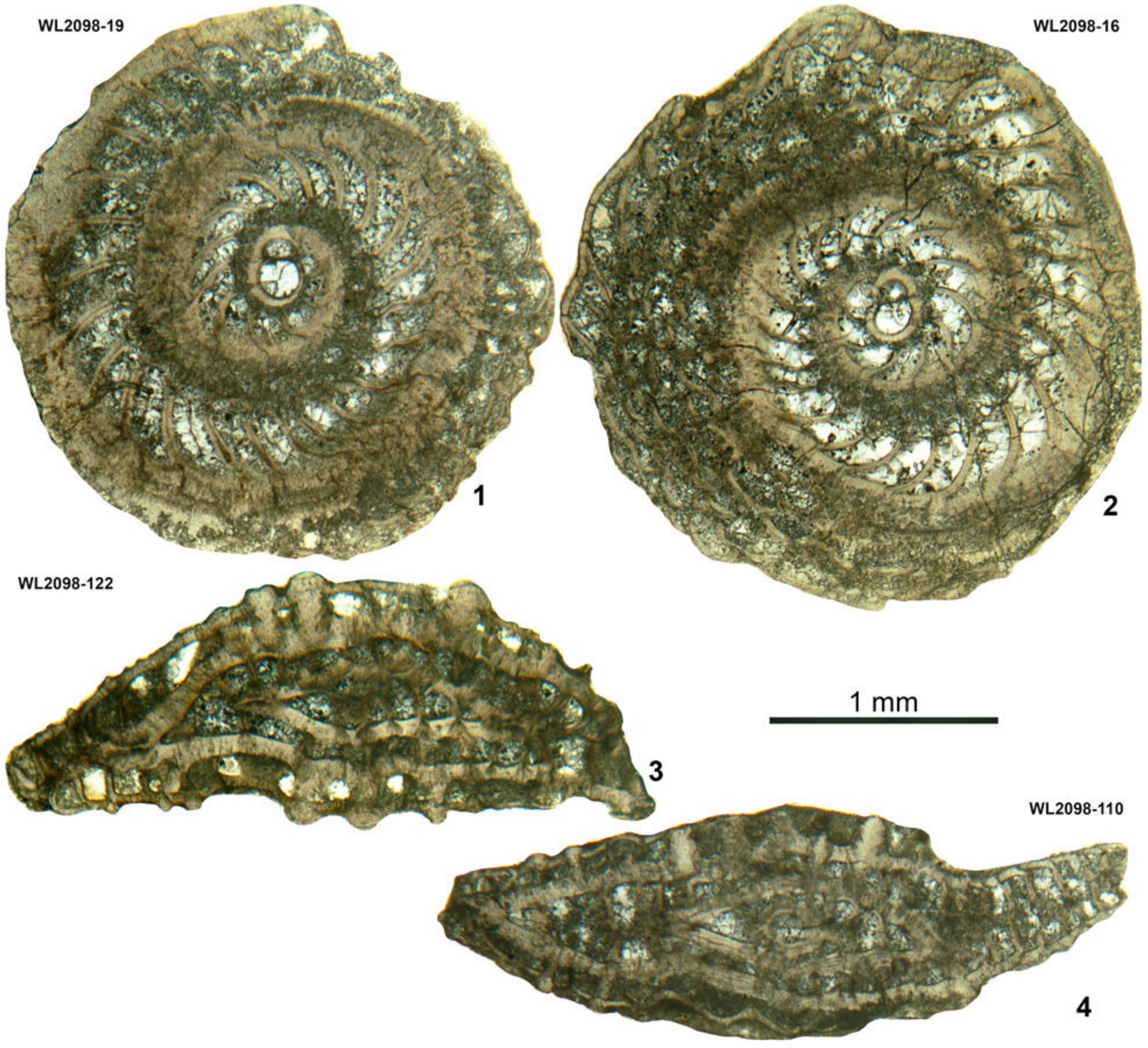


Figure 36: *Helicostegina dimorpha* Barker & Grimsdale, 1936. **1** (EO.WL2098-19), **2** (EO.WL2098-16): equatorial sections. **3** (EO.WL2098-122), **4** (EO.WL2098-110): axial sections. 4 shows a slightly longer flange, but occurs in a population which is assigned to *H. dimorpha*. Sample WL2098 (ABZ7), Farm Turn, St Mary, Jamaica.

Helicostegina jeannemairae

E. Robinson, Mitchell & Özcan, sp. nov.

(Figs. 41 - 47)

Diagnosis. Early growth stage as in *Heterostegina dimorpha* with alar prolongations open on the dorsal side and merging into subsidiary chamberlets on the ventral side. Adult test shows purely annular growth (alar prolongations absent in adult test) with an orbitoidiform (equatorial) layer and a ventral layer of subsidiary chamberlets giving a two-layered structure in axial section.

Type specimens. Holotype: UWIGM.WL3641-13 (Figs. 41.3, 43.6). Paratypes: UWIGM.WL 3641-2 to 6; UWIGM.UWLGM3641-8 to 9; UWIGM. WL3641-12; UWIGM.WL3641-14, UWIGM.WL 3641-16 to 21; UWIGM.WL3641-23 to 25. All from Chapelton Formation, Yellow Limestone (sample WL3641), Upper Rock Spring, parish of Westmoreland, Jamaica. There are several hundred additional paratypes in sample WL3641 that have not been numbered or cut.

Description. Tests are flat lenticular with swollen umbos and a diameter of up to 6.4 mm. The ornament consists of small scattered piles (pillars) across the whole test. The population is dominated by megalospheric specimens with very rare microspheric specimens. Microspheric specimens are only slightly larger (6.4 mm) than the megalospheric specimens (largest specimen is 5.7 mm).

Microspheric specimens have a very small proloculus that is followed by a primary spire of about 40 chambers. The spire is terminated by a retrovert chamber with two solons and this gives rise to the orbitoidiform layer.

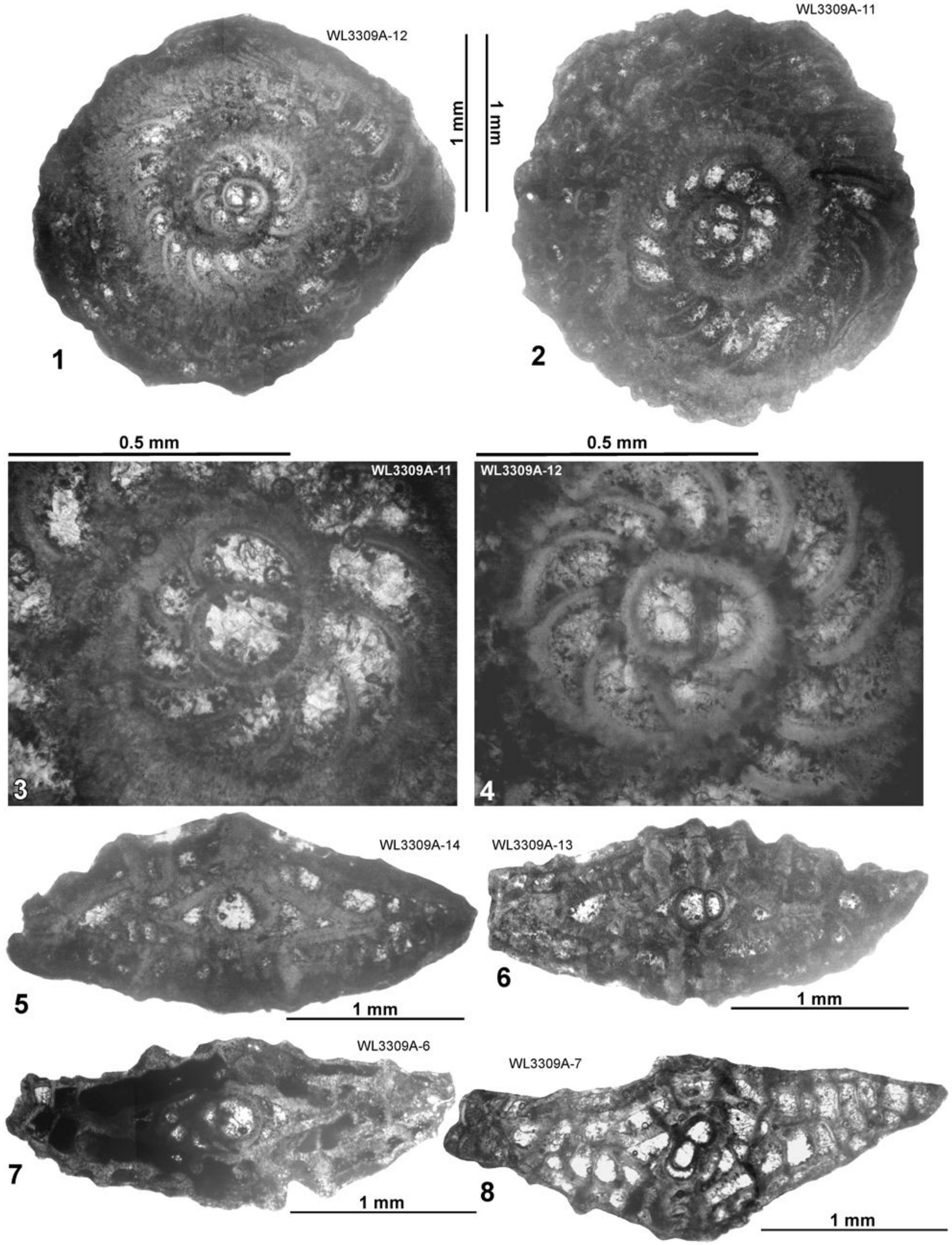


Figure 37: *Helicostegina dimorpha* Barker & Grimsdale, 1936. **1, 4** (UWIGM.WL3309A-12), equatorial section. **2-3** (UWIGM.WL3309A-11) equatorial section. **5** (UWIGM.WL3309A-14), axial section. **6** (UWIGM.WL3309A-13), axial section. **7** (UWIGM.WL3309A-6), axial section. **8** (UWIGM. WL3309A-7), axial section. Preston Hill Formation (ABZ7), Farm Turn (sample WL3309A), parish of St Mary, Jamaica.

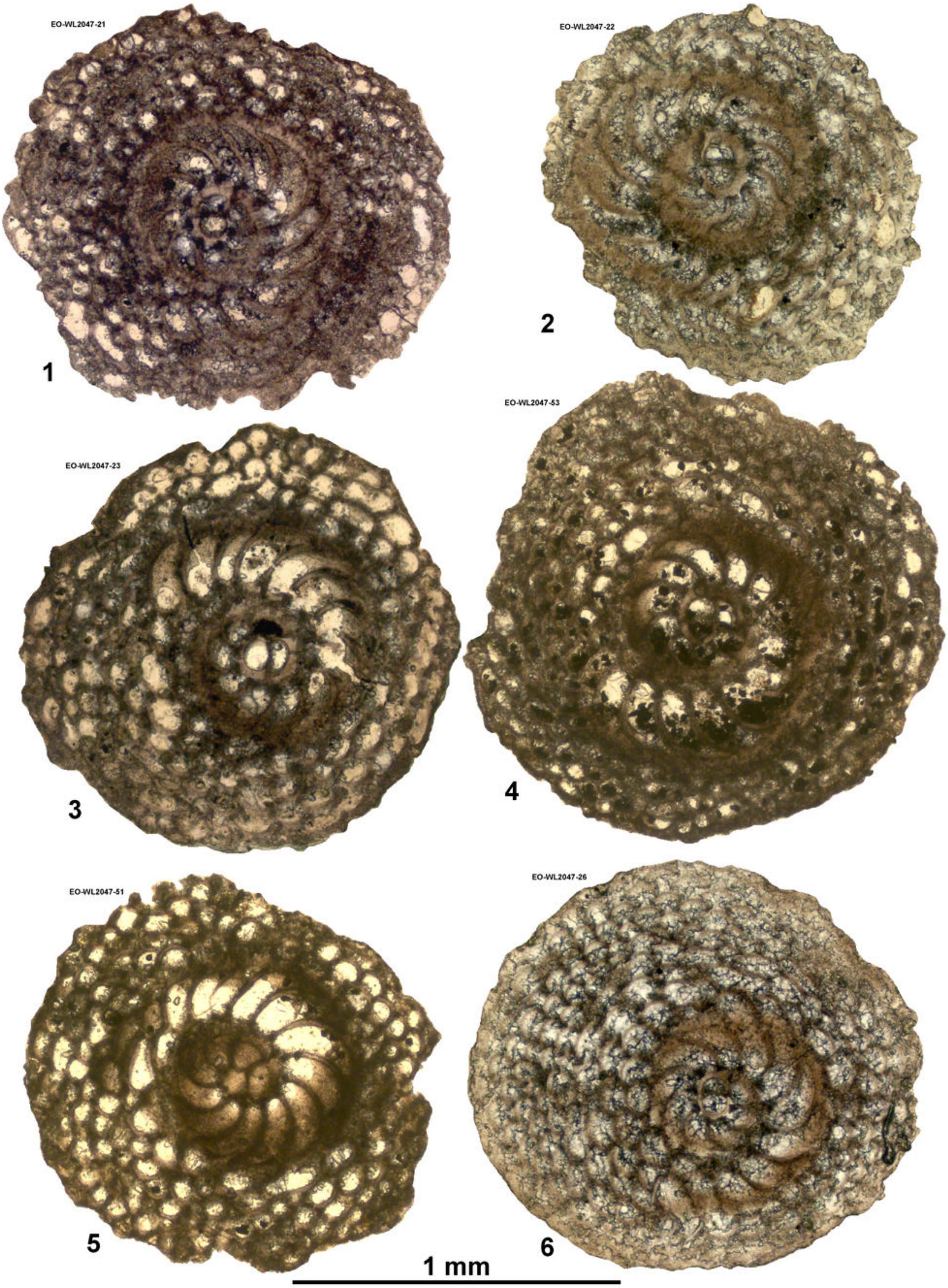


Figure 38: *Helicostegina jamaicensis* MITCHELL, E. ROBINSON & ÖZCAN sp. nov. **1** (EO.WL2047-21, paratype), **2** (EO.WL2047-22, paratype), **3** (EO.WL2047-23, paratype), **4** (EO.WL2047-53, paratype), **5** (EO.WL2047-51, holotype), **6** (EO.WL2047-26, paratype): equatorial sections. Note that the thickened spiral wall terminates before the margin of the test. Sample WL2047 (ABZ8), Preston Hill Formation, Lilyfield, St Ann, Jamaica.

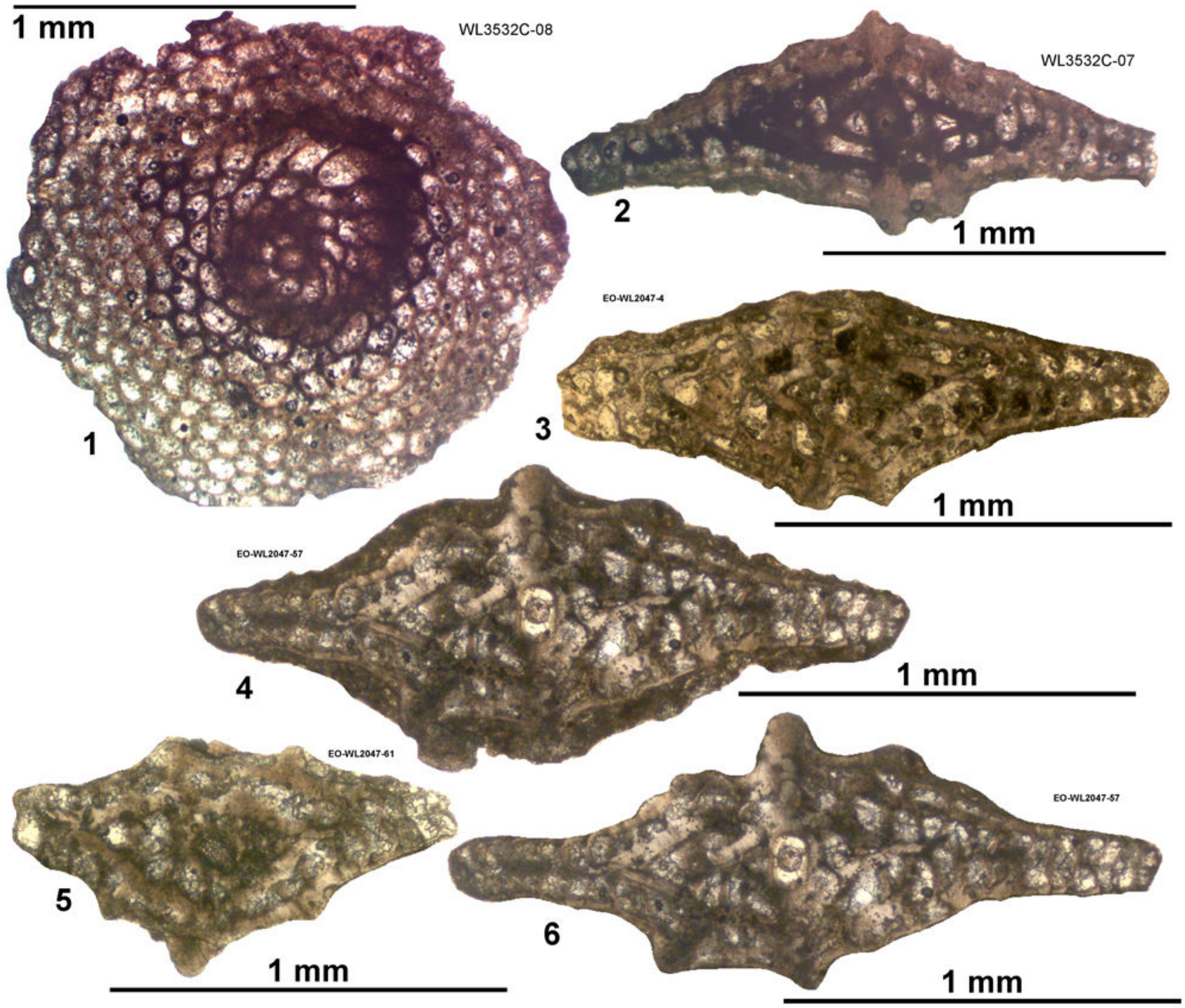


Figure 39: *Helicostegina jamaicensis* Mitchell, E. Robinson & Özcan sp. nov. Paratypes. **1** (UWIGM.WL3532C-08, paratype), equatorial section. **2** (UWIGM.WL3532C-07), **3** (EO.WL2047-4), **4** (EO.WL2047-57), **5** (EO.WL2047-41), **6** (EO.WL2047-57), axial sections. Samples WL2047 and WL3532C (ABZ8), Preston Hill Formation, Lilyfield, St Ann, Jamaica.

The megalospheric specimens have an embryo consisting of two chambers with a thickened chamber wall. The length of the embryo ranges from 278 to 400 µm (mean 340, SD 46.4, n = 10), with the proloculus being slightly larger than the deuteroloculus. The primary spire consists of one and a half whorls, is involute, and contains 15 to 23 chambers including the embryo (mean 19.1, st. dev. 2.88, n = 10). The primary spire contains subsidiary chamberlets on the ventral side, whereas the dorsal chambers extend onto the acute keel of the spire (this is developed as in *Helicostegina dimorpha*). The primary spire has a thickened wall which terminates at the point where orbitoidiform growth commences. The primary spire gives rise to two spirals (primary and secondary) through a chamber with two stolons (one forward directed and one retrovertly directed), and these spires coil around the periphery of the test and end in a closing chamber. Each chamber in the secondary spires gives rise to additional chamberlets which initiates orbitoidiform growth of the equatorial layer. The orbitoidiform chamberlets are low arcuate. The orbitoidiform layer occupies about four-fifths of the diameter of the test in large specimens. The ventral side of the test is composed of a single sheet of subsidiary chamberlets that develop from the sheet of secondary chamberlets on the ventral side of the primary spire. The chamberlets in the ventral subsidiary sheet have a typical orbitoidal form with two stolons as in the equatorial layer. Once orbitoidiform growth is initiated, there are no more alar prolongations and the test wall is compact without lateral chambers which results in the formation of a wide double flange. This indicates that growth of the adult test was facilitated by annular addition of orbitoidiform chamberlets to both the equatorial layer and to the ventral sheet of subsidiary chamberlets.

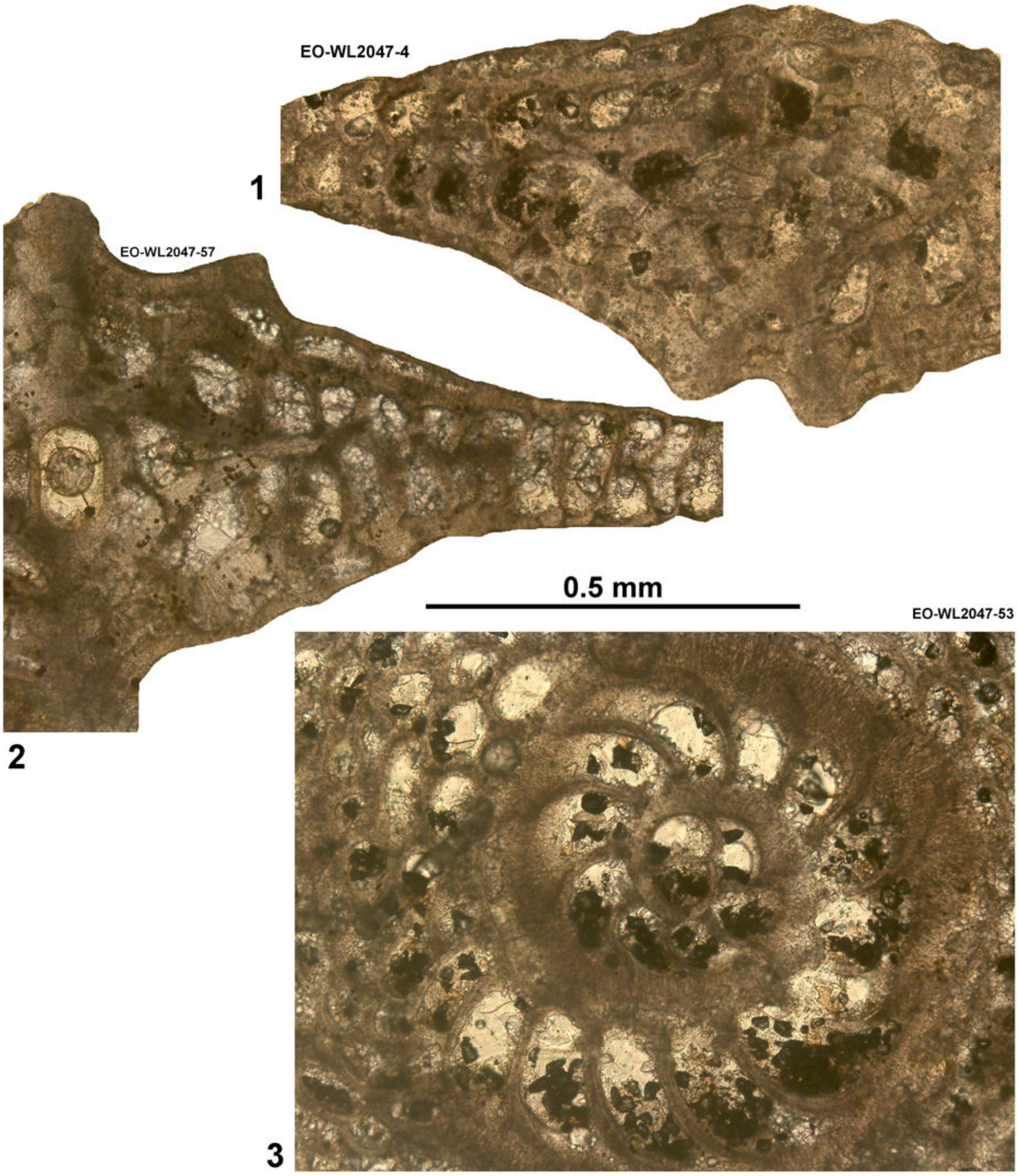


Figure 40: *Helicostegina jamaicensis* Mitchell, E. Robinson & Özcan sp. nov. Paratypes. **1** (EO.WL2047-4), **2** (EO.WL2047-57), details of axial sections; note the addition of lateral chambers. **3** (EO.WL2047-53), details of axial section showing the embryo (proloculus and deuteroloculus). Sample WL2047 (ABZ8), Preston Hill Formation, Lilyfield, St Ann, Jamaica.

Remarks. The species is named after the late Jeanne Mair Robinson who, with her children, discovered the first specimens of this species at Point, St James (Jamaica), although the type locality is situated in Westmoreland Jamaica where free specimens are abundant. The population from Point (Fig. 41) has more whorls in the spire than specimens from the type population and many have a one-winged morphology (Fig. 41.2-5, 7) in axial section. We regard these specimens as transitional to *H. dimorpha*, but because of the wide flange we place them in *H. jeannemairae* sp. nov. The species is common in some areas of western Jamaica (St. James and Westmoreland), but has not been found in the marlstones (Preston Hill Formation) or limestones (Chapelton Formation) along the North Coast Belt of Jamaica where *H. jamaicensis* sp. nov. is common. It may be that *H. jeannemairae* sp. nov. developed as a shallow-water species and *H. jamaicensis* sp. nov. as a deeper-water species.

Distribution. *Helicostegina jeannemairae* sp. nov. has only been found in sections in western Jamaica that lack zonally diagnostic forms. In St James it occurs in the Yellow Limestone above levels yielding *H.* cf. *dimorpha* and *Eolepidina* (probably lower ABZ8) and below levels yielding *Eo. gardnerae* (ABZ10), so an attribution to ABZ9 seems likely. At Rock Spring (Westmoreland) it occurs with only rare specimens of *Operculinoides* sp.

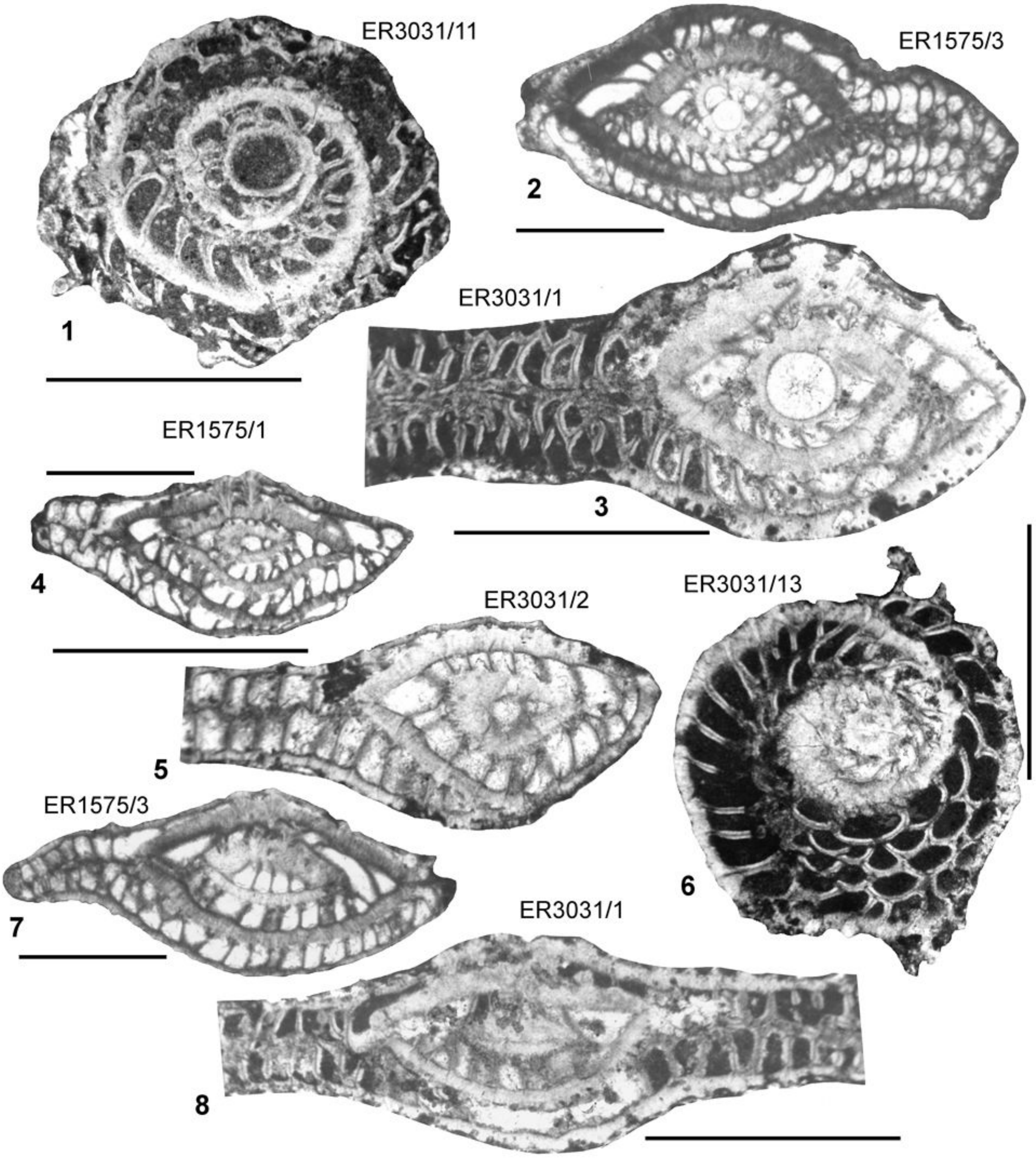


Figure 41: *Helicostegina jeannemairae* E. Robinson, Mitchell & Özcan sp. nov. Specimens in random orientations in thin section of rock. **1, 6**, off-centred equatorial sections. **2-5, 7-8**, off-centre axial sections. Note that some off-centred axial sections (**3-7**) show a single 'wing' and all axial sections show more whorls that in the type population of *H. jeannemairae*; we regard the Point population as transitional to *H. dimorpha*. Note that the flange is more strongly developed in specimens from sample ER3031 that in ER1575, with specimens from ER1575 be closer to *H. dimorpha*. Yellow Limestone, samples ER1575 and ER3031 (?lower ABZ9), Point, St James, Jamaica.

Family HELICOLEPIDINIDAE Tan, 1936

Diagnosis. The family is characterised by forms showing lenticular growth with the spiral and umbilical sides generally not determinable in axial sections. The equatorial layer consists of a primary spiral of chambers with equatorial chamberlets developing on the outside of the primary spiral. The alar prolongations on the ventral (spiral) side of the test are not subdivided into subsidiary chamberlets as in the Helicosteginidae, and lateral chamberlets are present on each side of the equatorial layer.

Genera included. *Helicosteginopsis* Caudri, 1975; and *Helicolepidina* Tobler, 1922.

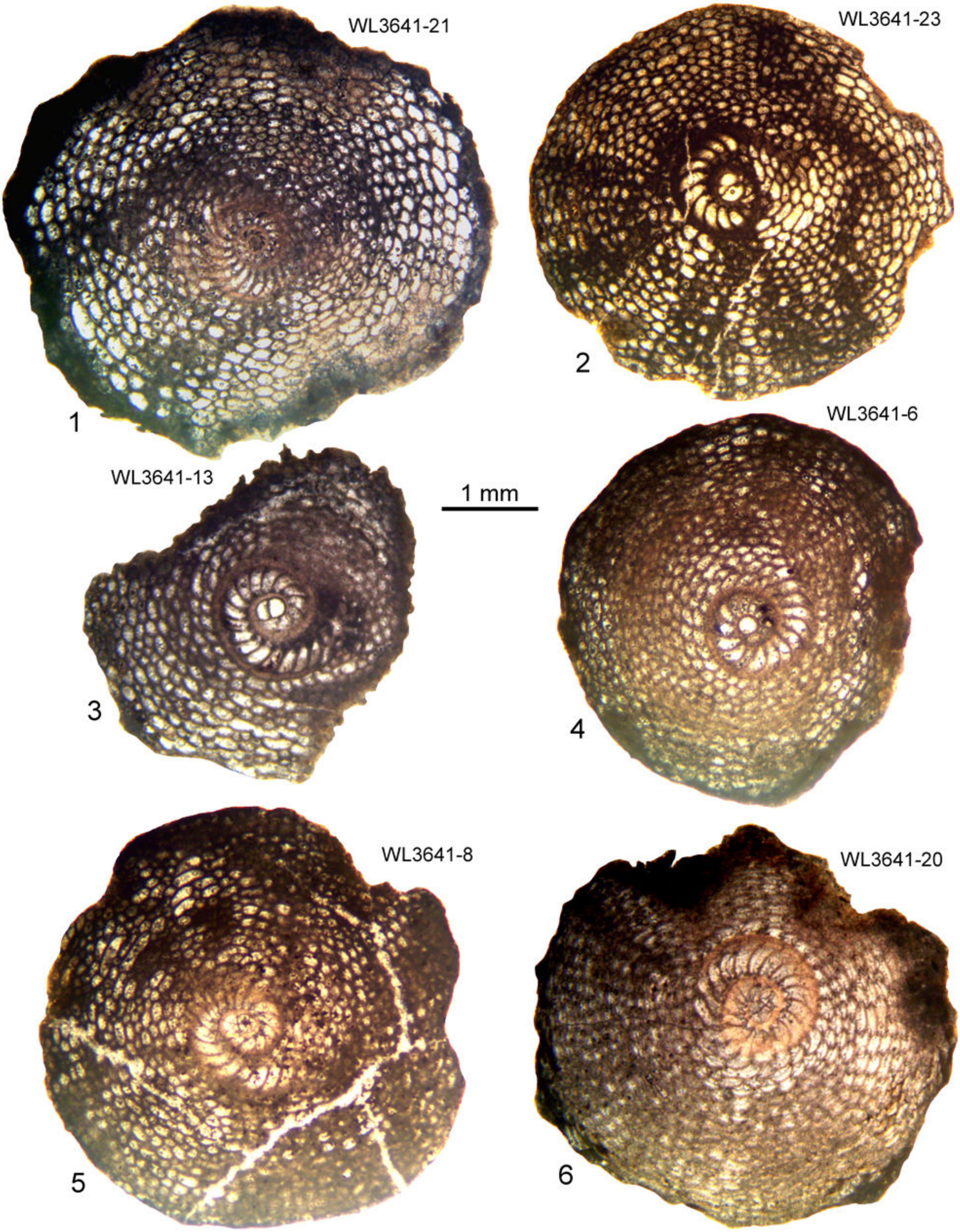


Figure 42: *Helicostegina jeannemairae* E. Robinson, Mitchell & Özcan sp. nov. Type population. Equatorial sections of microspheric (**1**: UWIGM.WL3641-21) and megalospheric (**2**, UWIGM.WL3641-23; **3**, UWIGM. WL3641-13; **4**, UWIGM.WL3641-6; **5**, UWIGM. WL3641-8; **6**, UWIGM.WL3641-20). Chapelton Formation (?upper ABZ9), Yellow Limestone (sample WL3641), Upper Rock Spring, parish of Westmoreland, Jamaica.

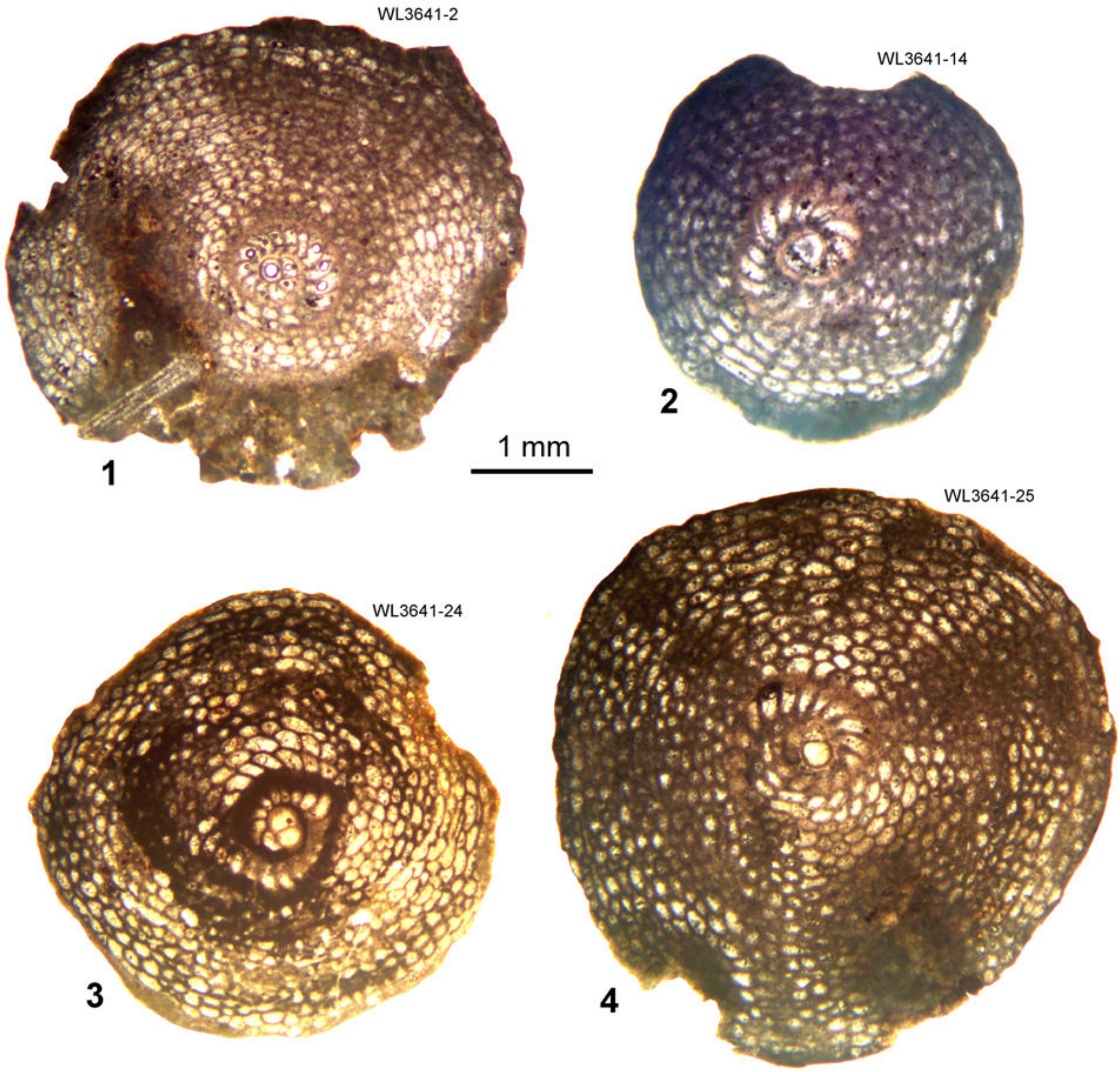


Figure 43: *Helicostegina jeannemairae* E. Robinson, Mitchell & Özcan sp. nov. Type population. Equatorial sections of megalospheric individuals (**1**, UWIGM.WL3641-2; **2**, UWIGM.WL3641-14; **3**, UWIGM. WL3641-24; **4**, UWIGM.WL 3641-25). Chapelton Formation (?upper ABZ9), Yellow Limestone (sample WL3641), Upper Rock Spring, parish of Westmoreland, Jamaica.

Remarks. The family is separated from the Helicosteginidae by the lack of a subsidiary sheet of chamberlets on the ventral (spiral) side of the test and the presence of lateral chamberlets on either side of the equatorial layer. We do not describe these forms as they are rare in our samples, but do provide our best estimates of ages.

Genus *Helicosteginopsis* Caudri, 1975

Type species. *Helicostegina soldadensis* Grimsdale in Vaughan & Cole, 1941.

Helicosteginopsis soldadensis (Grimsdale in Vaughan & Cole, 1941)

(Fig. 48.1, 3-4)

Previous descriptions. Grimsdale in Vaughan & Cole (1941); Caudri (1975, 1996); Adams (1987).

Age. The material from Trinidad comes from levels that have been assigned to the upper Eocene (Vaughan & Cole, 1941; Caudri, 1975, 1996), but contains reworked material from Paleocene and middle Eocene levels such that the age of the species cannot be determined from Trinidad. In Margarita Island (Caudri, 1974), Venezuela, *H. soldadensis* occurs in sample P.J.B.145 with *L. ariana*, *Orbitoina* spp. and *Helicolepidina spiralis trinitatis* [= *nortoni* Vaughan] and can be assigned to ABZ12. In Panama, Cole (1941) recorded *H. soldadensis* with *Eu. chaperi* and *H. ocalana* indicating ABZ16. We provisionally give a range estimate of zones ABZ12 to ABZ16.

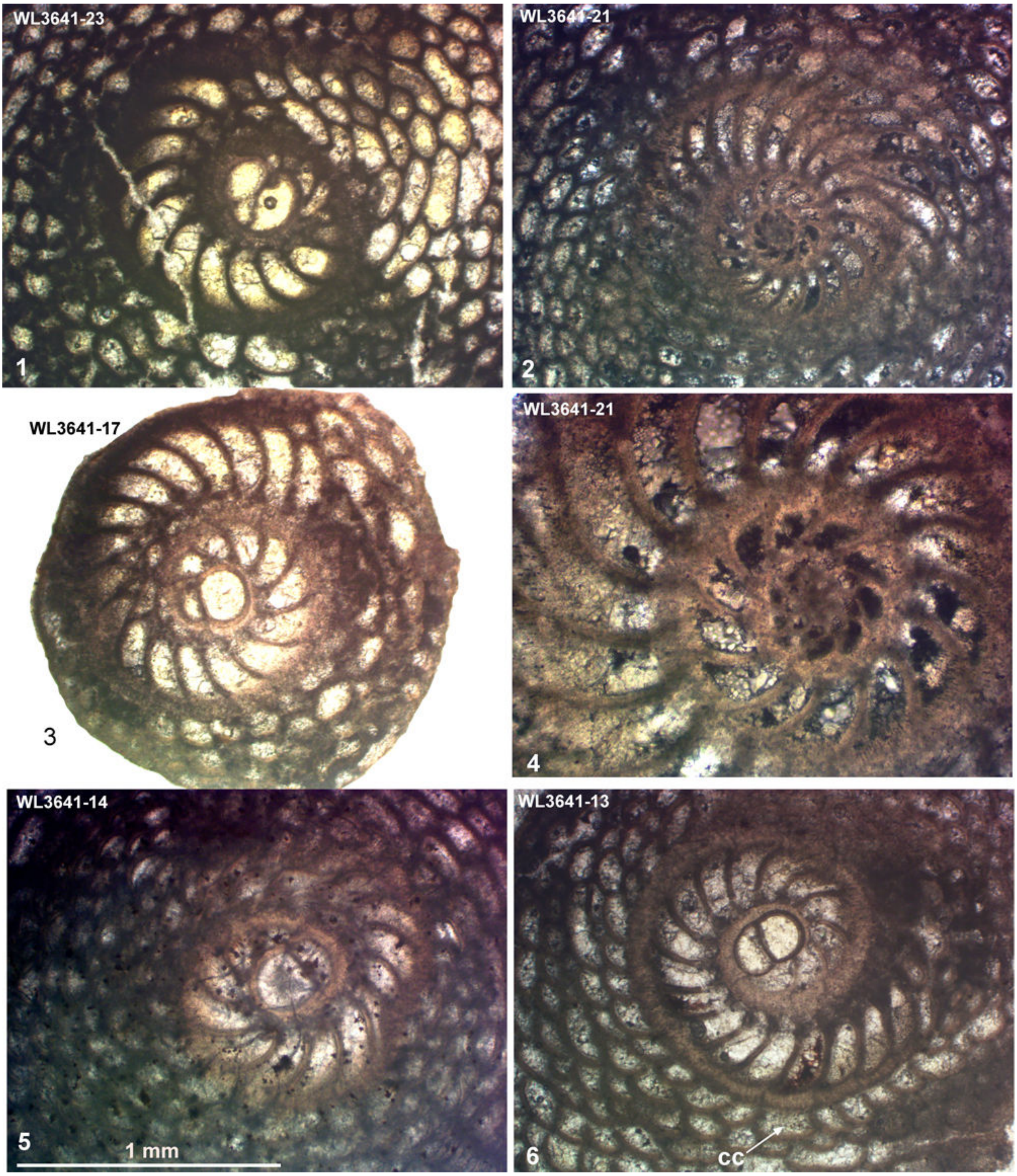


Figure 44: *Helicostegina jeannemairae* E. Robinson, Mitchell & Özcan sp. nov. Type population, details of spire. Equatorial sections of microspheric (**2, 4**, UWIGM.WL3641-21) and megalospheric individuals (**1**, UWIGM.WL3641-23; **3**, UWIGM.WL3641-17; **5**, UWIGM.WL3641-14; **6**, UWIGM.WL3641-13). Note closing chamber developed from two spires coiling around the shell wall of the primary spire. Chapelton Formation (?upper ABZ9), Yellow Limestone (sample WL3641), Upper Rock Spring, parish of Westmoreland, Jamaica.

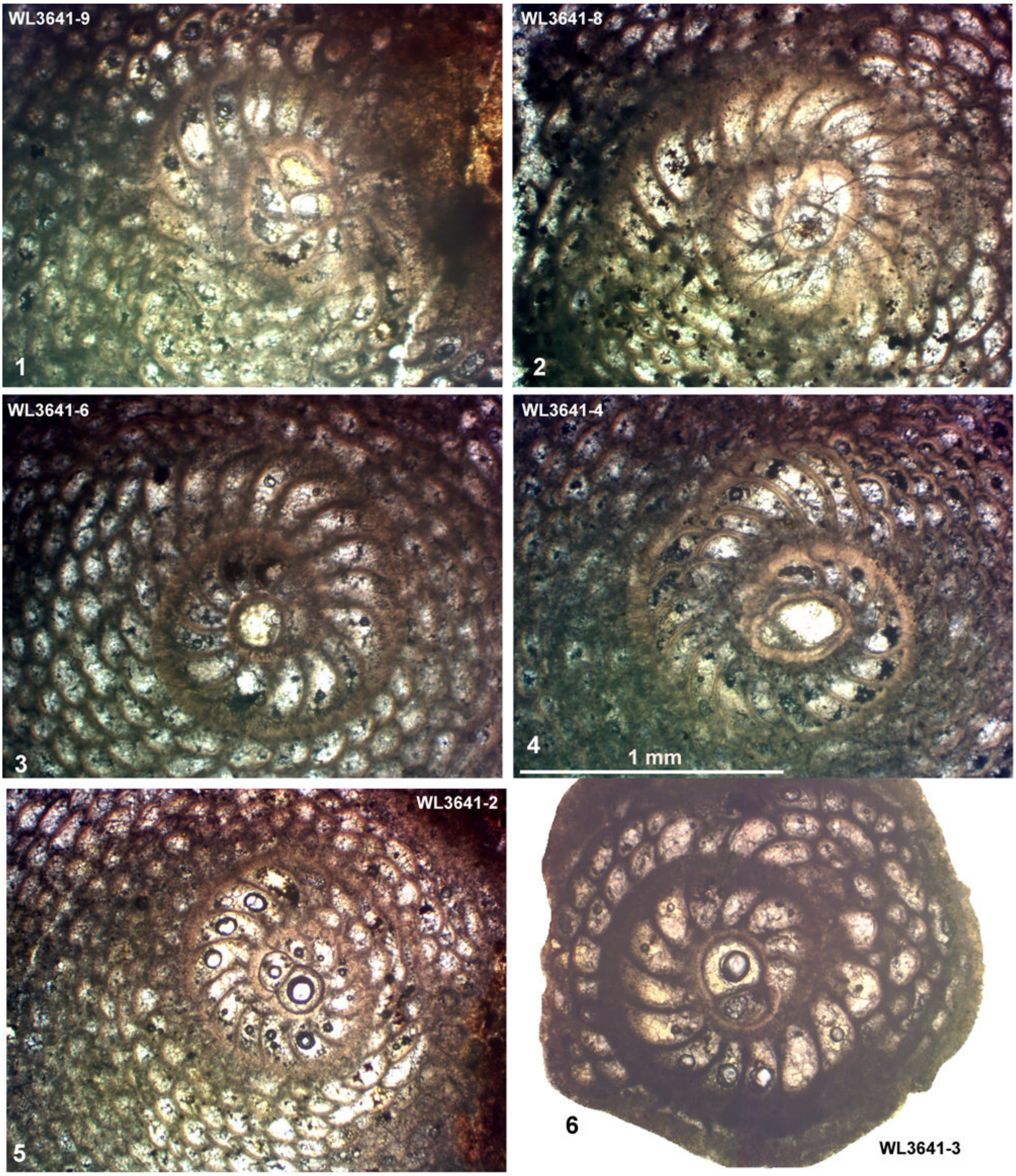


Figure 45: *Helicostegina jeannemairae* E. ROBINSON, MITCHELL & ÖZCAN sp. nov. Type population, details of spire. Equatorial sections of megalospheric individuals (**1**, UWIGM.WL3641-9; **2**, UWIGM.WL3641-8; **3**, UWIGM.WL3641-6; **4**, UWIGM.WL3641-4; **5**. UWIGM. WL3641-2; **6**, UWIGM.WL3641-3). Chapelton Formation (?upper ABZ9), Yellow Limestone (sample WL3641), Upper Rock Spring, parish of Westmoreland, Jamaica.

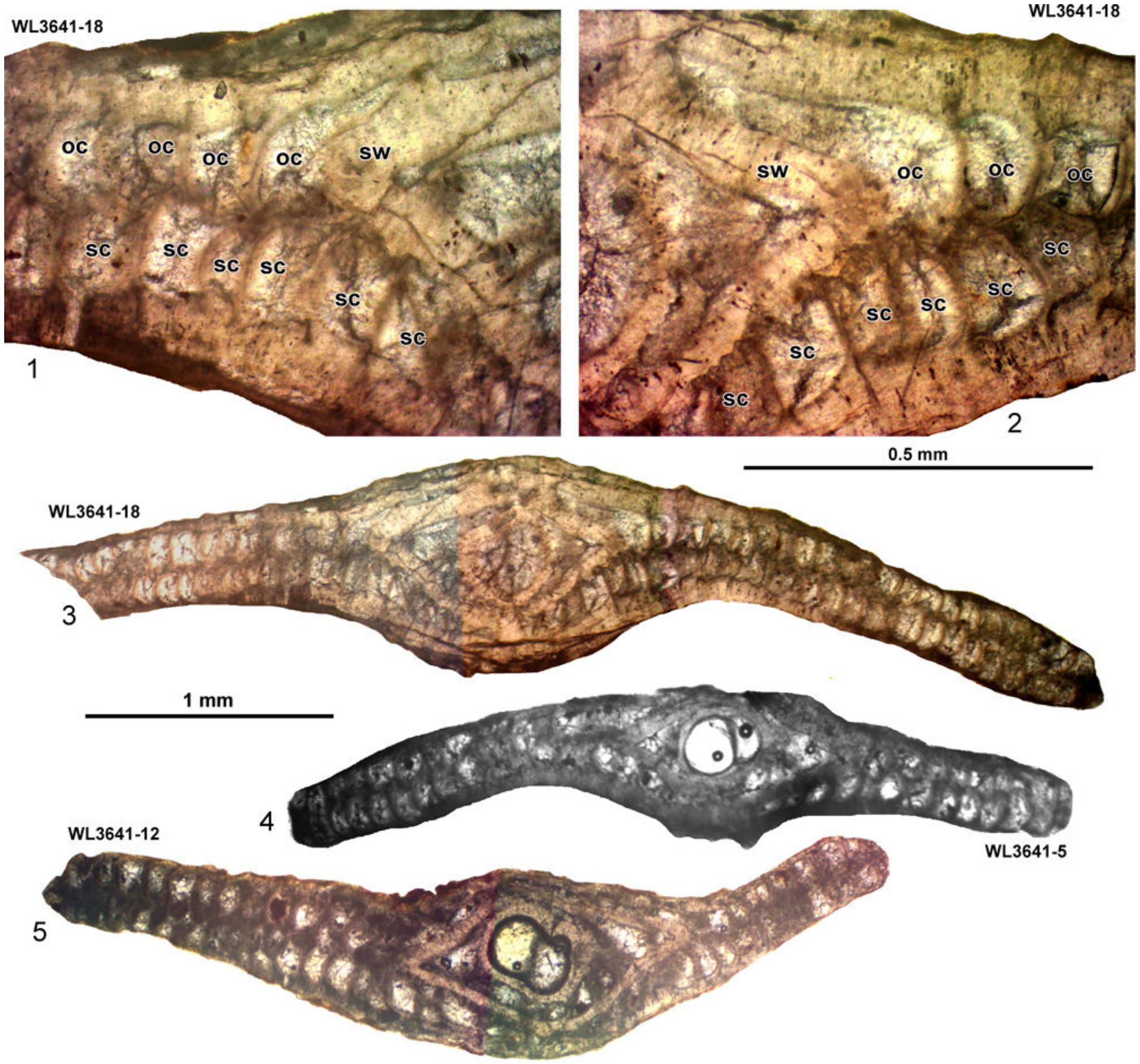


Figure 46: *Helicostegina jeannemairae* E. Robinson, Mitchell & Özcan sp. nov. Type population. Axial sections of megalospheric individuals (**1-3**, UWIGM.WL3641-18; **4**, UWIGM.WL3641-5; **5**, UWIGM. WL3641-12). sw, spiral wall; oc, orbitoidiform chamber; sc, subsidiary chamberlet. Chapelton Formation (?upper ABZ9), Yellow Limestone (sample WL3641), Upper Rock Spring, parish of Westmoreland, Jamaica.

Genus *Helicolepidina* Tobler, 1922

Type species. *Lepidocyclina (Helicolepidina) spiralis* Tobler, 1922.

Synonyms. *Helicocyclina* Tan, 1936 (type species: *Helicolepidina paucispira* Barker & Grimsdale, 1936).

Helicolepidina sp. A

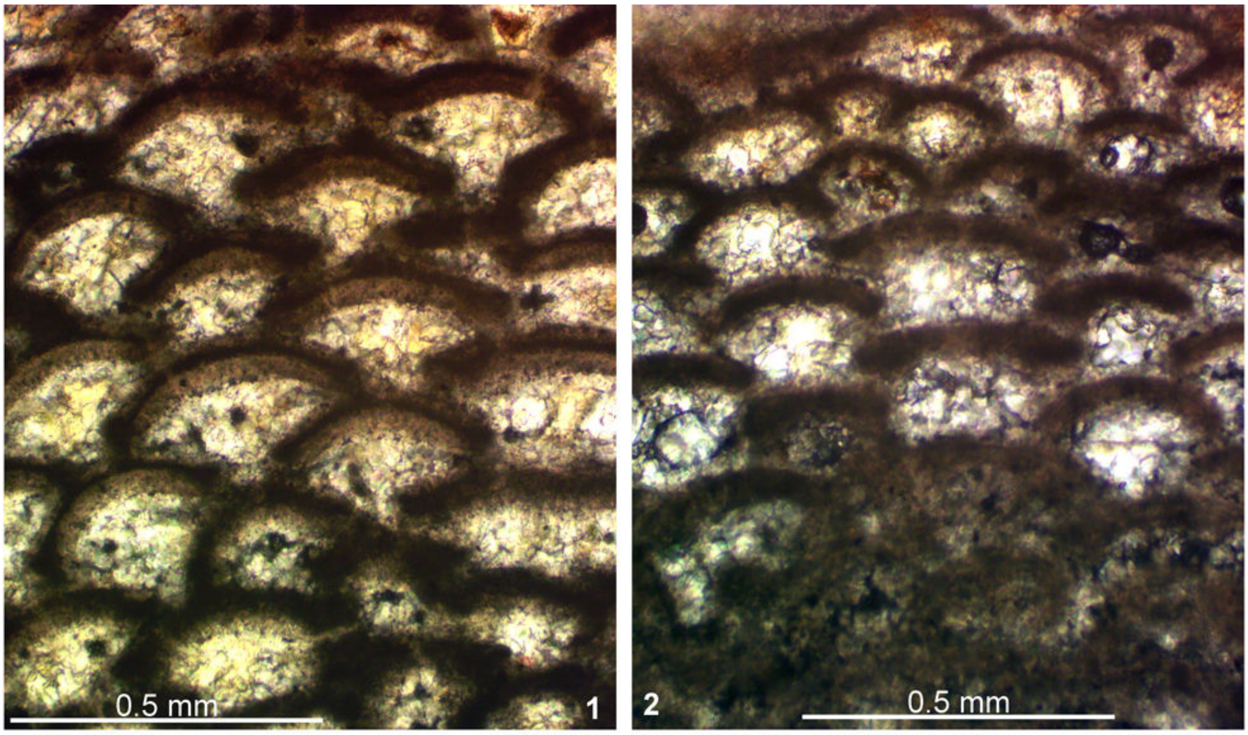
(Fig. 48.2)

Remarks. Barker and Grimsdale (1936, Pl. 35, fig. 4) figured a specimen that they ascribed to *Eulinderina guayabalensis* var. *regularis* Barker & Grimsdale, but differs in having some equatorial chamberlets developing on the outside of the primary spire (Fig. 49.4). This form does not have a thick spiral wall. We ascribe this specimen (from the ABZ7- ABZ8 boundary zone) to *Helicolepidina* sp. A.

Helicolepidina spiralis Tobler, 1922, and *Helicolepidina nortoni* Vaughan, 1936

(Fig. 49.1)

This group of species has been discussed by Raadshooven (1951) who recognized six forms (morphotypes) with some stratigraphic significance; his forms C and D correspond to *H. spiralis* Tobler and his forms E and F, to *H. nortoni* (= *H. spiralis trinitatis* Brönnimann). Caudri (1975) recorded *H. nortoni* (her *H. spiralis trinitatis*) from ABZ12 on Margarita Island, Venezuela. Cole (1952) recorded *H. nortoni* (as *H. spiralis*) from Panama in samples lacking both *Pl. tobleri* and *H. ocalana* (ABZ15) and in samples with *H. ocalana* (ABZ16). Thus we infer a range of zones ABZ12 to ABZ16 to *H. nortoni*. We assign tentative ages of ABZ7 to ABZ8 for *H.* sp. 1 (forms A and B of Raadshooven, 1951) and ABZ8 and ABZ10 for *H. spiralis*, based on Raadshooven (1951); further work is needed to confirm the ranges.



Orbitoidal layer WL3641-23 Spiral sheet of subsidiary chamberlets WL3641-19

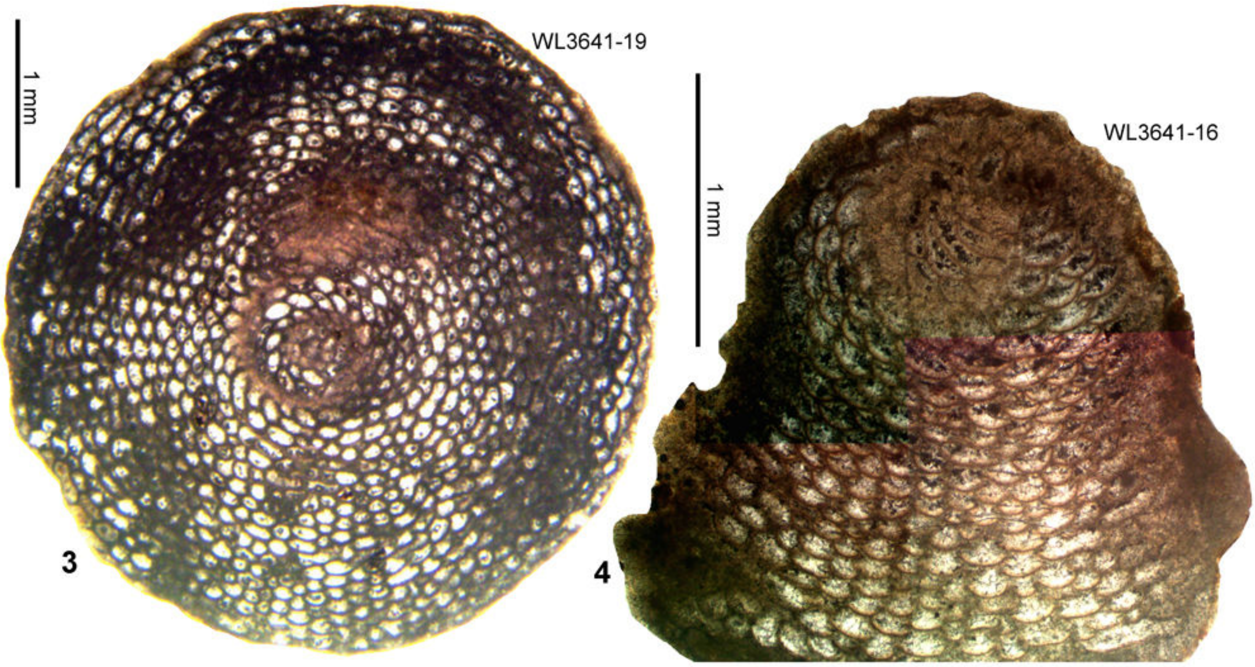


Figure 47: *Helicostegina jeannemairae* E. ROBINSON, MITCHELL & ÖZCAN sp. nov. Type population. **1** (UWIGM.WL 3641-23), detail showing stolons in the equatorial layer of chamberlets. **2** (UWIGM.WL3641-19), detail showing stolons in the subsidiary ventral layer of chamberlets. **3** (UWIGM.WL3641-19), section cut parallel to the equatorial plane through a rather symmetrical specimen showing the development of the subsidiary chamberlets in the ventral sheet of subsidiary chamberlets (a typical equatorial layer was ground away during the making of the section). **4** (UWIGM.WL3641-16), tangential section through the ventral sheet of subsidiary chamberlets. Chapelton Formation (?upper ABZ9), Yellow Limestone (sample WL3641), Upper Rock Spring, parish of Westmoreland, Jamaica.

Helicolepidina polygyralis BARKER, 1932
(Fig. 49.3-4)

Remarks. BARKER (1932, 1934) placed megalospheric forms with diameters of 1.6 - 2.4 mm and 2.5 - 3 whorls in this species; it therefore has more whorls than other species of *Helicolepidina*. CAUDRI (1974) recorded *H. polygyralis* from ABZ9 on Margarita Island, Venezuela.

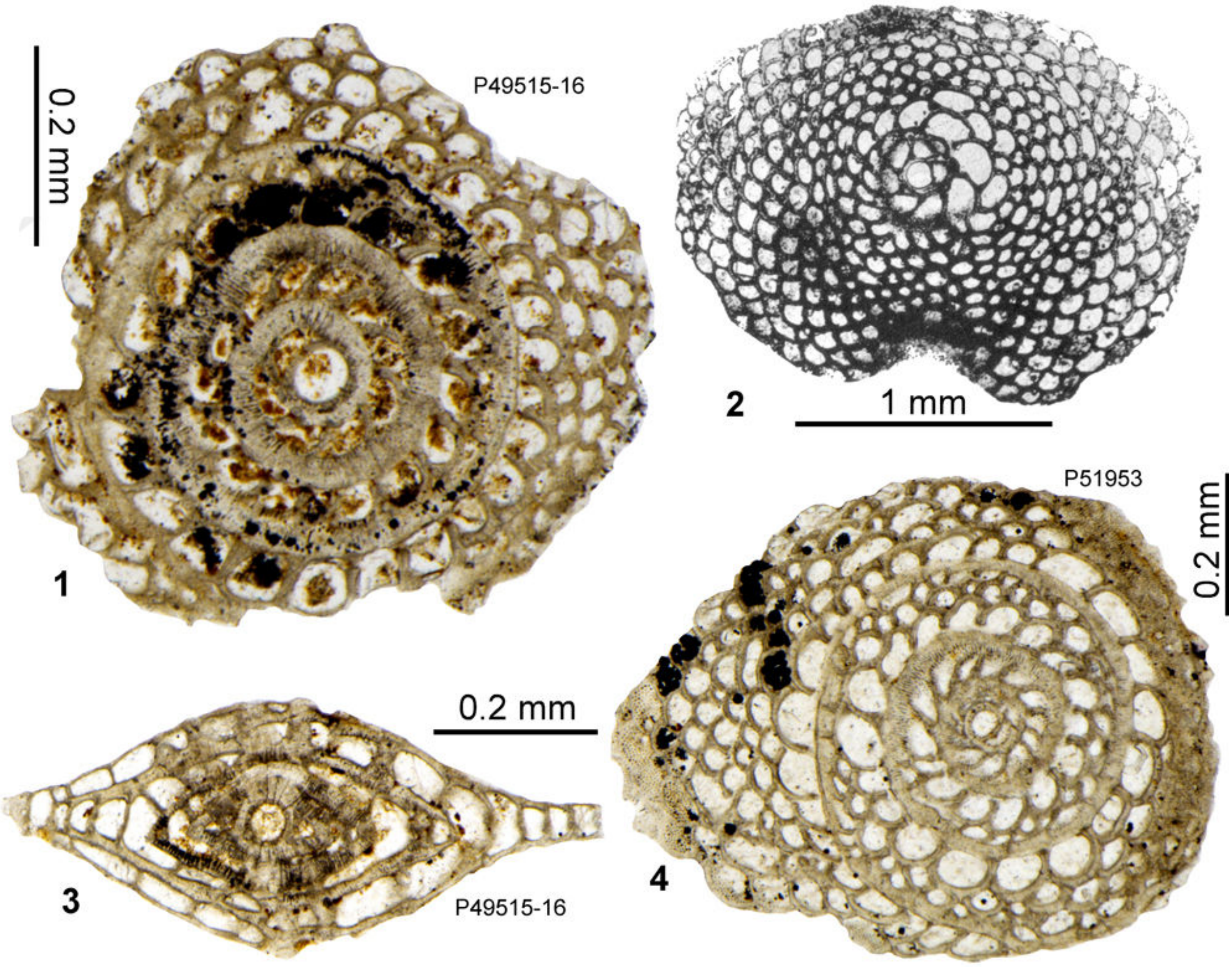


Figure 48: 1, 3-4, *Helicosteginopsis soldadensis* (Grimsdale): **1** (BMNH.P49515-16), megalospheric specimen, equatorial section; **3** (BMNH.P49515-16), megalospheric specimen, axial section: note symmetrical development of lateral chambers and single spiral (equatorial) layer. **4** (BMNH.P51953), megalospheric specimen, equatorial section; Soldado Rock, Trinidad (T.F. Grimsdale collection). **2**, *Helicolepidina* sp. (reproduced from figure of Barker & Grimsdale, 1936, Pl. 35, fig. 4, *Eulinderina guayabalensis* var. *regularis*), megalospheric form, equatorial section, close to village of Yecautla, Veracruz, Mexico.

Helicolepidina paucispira
Barker & Grimsdale, 1936
(Fig. 49.2)

Remarks. Barker and Grimsdale referred *H. paucispira* to the upper Eocene. Cole (1945, p. 17) reported this species from water wells at Tallahassee in the Upper Eocene of Florida which can be assigned to either upper ABZ15 or ABZ16 due to the presence of *Eu. chaperi*.

Family PSEUDOLEPIDINIDAE
Mitchell, E. Robinson & Özcan fam. nov.

Diagnosis. The family is characterised by the development of a double equatorial layer together with lateral chambers on both the dorsal (umbilical) and ventral (spiral) sides. The double equatorial layer develops from an initial single equatorial layer.

Remarks. The biloculine embryo is joined by a further chamber on the ventral side that we consider to be part of the embryo. There is/are one or two PACs developed in addition to this third embryonic chamber. *Pseudolepidina* developed a lepidocyclinid orbitoidiform morphology before the Lepidocyclinidae and therefore cannot be derived from that stock. We also see it difficult to generate *Pseudolepidina* from the Helicosteginidae or the Helicolepidinae, again because of its advanced equatorial plan. The subfamily appears to be a separate radiation, presumably from an unknown rotalid ancestor.

Genera included. *Pseudolepidina* Barker & Grimsdale, 1937 (type species: *Pseudolepidina trimera* Barker & Grimsdale, 1937); *Triplalepidina* Vaughan & Cole, 1938 (type species: *Triplalepidina veracruziana* Vaughan & Cole, 1938). We do not consider *Triplalepidina* in this work as we do not have specimens of this genus.

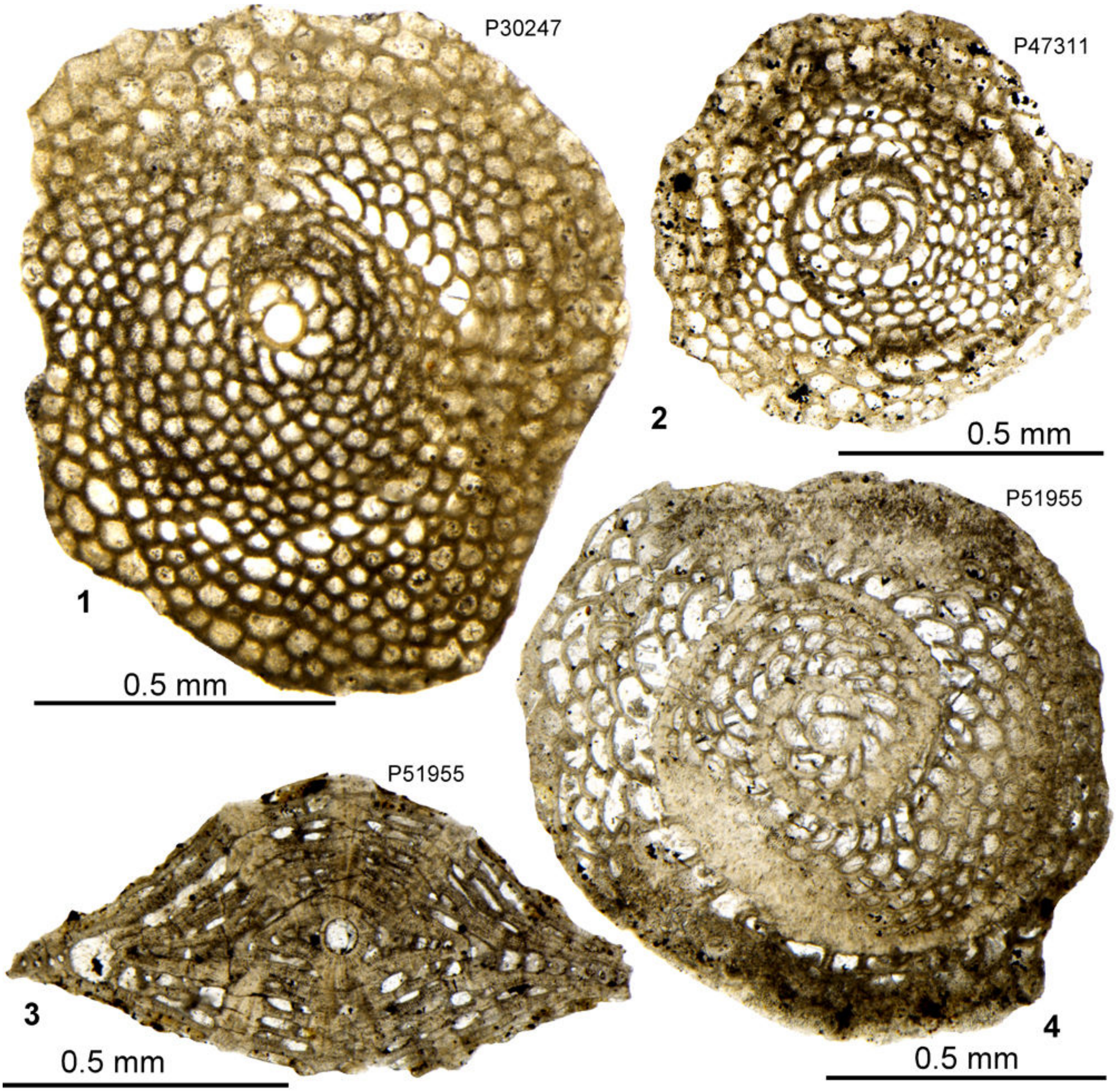


Figure 49: 1, *Helicolepidina spiralis* Tobler, 1922 (BMNH.P30247), megalospheric specimen, equatorial section; El Alto, north-western Peru. **2**, *Helicolepidina paucispira* Barker & Grimsdale, 1936 (BMNH.P47311), megalospheric specimen, equatorial section; Ecuador. **3-4** (BMNH.P51955), *Helicolepidina polygyralis* Barker, 1932: **3**, megalospheric specimen, axial section (note the single spiral-equatorial layer); **4**, megalospheric specimen, equatorial section: Ancon Peninsula, Santa Elena Peninsula, Ecuador.

Genus *Pseudolepidina*
Barker & Grimsdale, 1937

Type species. *Pseudolepidina trimera* Barker & Grimsdale, 1937 from the Lutetian of Jenny station 1573, 11 km SE of Sabaneta, state of Veracruz, Mexico.

Diagnosis. A genus of Pseudolepidinidae developing a double equatorial layer, but lacking a compact shell layer between the two parts of the equatorial layer; with a 'third PAC' developed; and well-developed lateral chamberlets.

Remarks. *Pseudolepidina* is distinguished from *Triplalepidina* in lacking a compact shell layer between the two parts of the double equatorial layer.

Pseudolepidina trimera
Barker & Grimsdale, 1937

(Figs. 50 - 55)

Previous descriptions and figures. Barker & Grimsdale, 1937, p. 172, Pl. V. figs. 1-3; Pl. VIII, figs. 1-5; Adams, 1987, p. 299, Pl. 3, figs. 11-16.

Recognition. The double equatorial layer as seen in axial sections is diagnostic, particularly when the third PAC is visible in such sections. Oblique sections of *Lepidocyclina* or *Orbitoina* may give the impression of showing two equatorial layers and can be confused with *Pseudolepidina*, so the presence of the additional PAC is critical to identifications of specimens in random

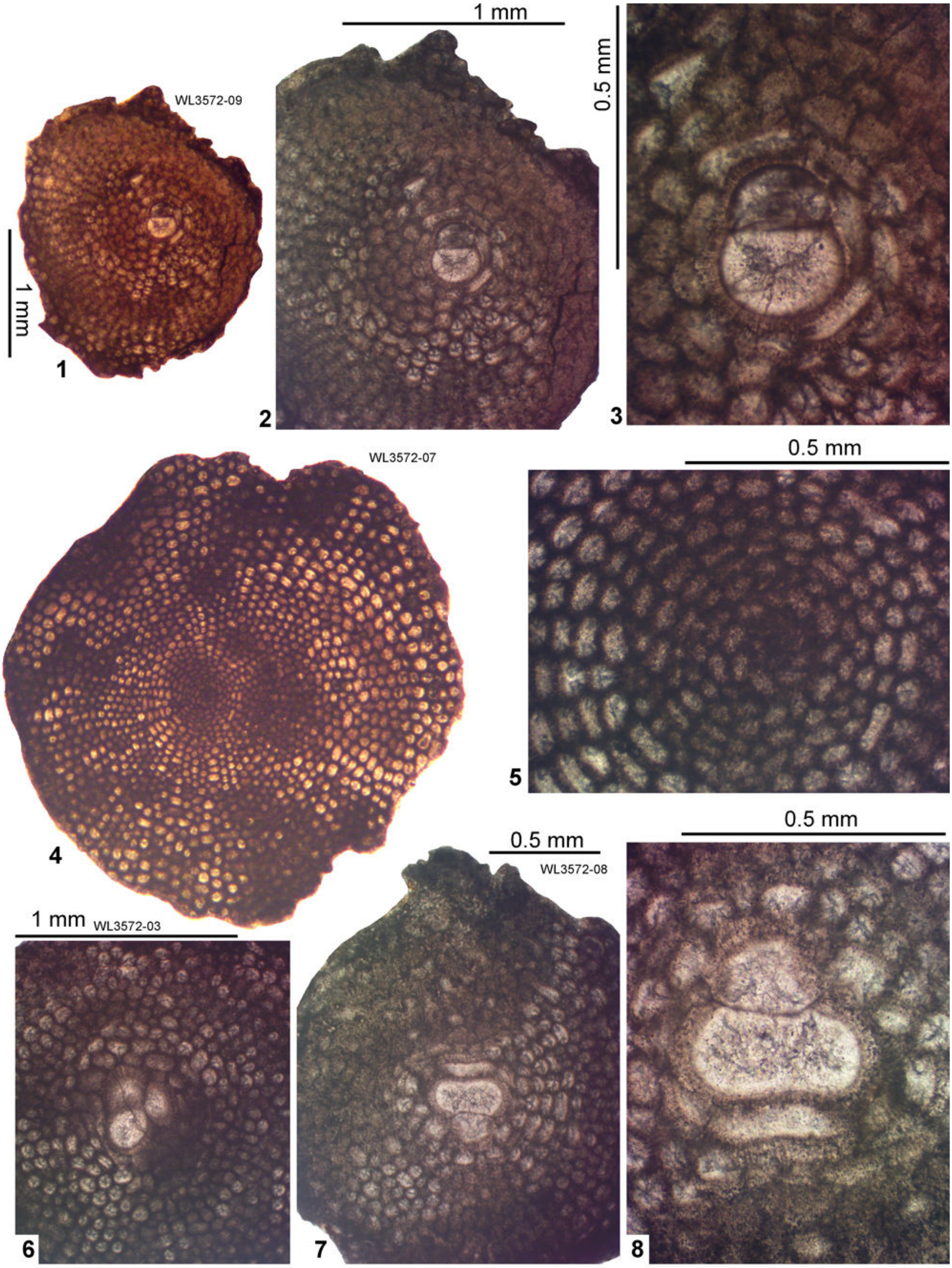


Figure 50: *Pseudolepidina trimera* BARKER & GRIMSDALE, 1937. **1-3** (UWIGM.WL3572-09), megalospheric forms, equatorial section showing two PACs and four unequal spirals of epiembryonic chambers. **4-5** (UWIGM.WL3572-07), microspheric form, equatorial section. **6** (UWIGM.WL3572-03), megalospheric form showing one obvious PAC. **7-8** (UWIGM.WL3572-08), megalospheric form with deformed embryo showing three chambers with four PACs. Yellow Limestone (ABZ7), Grants Pen, St Thomas, Jamaica.

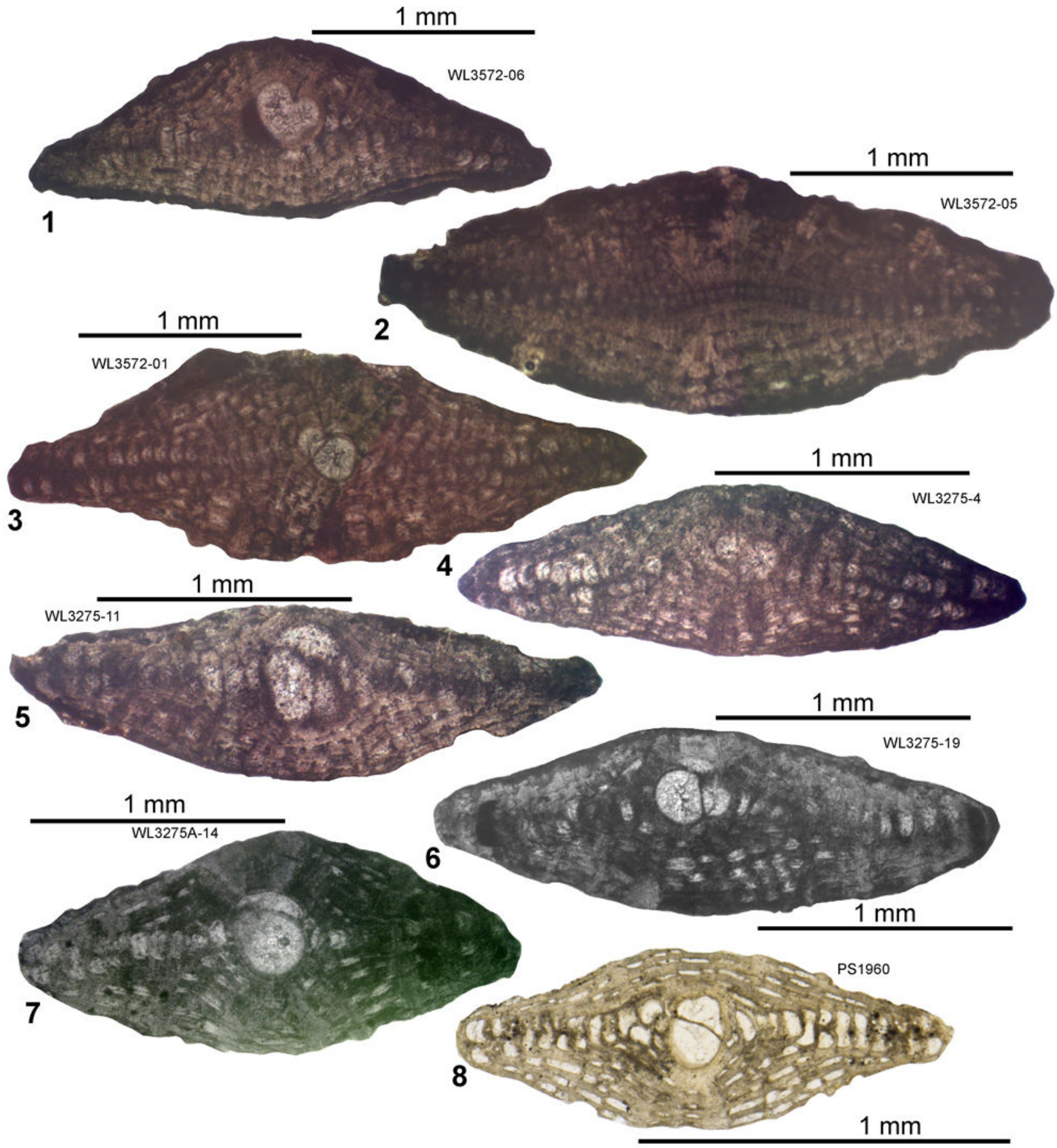


Figure 51: *Pseudolepidina trimera* Barker & Grimsdale, 1937. Axial sections of megalospheric (1, 3-8) and microspheric (2) forms. **1** (UWIGM.WL3572-06), **2** (UWIGM.WL3572-05), **3** (UWIGM.WL3572-01), Yellow Limestone (sample WL3572), Grants Pen (attributed to ABZ7), St Thomas, Jamaica. **4** (UWIGM.WL3275-4), **5** (UWIGM.WL3275-11), **6** (UWIGM.Wl3275-19), **7** (UWIGM.Wl3275A-14), Yellow Limestone, type section of the 'Swanswick' Formation (samples WL3275 and WL3275A), Swanswick House (ABZ7), Trelwany, Jamaica. **8** (BMNH.PS1960), locality with *Eulinderina regularis* and *Eolepidina guayabalensis* (ABZ7), close to the village of Yecuatla, state of Veracruz, Mexico.

orientations in limestone thin sections. There is considerable variation in the embryo and PACs with specimens having one or two PACs when cut in equatorial section; the position of the 'third PAC' (which we regard as part of the embryo) seems variable and it may also be seen in some equatorial sections.

Remarks. The type series of Barker and Grimsdale (1937) came from Jenny station 1573, 11 km SE of Sabaneta, state of Veracruz, Mexico, where it was associated with *H. gyralis* and *Operculinoides jennyi* (Barker & Grimsdale, 1936, 1937; Barker, 1939) and can be assigned to ABZ7. Adams (1987, Pl. 3, figs. 15-16, rephotographed

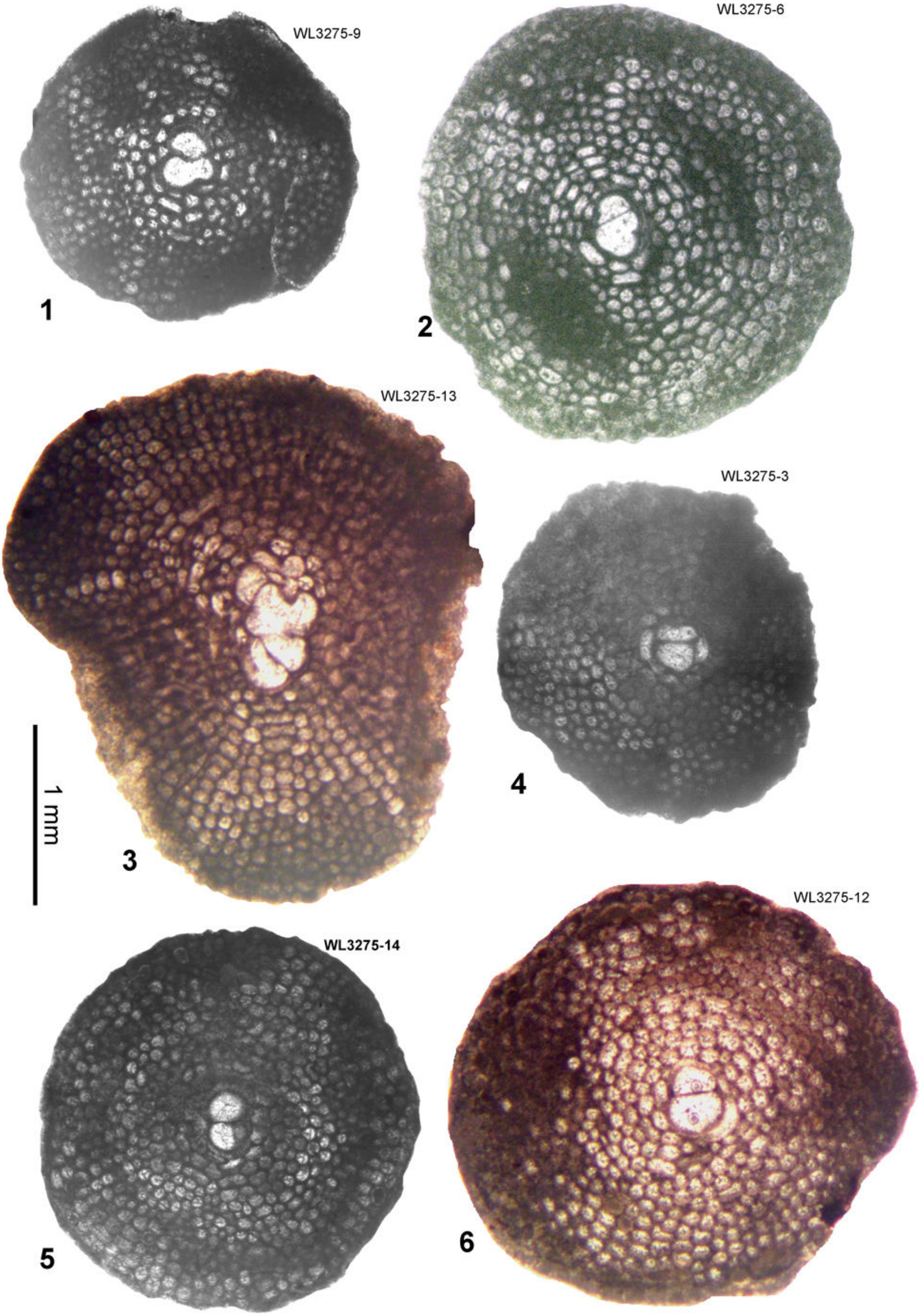


Figure 52: *Pseudolepidina trimera* Barker & Grimsdale, 1937. Megalospheric forms. **1** (UWIGM.WL3275-9), **2** (UWIGM.WL3275-6), **3** (UWIGM.WL3275-13), **4** (UWIGM. WL3275-3), **5** (UWIGM.WL3275-14), **6** (UWIGM.WL3275-12): Yellow Limestone, type section of the 'Swanswick' Formation (sample WL3275), Swanswick House (ABZ7), Trelwany, Jamaica.

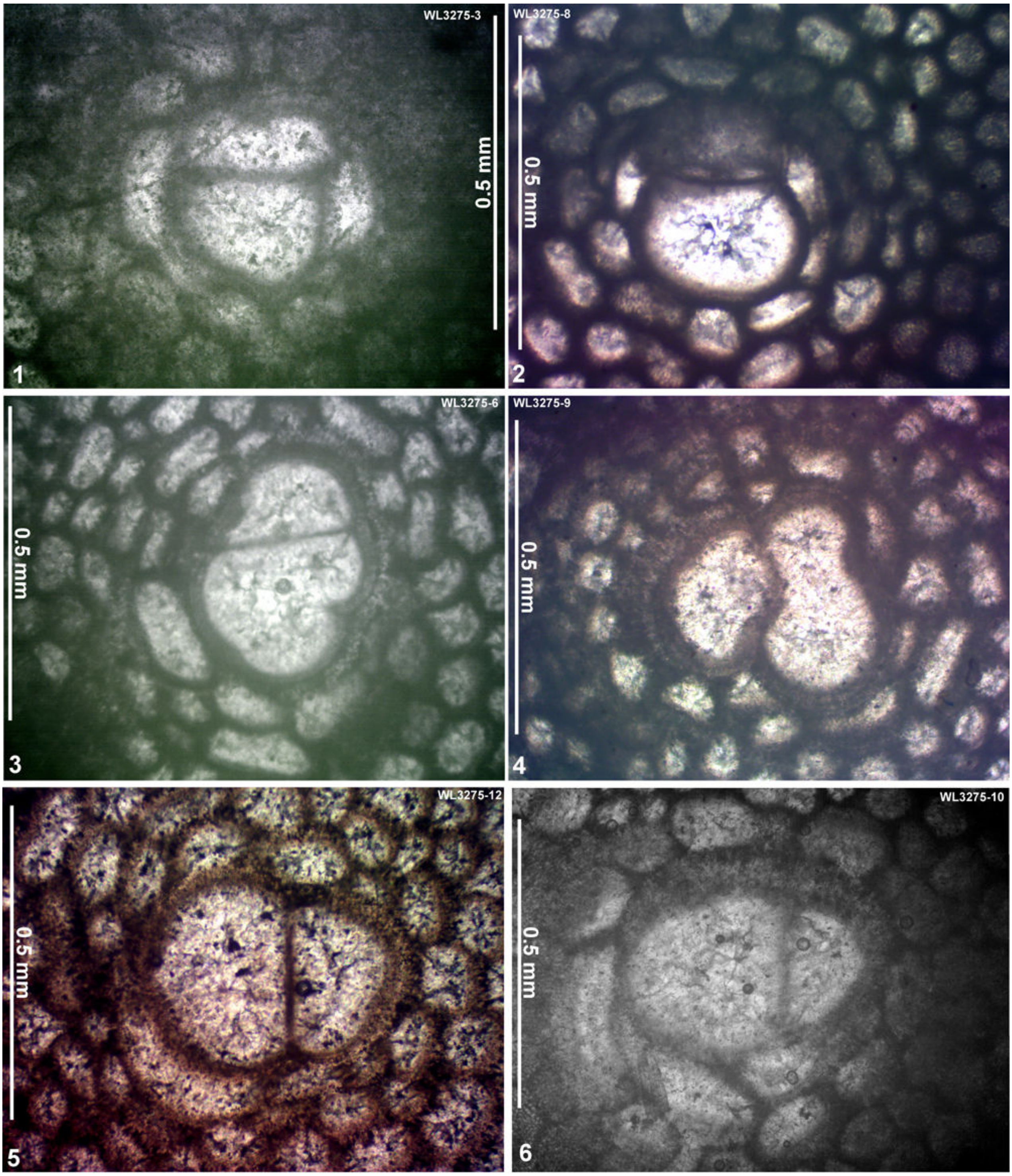


Figure 53: *Pseudolepidina trimera* Barker & Grimsdale, 1937. Embryo in equatorial section (some specimens rotated so that peri-embryonic chambers can be shown). **1** (UWIGM.WL3275-3), specimen with 'two' PACs; **2** (UWIGM.WL3275-8), specimen with 'two'PACS; **3** (UWIGM.WL3275-6), specimen with irregular peri-embryonic chambers); **4** (UWIGM.WL3275-9) specimen with irregular embryo; **5** (UWIGM.WL3275-12), specimen with one large chamber (third PAC?); **6** (UWIGM.WL3275-10), specimen with one? PAC: Yellow Limestone, type section of the 'Swanswick' Formation (sample WL3275), Swanswick House (ABZ7), Trelwany, Jamaica.

in Fig. 54.8 here) figured a specimen from Goldschmidt station 837, close to the village of Yecuatla, state of Veracruz, Mexico, where it was associated with *Eulinderina regularis* and *Eolepidina antillea* (reported as *Eulinderina semiradiata*: Barker & Grimsdale, 1936); this can be assigned to the ABZ7- ABZ8 transition interval. Robinson (2000) recorded *Ps. trimera* from the type Swanswick Formation and from a level in the Chapelton Formation of Jamaica. We have specimens from the type Swanswick Formation at Swanswick House and this can be assigned to ABZ7. The occurrence in the Chapelton Formation needs confirmation, and we would assign this to

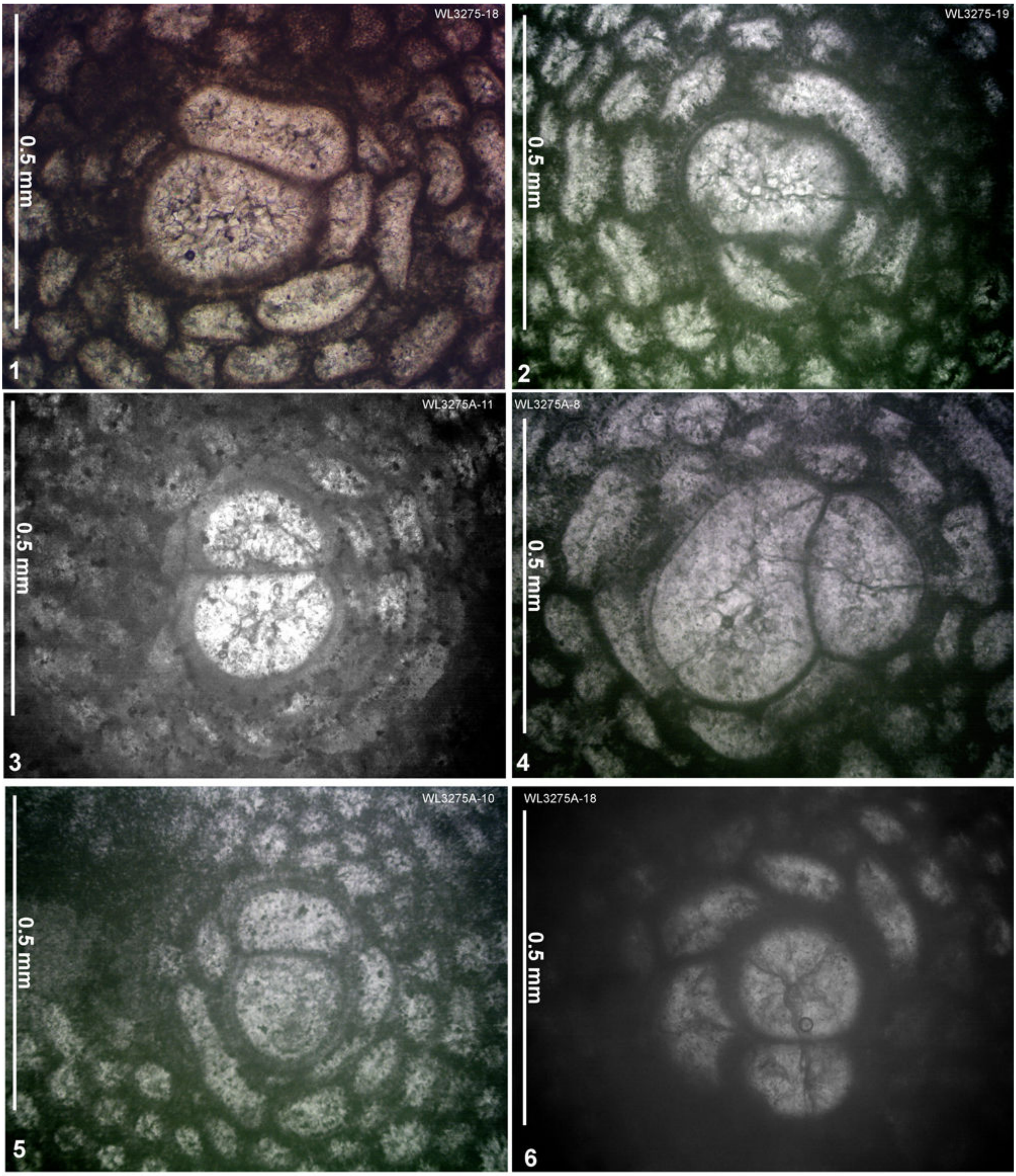


Figure 54: *Pseudolepidina trimera* BARKER & GRIMSDALE, 1937. Embryo in equatorial section (some specimens rotated so that peri-embryonic chambers can be shown). **1** (UWIGM.WL3275-18), specimen with 'two' PACs and irregular spires; **2** (UWIGM.WL3275-19), specimen with irregular embryo; **3** (UWIGM.WL3275A-11), specimen with one? PAC); **4** (UWIGM.WL3275A-8) specimen with irregular embryo and two PACs; **5** (UWIGM.WL3275A-10), specimen with two PACs; **6** (UWIGM.WL3275A-18), *Pseudolepidina* cf. *trimera*, specimen with one PAC and a clear asymmetrical spire developed from it: Yellow Limestone, type section of the 'Swanswick' Formation (samples WL3275 and WL3275A), Swanswick House (ABZ7), Trelwany, Jamaica.

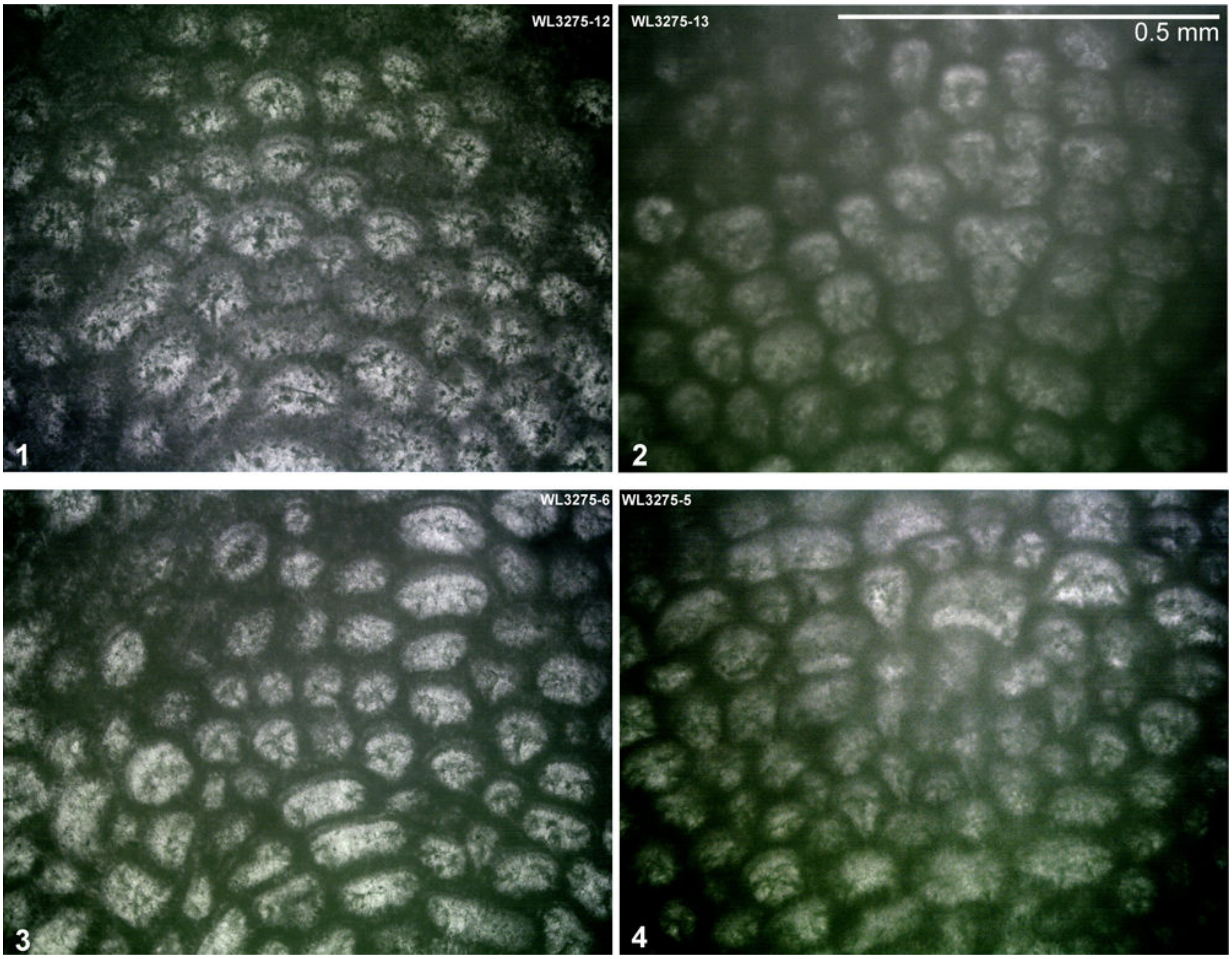


Figure 55: *Pseudolepidina trimera* Barker & Grimsdale, 1937. Equatorial chamberlets shown in equatorial section. **1** (UWIGM.WL3275-12), **2** (UWIGM.WL3275-13), **3** (UWIGM.WL3275-6), **4** (UWIGM.WL3275-5): Yellow Limestone, type section of the 'Swanswick' Formation (sample WL3275), Swanswick House (ABZ7), Trelwany, Jamaica. Chamberlets are broadly arranged in radial rows (at least for short sections) and consist of both wide and narrow forms. Radially, chamberlets get progressively wider until they are replaced by two rows of chamberlets.

the early Bartonian (maybe ABZ12 or ABZ13) - we do not show this occurrence on the stratigraphic chart (Fig. 6) since it needs confirmation.

Family LEPIDOCYCLINIDAE
Scheffen, 1932

Diagnosis. A family developed from a spiral (eulinderine) ancestor without alar prolongations. We recognize two subfamilies (Lepidocyclininae and Orbitoininae subfam. nov.) which each show a progressive reduction in the primary spire from eulinderine to polylepidine to lepidocycline to nephrolepidine or eulepidine. All but the most primitive forms have 'lateral' chamberlets developed.

Remarks. The Lepidocyclinidae show clear and separate radiations of genera that are obvious from the detailed work we have undertaken in Jamaica. This has been suggested previously for the Eocene lepidocyclines (*e.g.*, Grimsdale, 1959; Vlerk, 1959; Sirotti, 1983; Butterlin, 1987), but age relationships between different forms have previously been poorly constrained. From the samples collected from Jamaica we can see two clear radiations, which we place in separate subfamilies: the Lepidocyclininae and Orbitoininae. The largest problem is with homeomorphy, as each radiation gives rise to advanced lepidocycline morphologies which are difficult to distinguish from each other on morphological features (particularly in random thin sections). This classification has the advantage of retaining all lepidocycline-like forms in a single family, but separating them into their separate radiations. Although the orbitoidiform plan has been used to define families or subfamilies previously (*e.g.*, Loeblich & Tappan, 1964, 1988; Adams, 1987; BouDagher-Fadel, 2018), we believe that individual phylogenetic radiations should not be arbitrarily split into subfamilies based on the acquisition of an orbitoidiform growth plan. If such a course was taken, at least four separate subfamilies would be required in the Lepidocyclinidae. We therefore give subfamily status to the two individual evolving clades that show a progressive change from cyclic to orbitoidiform growth.

Each radiation shows a progressive change up section. Early forms have an embryo consisting of a proloculus and a deuteroloculus followed by a short spire of large, peri-embryonic chambers (eulinderine forms) that gives rise to a chamber (R) with a retrovert aperture from which two spires (primary and secondary) of relatively large peri-embryonic chambers emanate. Up section, the position or R progressively decreases until the development of first one PAC (unilepidine) and then two PACs (polylepidine). With one PAC two spirals of peri-embryonic chambers extend around the embryo and meet at a closing chamber. With two PACs three or four, asymmetrical spirals of peri-embryonic chambers extend around the embryo with two closing chambers (EVA, 1980). A true orbitoidiform growth plan (lepidocycline) is achieved when the four spires emanating from the PACs become bilaterally symmetrical about the embryonic (protoconch-deuteroconch) axis. Subsequent development sees additional stolons connecting adauxilary chambers to the protoconch and/or deuteroconch, and a reduction in the size (and consequent increase in number) of the peri-embryonic chambers. Further development sees an increase in the width of the deuteroconch which then partially envelops the protoconch (nephrolepidine to eulepidine forms).

Equatorial chambers and chamberlets can be divided into several types. The first two chambers represent the embryo. In the earliest forms there is only a single stolon connecting the proloculus to the deuteroloculus. Subsequent chambers in the primary spire of early forms have two stolons: a single stolon connecting back to the embryo, or earlier chambers and a single stolon connecting to subsequent chambers. Once an R chamber, one PAC, or two PACs are developed (or for that matter adauxilary chambers), these chambers and any subsequently peri-embryonic chambers have three stolons, one connecting to the chamber that the chamber arises from and two connecting to subsequent chambers/chamberlets (note, that the presence of adauxiliary chambers adds to the numbers of stolons connecting to the protoconch and/or deuteroconch). The closing chamber(s) mark(s) a change to four or six stolons and all subsequent chamberlets after this have either four stolons or six stolons. We define equatorial chambers as those representing the embryo and the peri-embryonic chambers (including any closing chambers) and equatorial chamberlets as those that arise from the peri-embryonic and closing chambers.

There are three broad arrangements of equatorial chamberlets when viewed in equatorial sections. The first has a predominantly radial form and occurs in *Eolepidina* and *Orb. rdouvillei* (similar patterns are seen in *Pseudolepidina*). The second only shows arcs of equatorial chamberlets with neither a prominent radial nor a prominent concentric arrangement of chamberlets and occurs in *Lep. ariana*. The third is characterised by a series of concentric or annular rings of equatorial chamberlets and occurs in *Lep. ocalana*, *Eulepidina chaperi* and *Eulepidina undosa*. These arrangements result from the way that chamberlets are arranged, from the chamberlet shapes and from the distribution of stolons (four versus six) connecting chamberlets. The form of these arrangements is not of generic significance, since they repeatedly occur at similar stages in the development of different lineages.

Subfamily LEPIDOCYCLININAE SCHEFFEN, 1932

The breakdown of the Lepidocyclininae into genera has been demonstrated by ROBINSON & JIANG (1995) and ROBINSON (1996, 1997) and we follow their scheme here, with modifications, recognizing eulinderine (R > 7, no lateral chambers), eolepidine (R > 3, with lateral chambers), unilepidine (R = 3), polylepidine (R = 2), lepidocycline (R = 2) and eulepidine morphologies (Fig. 56). Different stages of development are given generic status and have useful biostratigraphic value. The described genera are somewhat arbitrary and are retained here for historical reasons rather than because they are fully merited. We discuss the use of generic names under each genus below. The proloculus/protoconch and embryo sizes in the Lepidocyclininae gets larger through the Eocene, although there are periods of stasis (Figs. 57 - 59), and the embryo is generally larger than the embryo size of co-occurring populations of the Orbitoininae (other than for *Pliolepidina*).

FROST and LANGENHEIM (1974) synonymised many species in this group (although their figured populations can often be assigned to individual species as recognized here) and their scheme clearly obscures the biostratigraphic value demonstrated by ROBINSON and JIANG (1995) and ROBINSON (1996, 1997). We do not follow FROST and LANGENHEIM's (1974) synonyms here, but develop our own classification of these forms. Many studies are based on random sections in thin sections of rock samples (*e.g.*, ROBINSON & WRIGHT, 1993; SERRA-KIEL *et al.*, 2007); yet many random sections are difficult to place in the evolutionary scheme as understood here and, if possible, workers should try to obtain free specimens to produce orientated sections for better biostratigraphic resolution. An alternative is to cut large numbers of random sections hoping to get some more-or-less equatorial sections by chance. Yet some genera (*e.g.*, *Eulinderina*) and species (*e.g.*, *Lepidocyclina macdonaldi*) are very distinctive in random sections, and provide some useful biostratigraphic resolution.

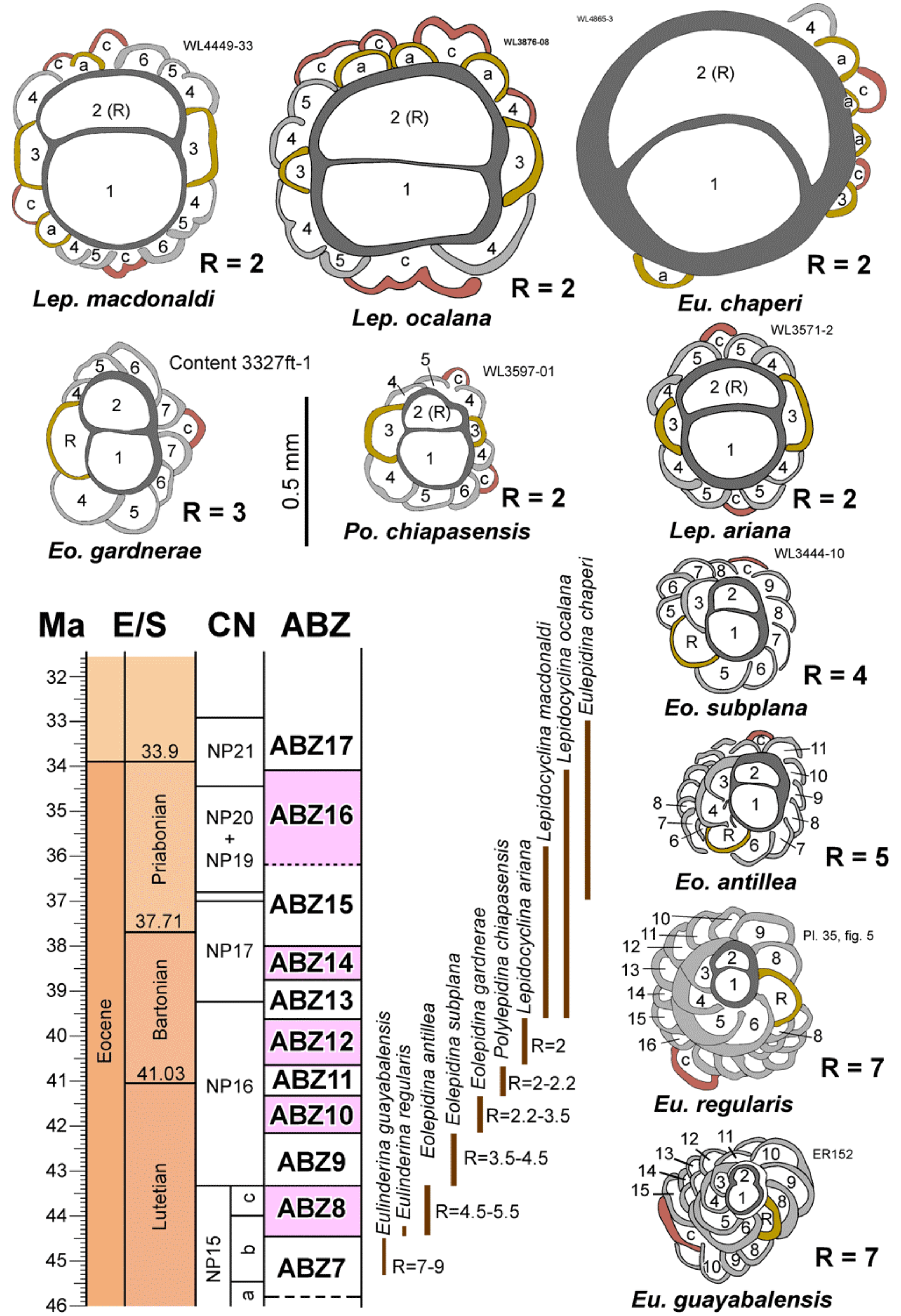


Figure 56: Evolution and stratigraphic distribution of the Lepidocyclininae showing typical equatorial arrangements of chambers for each species.

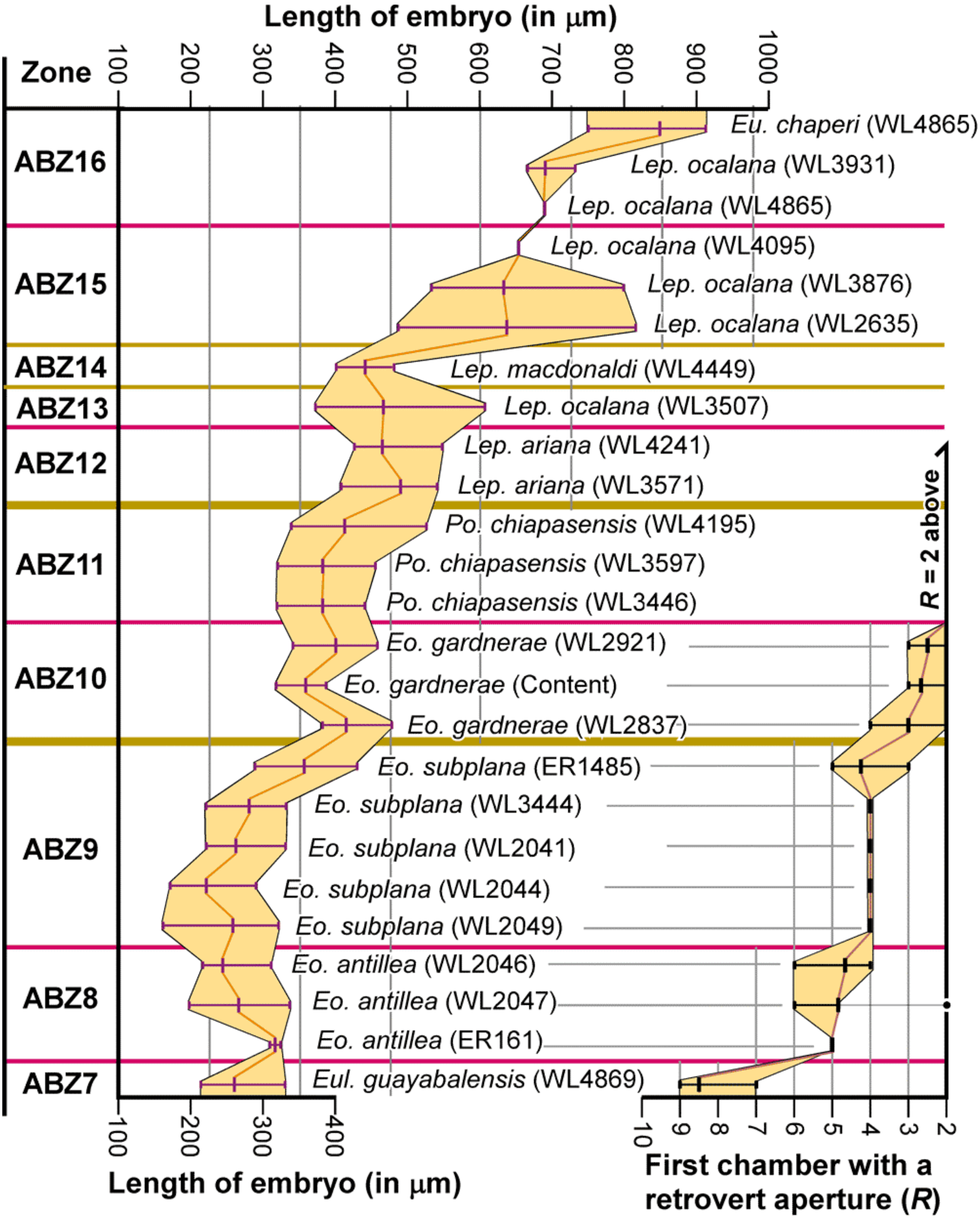


Figure 57: Range in R values and length of embryos (Ele) in populations of Lepidocyclininae from Jamaica (and St Bartholomew). Note periods of stasis in embryo size punctuated by significant changes at the top of ABZ9, ABZ11 and ABZ14 (all of which correspond to sequence boundaries) and within ABZ16 (which is due to the appearance of *Eu. chaperi*).

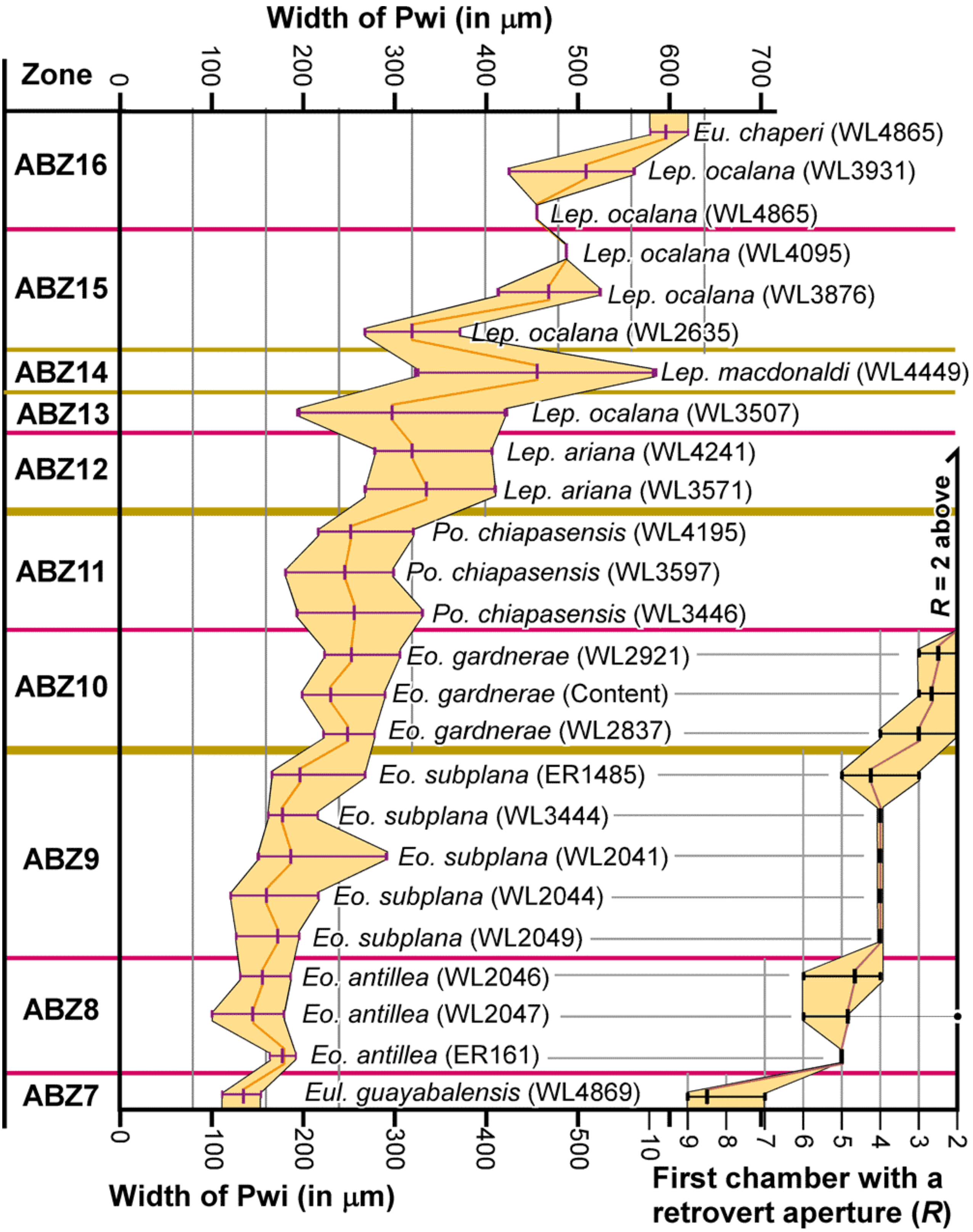


Figure 58: Range in R values and width of proloculus/protoconch (Pwi) in populations of Lepidocyclininae from Jamaica (and St Bartholomew). Note periods of stasis in proloculus/protoconch size punctuated by significant changes at the top of ABZ9, ABZ11 and ABZ14 (all of which correspond to sequence boundaries) and within ABZ16 (which is due to the appearance of *Eu. chaperi*).

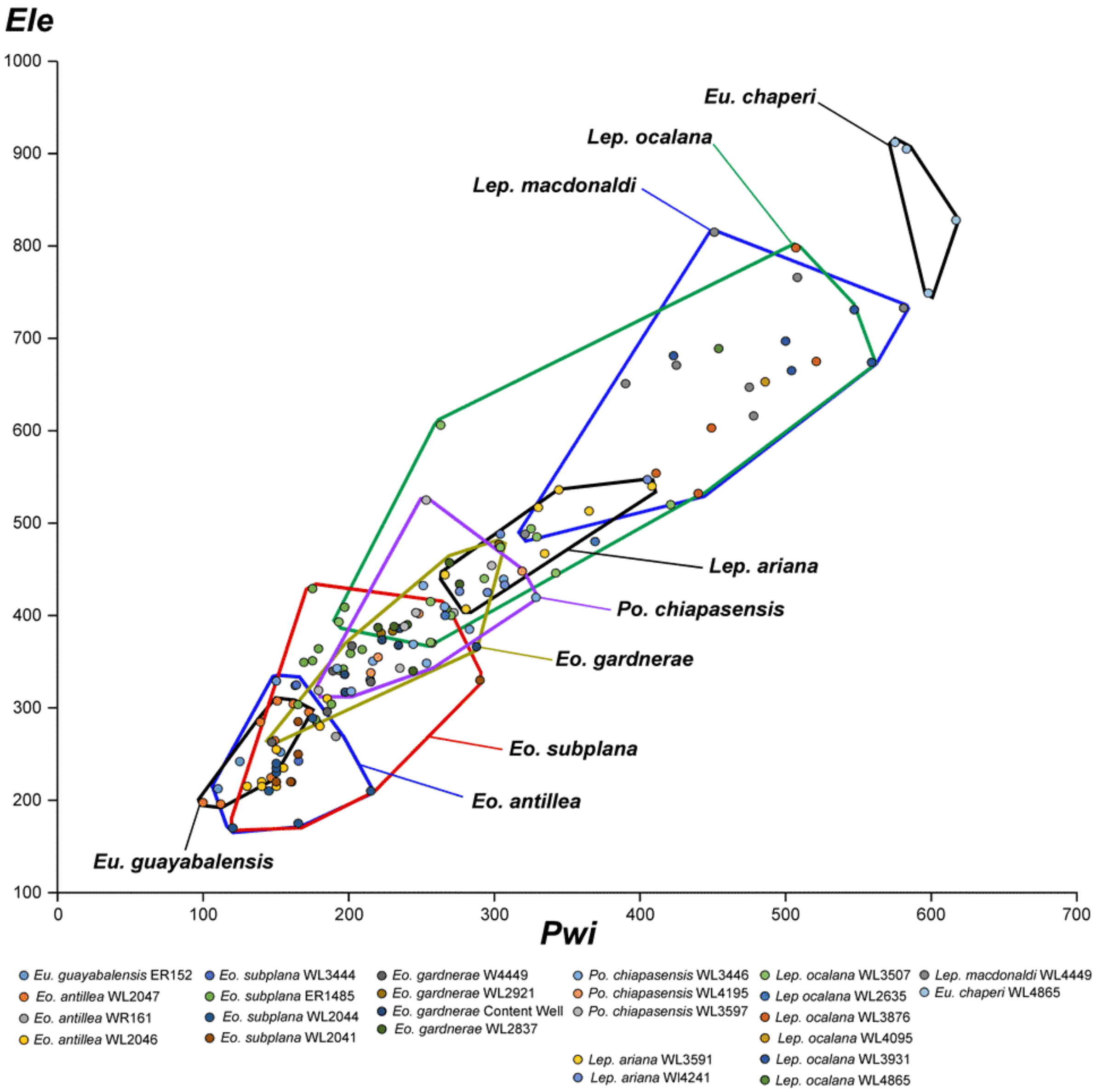


Figure 59: Scatter plot of length of embryo (Ele) versus width of proloculus/protoconch (Pwi) for populations of Lepidocyclininae from Jamaica (and St Bartholomew) with fields for species indicated. Note that there is extensive overlap of the different species fields.

Robinson (1996, 1997) introduced mean R values (Ṝ), being the mean number of chambers (including the protoloculus and deuteroloculus) to the first retrovert chamber in populations of eulinderine and polylepidine forms. He showed that Ṝ values fell within narrow limits within populations, and many additional populations analysed from Jamaica in this work show a similar narrow limit for Ṝ in any one sample. We therefore define limits for mean R size for identifying species here (Table 17). We also provide measurements for the embryo (combined length of the proloculus and deuterolocus or protoconch and deuteroconch, including the thickness of the walls; Ele, Table 18) and width of the proloculus/protoconch excluding walls (Pwi, Table 19) for different species as given in the literature and in measured specimens/populations for Jamaica. The transition from typical four-spired lepidocyclines (*L. ariana*) to lepidocyclines with adauxilary chambers (*L. macdonaldi*, *L. ocalana*), to nephrolepidine-like forms (*Eu. chaperi*) is not straight forward and needs to be investigated in more detail. Other recent papers (*e.g.*, Molina *et al.*, 2015, Pl. 1.5; Hohenegger & Torres Silva, 2020, Fig. 2) confuse isolepidine forms (*L. ocalana*) with adauxilary chambers for nephrolepidine forms (*Eu. chaperi*).

Numerous generic names have been proposed for the Lepidocyclininae, many of which have been synonymised. The names retained here break the lineage(s) up into a series of genera, and the generic names have a long historical usage. Our placement of species into different genera is based on our revised definitions of the genera as indicated below.

Table 17: Criteria for distinguishing species of *Eulinderina*, *Eolepidina* and *Polylepidina* based on mean R values.

Species	Range of mean R values	'Lateral' chamberlets?
Eulinderina guayabalensis (Nuttall)	7 - 9	No
Eulinderina regularis (Barker & Grimsdale)	5.5 - 7	No
Eolepidina antillea (Cushman)	4.5 - 5.5	Yes
Eolepidina subplana (Barker & Grimsdale)	3.5 - 4.5	Yes
Eolepidina gardnerae (Cole)	2.2 - 3.5	Yes
Polylepidina chiapasensis (Vaughan)	2 - 2.2	Yes
Lepidocyclina spp.	2	Yes

Table 18: Measurements of mean R and the length of the nucleoconch (or first two chambers) including the walls for specimens/species of Lepidocyclininae from Jamaica and elsewhere. Measurements include nucleoconch (chamber) walls.

Species	Sample	Ṝ	Zone	Length of nucleus (µm)				Source
				range	mean	SD	n	
Eu. guayabalensis	Mexico	7 - 9	ABZ7	160 - 230	-	-	-	B & G, 1936
Eu. guayabalensis	ER152/WL4869	8.25	ABZ7	242 - 332	269	51.0	4	Our measurements
Eu. regularis	Mexico	6 - 7	ABZ7/6	220 - 260	-	-	-	B & G, 1936
Eo. 'semiradiata'	Mexico	3 - 5	ABZ7/6	330 - 430	-	-	-	B & G, 1936
Eo. antillea	WL2047A	5	ABZ8	196 - 307	262	44.6	9	Our measurements
Eo. antillea	ER161	5	ABZ8	308 - 323	316	21.3	2	Our measurements
Eo. antillea	WL2046	4.7	ABZ8	215 - 310	243	33.5	9	Our measurements
Eo. subplana	WL3444	4	ABZ9	220 - 300	279	56.6	4	Our measurements
Eo. subplana	ER1485	3.82 (11)	ABZ9	304 - 429	371	38.8	9	Our measurements
Eo. subplana	WL2044	4	ABZ9	170 - 289	220	38.2	8	Our measurements
Eo. gardnerae	WL4449 †	3 †	ABZ14	263 - 367	319	40.3	5	Our measurements
Eo. gardnerae	WL2921	3	ABZ10	381 - 477	414	54.9	3	Our measurements
Eo. gardnerae	Content Well	2.7	ABZ10	317 - 386	358	25.9	6	Our measurements
Eo. gardnerae	WL2837	2.5	ABZ10	340 - 457	399	41.0	6	Our measurements
Po. chiapasensis	WL3446	2	ABZ11	318 - 439	381	42.1	10	Our measurements
Po. chiapasensis	WL4195	2	ABZ11	338 - 525	412	67.8	6	Our measurements
Po. chiapasensis	WL3597	2	ABZ11	319 - 454	381	52.8	5	Our measurements
Lep. ariana	WL3571	2	ABZ12	371 - 463	422	41.9	5	Our measurements
Lep. ariana	WL4241	2	ABZ12	425 - 547	464	53.4	5	Our measurements
Lep. ariana	Margarita	2	ABZ12	385 - 605	449	77.4	8	*Butterlin, 1970
Lep ocalana	WL2635	2	ABZ13	479	-	-	1	Our measurements
Lep. ocalana	WL3507	2	ABZ13	371 - 606	459	67.5	11	Our measurements
Lep. ocalana	WL3876/3876A	2	ABZ15	532 - 798	632	107.6	5	Our measurements
L. montgomeriensis	Moodys Branch	2	ABZ15	433 - 833	-	-	-	G & H, 1935
Lep. macdonaldi	WL4449	2	ABZ15	488 - 766	660	124.1	4	Our measurements
Lep. macdonaldi	Jamaica	2		520 - 720	620	-	3	*Cole, 1956
Lep. ocalana	WL4095	2	ABZ15	673	-	-	1	Our measurements
Lep. ocalana	WL3931	2	ABZ16	665 - 731	690	25.9	5	Our measurements
Eulepidina chaperi	WL4865	2	ABZ16	749 - 912	849	76.5	4	Our measurements

* specimens measured from illustrations in publications (which is dependent on accuracy of plate reproduction when only magnifications were given). † specimens regarded as reworked. B & G, 1936 = Barker & Grimsdale, 1936; G & H, 1935 = Gravell & Hanna, 1935.

Genera included. *Eulinderina* Barker & Grimsdale, 1936; *Eolepidina* Tan, 1939; *Polylepidina* Vaughan, 1924; *Lepidocyclina* Gümbel, 1868; *Eulepidina* Douvillé, 1911.

Genus *Eulinderina*
Barker & Grimsdale, 1936

Diagnosis. Lepidocyclininid with a primary spire comprising six or more chambers before the first retrovert chamber (*i.e.*, the chamber that gives rise to two separate spires); lateral chamberlets absent.

Remarks. We formally define limits of Ṝ for the two species of *Eulinderina* here for use for biostratigraphic purposes (Table 17). The two taxa assigned to *Eulinderina*, *Eu. guayabalensis* (Nuttall, 1930) (Ṝ = 7 - 9) and *Eu. regularis* Barker & Grimsdale, 1936 (Ṝ = 5.5 - 7), appear to be rare outside of Mexico and are not currently incorporated into the zonation. It is likely that the Lepidocyclininae initially evolved in Mexico (close to where Jamaica was situated at the time: Pindell, 2009; Mitchell, 2020) during the Lutetian and subsequently spread across the American LBF bioprovince.

Table 19: Measurements of mean R and the width of the proloculus/protoconch (Pwi) excluding the walls for specimens/species of Lepidocyclininae from Jamaica and elsewhere. Measurements include nucleoconch (chamber) walls.

Species	Sample	$\bar{R}$	Zone	Width of Proloculus/Protoconch (µm)				Source
				range	mean	SD	n	
Eu. guayabalensis	Mexico	7 - 9	ABZ7	85 - 115	-	-	-	B & G, 1936
Eu. guayabalensis	ER152/WL4869	8.25	ABZ7	212 - 329	259	49.7	4	Our measurements
Eu. regularis	Mexico	6 - 7	ABZ7/6	120	-	-	-	B & G, 1936
Eo. 'semiradiata'	Mexico	3 - 5	ABZ7/6	180 - 220	-	-	-	B & G, 1936
Eo. antillea	WL2047	5	ABZ8	196 - 307	262	44.6	9	Our measurements
Eo. antillea	ER161	5	ABZ8	269 - 324	297	38.9	2	Our measurements
Eo. antillea	WL2046	4.7	ABZ8	215 - 310	246	34.6	8	Our measurements
Eo. subplana	WL3444	4	ABZ9	220 - 330	279	56.6	4	Our measurements
Eo. subplana	ER1485	3.82	ABZ9	288 - 429	356	40.9	14	Our measurements
Eo. subplana	WL2044	4	ABZ9	170 - 289	220	38.2	8	Our measurements
Eo. gardnerae	WL4449 †	3	ABZ14	263 - 367	319	40.3	5	Our measurements
Eo. gardnerae	WL2921	3	ABZ10	381 - 477	414	54.9	3	Our measurements
Eo. gardnerae	Content Well	2.7	ABZ10	317 - 386	358	25.9	6	Our measurements
Eo. gardnerae	WL2837	2.5	ABZ10	340 - 457	399	41.0	6	Our measurements
Po. chiapasensis	WL3446	2	ABZ11	318 - 439	381	42.1	10	Our measurements
Po. chiapasensis	WL4195	2	ABZ11	338 - 525	412	67.8	6	Our measurements
Po. chiapasensis	WL3597	2	ABZ11	319 - 454	381	52.8	5	Our measurements
Lep. ariana	WL3571	2	ABZ12	407 - 540	489	50.7	7	Our measurements
Lep. ariana	WL4241	2	ABZ12	425 - 547	464	53.4	5	Our measurements
Lep ocalana	WL2635	2	ABZ13	400 - 480	440	56.6	2	Our measurements
Lep. ocalana	WL3507	2	ABZ13	371 - 606	459	67.5	11	Our measurements
Lep. ocalana	WL3876/3876A	2	ABZ15	532 - 798	632	107.6	5	Our measurements
Lep. macdonaldi	WL4449	2	ABZ15	488 - 815	673	100.7	8	Our measurements
Lep. ocalana	WL4095	2	ABZ15	-	653	-	1	Our measurements
Lep. ocalana	WL3931	2	ABZ16	665 - 731	690	25.9	5	Our measurements
Lep. ocalana	WL4865	2	ABZ16	-	689	-	1	Our measurements
Eulepidina chaperi	WL4865	2	ABZ16	749 - 912	849	76.5	4	Our measurements

Eulinderina guayabalensis

(Nuttall, 1930)

(Figs. 60, 61.1-5)

Previous descriptions. Barker & Grimsdale, 1936, p. 238, Pl. 32, figs. 8-9; Pl. 34, figs. 8, 10-11.

Recognition. *Eu. guayabalensis* is recognised by its long primary spire before the development of a retrovert aperture, and also by its lack of lateral chamberlets and a laminate shell seen in axial section.

Remarks. *Eu. guayabalensis* appears to be rare outside of Mexico. We have several specimens from the Preston Hill Formation (samples ER152 and WL4869) from Grants Town (St Mary, Jamaica) with R values of 7 and 9 (mean = 8.5, n = 4). Barker and Grimsdale (1936) give the length of the embryo of *Eu. guayabalensis* as 160-230 µm, which is notably smaller than specimens of this species from Jamaica that have an embryo with a length of 212-329 µm. The age of the material described by Barker and Grimsdale (1936) is difficult to assign to our biostratigraphic zonation because they did not list associated species (particularly nummulitids); it could be that their material was from ABZ6 rather than ABZ7, but this will have to await studies of topotype material. Samples ER152 and WL4869, both from the Preston Hill Formation at Grants Town, yield *Eu. guayabalensis* in association with *Operculinoides* and orthophragmines (Robinson & Mitchell, 1999, p. 35; herein) and are assigned to ABZ7 and NP15b. For the present, we assume that *Eu. guayabalensis* is likely restricted to ABZ7.

Eulinderina regularis

Barker & Grimsdale, 1936

(Fig. 61.6-9)

Previous descriptions. Barker & Grimsdale, 1936, p. 238, Pl. 30, figs. 7, 9; Pl. 32, figs. 10-11; Pl. 35, figs. 4-5; Pl. 37, fig. 5.

Recognition. *Eu. regularis* is recognised by its shorter primary spire before the development of a retrovert aperture, and also by its lack of lateral chamberlets and a compact shell seen in axial section.

Remarks. Barker and Grimsdale (1936) recorded *Eu. regularis* (their *Eu. guayabalensis* var. *regularis*) from the same locality as *Eolepidina semiradiata* (= *Eolepidina antillea*); this suggests that this locality (assuming the material was from the same sample, rather than locality) contains an assemblage of specimens at the transition between *Eulinderina* and *Eolepidina*. We have not

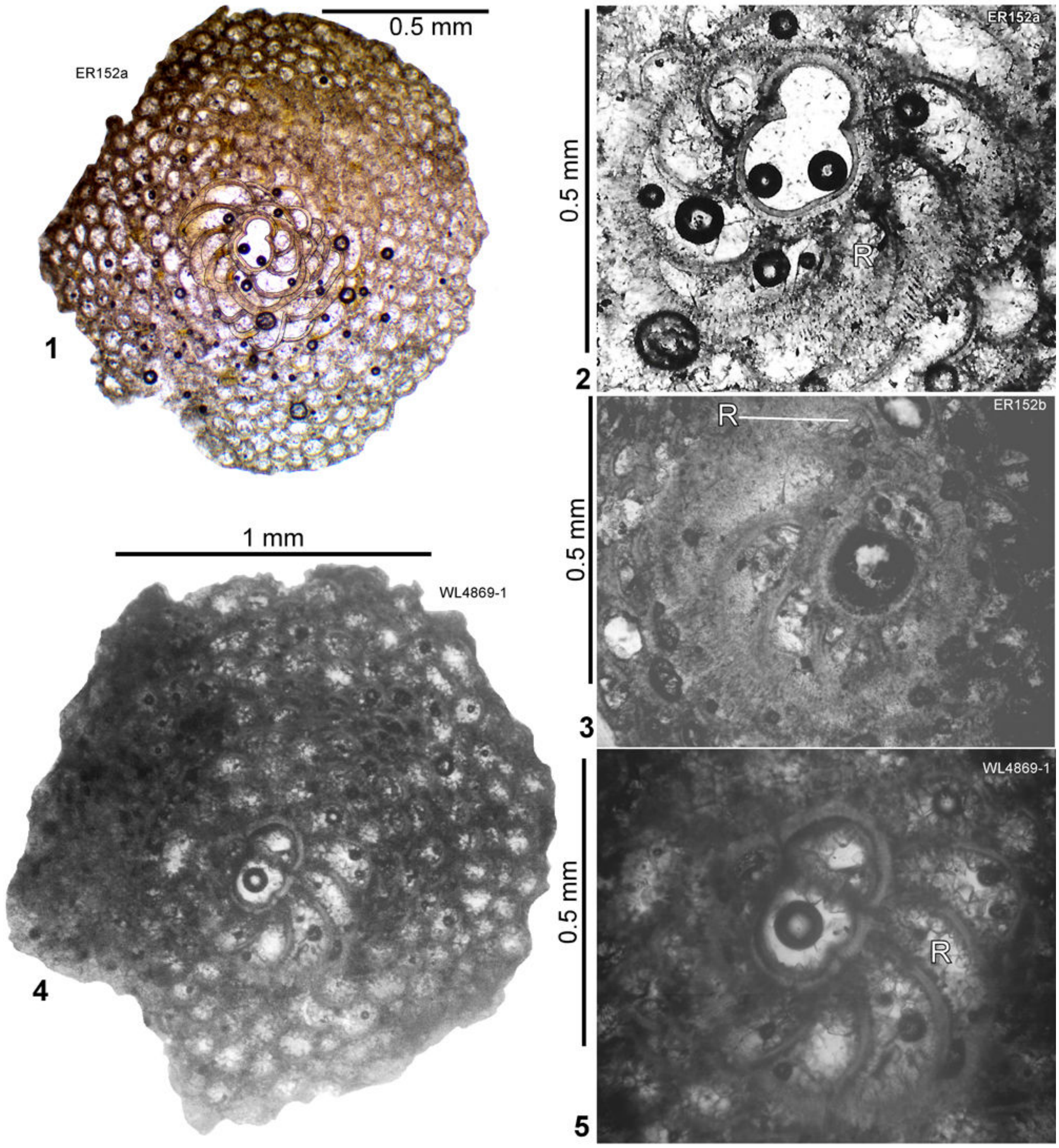


Figure 60: A-B, *Eulinderina guayabalensis* (Nuttall, 1930), megalospheric forms. **1-2** (ER152a), equatorial section (R = 7). **3** (ER152b), equatorial section (R = 9). **4-5** (WL4869-1), equatorial section (R = 9). Preston Hill Formation (samples ER152 and WL4869), Grants Town, parish of St Mary, Jamaica.

recorded *Eu. regularis* from Jamaica. In Mexico, its occurrence with *Eolepidina antillea* (reported as *Eu. semiradiata*) and *Ps. trimera* (Barker & Grimsdale, 1936; Adams, 1987) indicates it occurs around the ABZ7 to ABZ8 transition.

Genus *Eolepidina* Tan, 1939

Type species. *Eulinderina semiradiata* Barker & Grimsdale, 1936 (junior synonym of *Lepidocyclina antillea* Cushman, 1919) from the Lutetian, close to the village of Yecuatla, state of Veracruz, Mexico (Barker & Grimsdale, 1936).

Diagnosis. A Lepidocyclininae with a short primary spire of equatorial chambers (from 3 to 6), none or one PAC, and vacuole-like lateral chambers.

Discussion. *Eolepidina* is distinguished from *Eulinderina* by the presence of lateral chamberlets. The type locality of *Eo. semiradiata* (= *Eo. antillea*) appears to show specimens in transition between *Eulinderina* and *Eolepidina*. Because the presence or absence of lateral chamberlets is easily determined in random sections (as seen in thin sections of rock samples), the separation of the two genera is certainly warranted for biostratigraphic purposes.

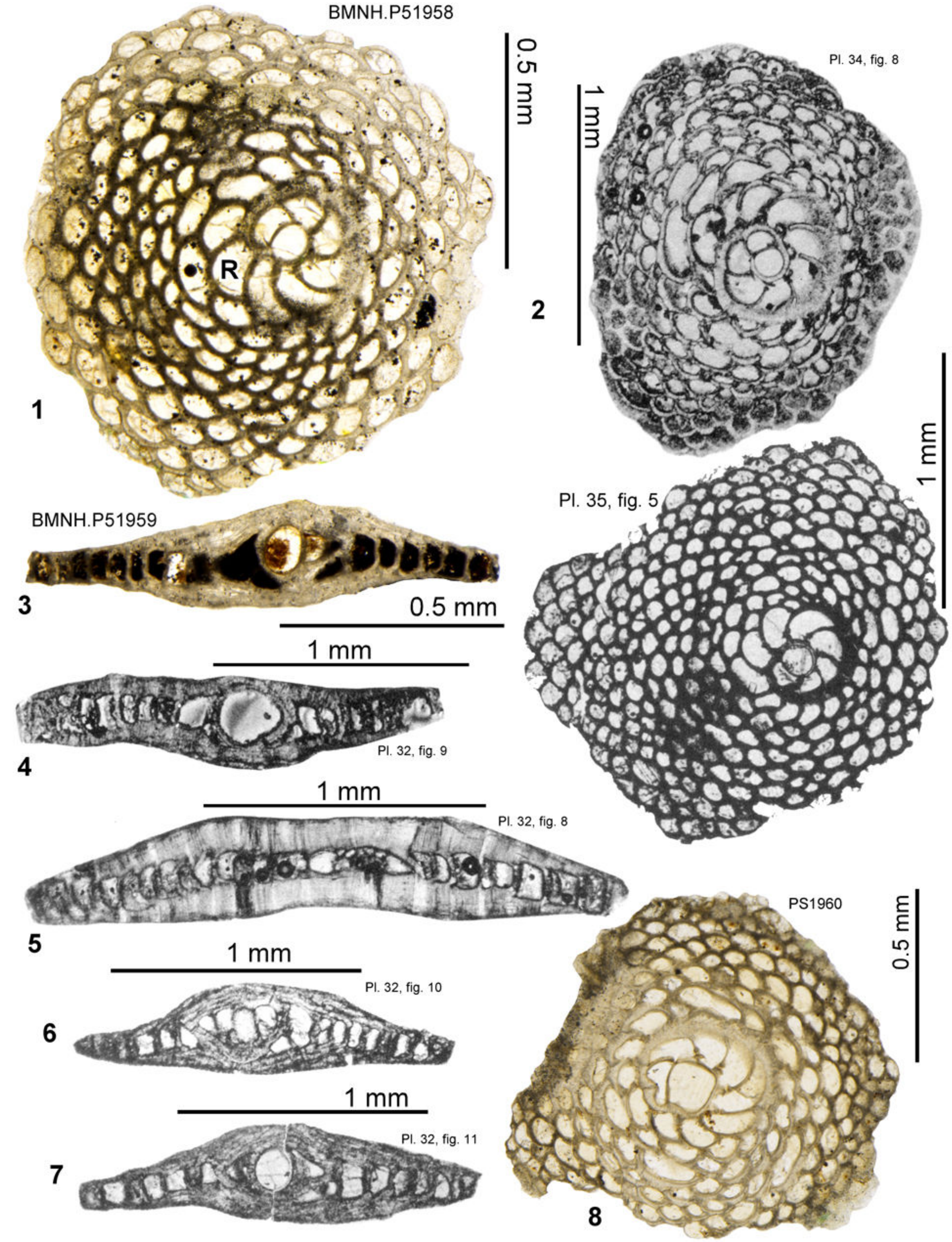


Figure 61: 1-5 *Eulinderina guayabalensis* (Nuttall, 1930) and 58.6-8 *Eulinderina regularis* Barker & Grimsdale, 1936. **1** (topotype: BMNH.P51958), megalospheric specimen, equatorial section (R = 8). **2** (reproduction of original specimen of Barker & Grimsdale, 1936, Pl. 34, fig. 8) equatorial section (R = 9), **3** (BMNH.P51959), megalospheric specimen, axial section (note absence of lateral chambers). **4** (reproduction of original specimen of Barker & Grimsdale, 1936, Pl. 32, fig. 9), axial section of megalospheric form. **5** (reproduction of original specimen of Barker & Grimsdale, 1936, Pl. 32, fig. 8), axial section of microspheric form. **6 -7** (reproduction of original specimen of Barker & Grimsdale, 1936, Pl. 35, figs. 10-11), axial sections of megalospheric specimens. **8** (topotype: BMNH.PS1960), equatorial section (R = 8). **1-5**, close to the village of Yecuatla, state of Veracruz, Mexico. **6-8**, Mexican Eagle Oil Company Well No. 5 (4,590 ft depth), Mexico. **5**, Union Oil Company Miahuapan No. 3-A well (3,100 to 4,100 ft depth), Mexico.

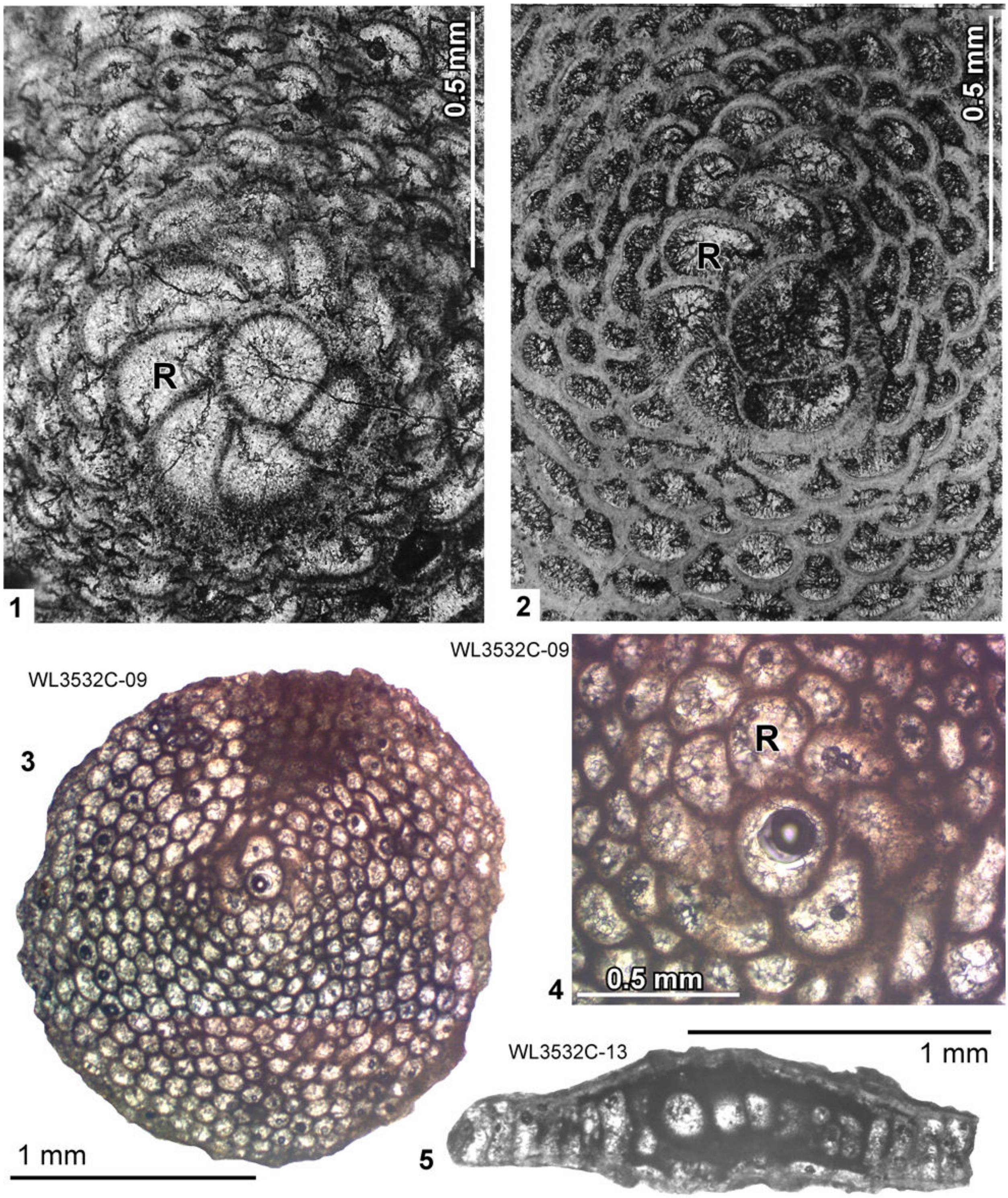


Figure 62: *Eolepidina antillea* (CUSHMAN, 1919). **1** (unfigured specimen from COLE, 1960), equatorial section. **2** (original of COLE, 1960, Pl. 13, fig. 5, figured as *Lepidocyclina* (*Polylepidina*) *antillea* CUSHMAN), equatorial section. **3** (UWIGM.WL3532C-09), equatorial section. **4** (UWIGM.WL3532C-09), detail of equatorial section showing primary spire with R = 5. **5** (UWIGM.WL3532C-13), axial section (note presence of irregular lateral chamberlets. A-B, Saint Bartholomew. C-E, Preston Hill Formation, Bamboo, parish of St Ann, Jamaica.

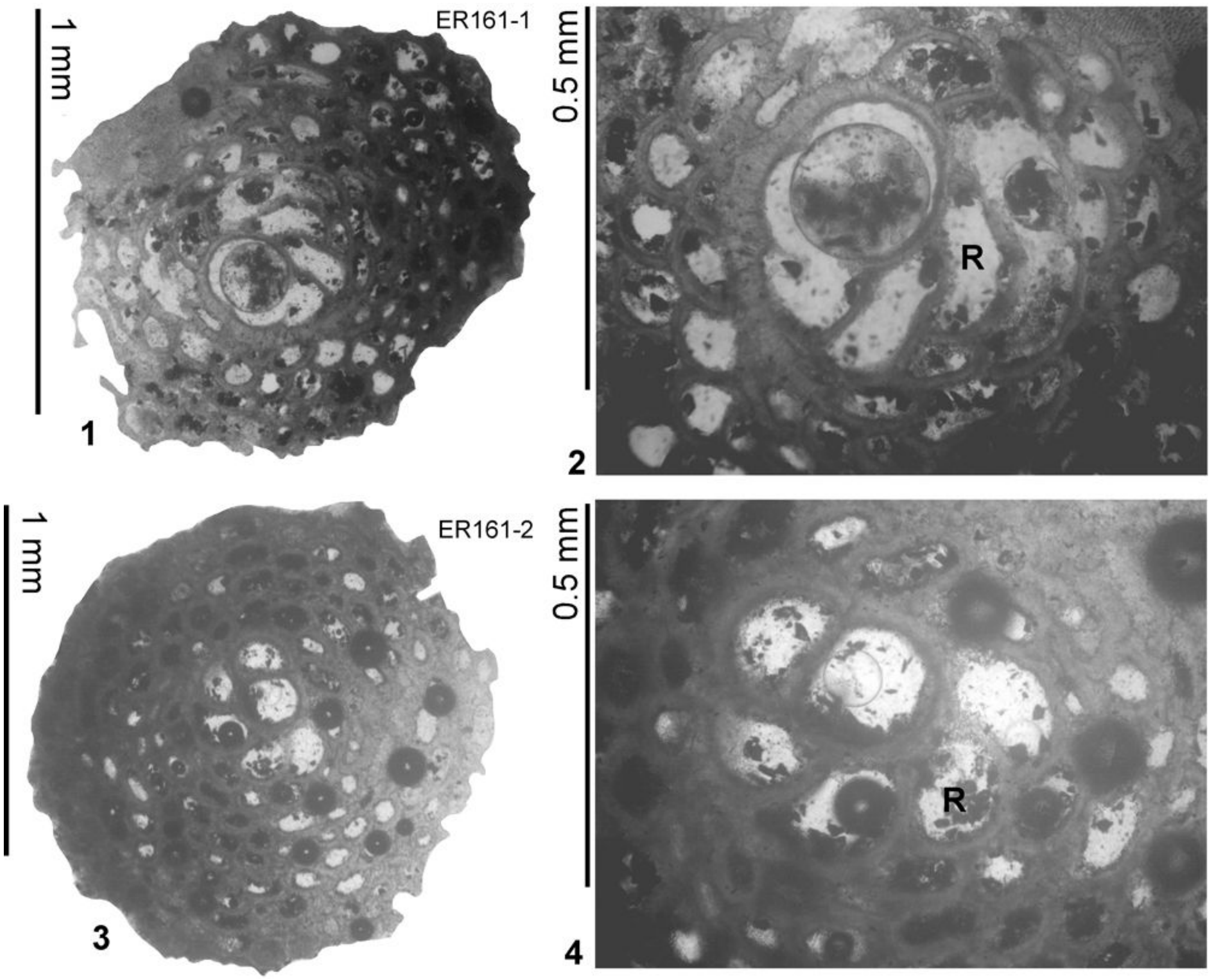


Figure 63: *Eolepidina antillea* (CUSHMAN, 1919). **1-2** (UWIGM.ER161-1), equatorial sections. **3-4** (UWIGM. ER161-2), equatorial sections. Sample ER161, stratotype of the Preston Hill Formation (which disappeared due to a landslide), Preston Hill, parish of St Mary, Jamaica.

We recognize three species of *Eolepidina*: *Eo. antillea*, *Eo. subplana* and *Eo. gardnerae*. The last species has one PAC and has been placed in *Polylepidina* by some workers (*e.g.*, COLE, 1929). We define *Polylepidina* as containing two PACs with three or four asymmetric spires of peri-embryonic chambers, which leads us to place the species *gardnerae* in the genus *Eolepidina*.

Eolepidina antillea (CUSHMAN, 1919)

(Figs. 62 - 66)

Previous descriptions and figures. COLE, 1960, Pl. 11, figs. 6, 13; Pl. 12, figs. 1-8.

Remarks. *Eo. antillea* has an ornament consisting of scattered pustules, and we define that $\bar{R}$ = 5.5 - 4.5. The secondary spire of chambers developed from the first retrovert chamber is often short with small chambers and contrasts with the primary spire developed from the first retrovert chamber which is long with larger chambers. We follow the revision of *Eo. antillea* as proposed by COLE (1960) and ROBINSON (1996). We synonymise *Eulinderina semiradiata* BARKER & GRIMSDALE, 1936 with *Eo. antillea* here. *Eo. antillea* occurs in the Preston Hill Formation in the North Coast Belt and northern Wag Water Belt in Jamaica, where it is associated with *Operculinoides* and small *Nummulites*. It is the nominate taxon for ABZ8. At the type locality in St Bartholomew (recollected as samples ER1524-ER1526), *Eo. antillea* occurs with *Fallotella* cf. *cookie*.

Some specimens show a thick spiral wall which extends up to the chamber before the chamber with the first retrovert aperture (*e.g.*, Fig. 66.2). Other specimens (*e.g.*, Fig. 66.3-4) lack a thickened spiral wall, but occur with specimens which have a thickened spiral wall. Further work is needed to determine if these are separate morphospecies, or simply variants of a single morphospecies.

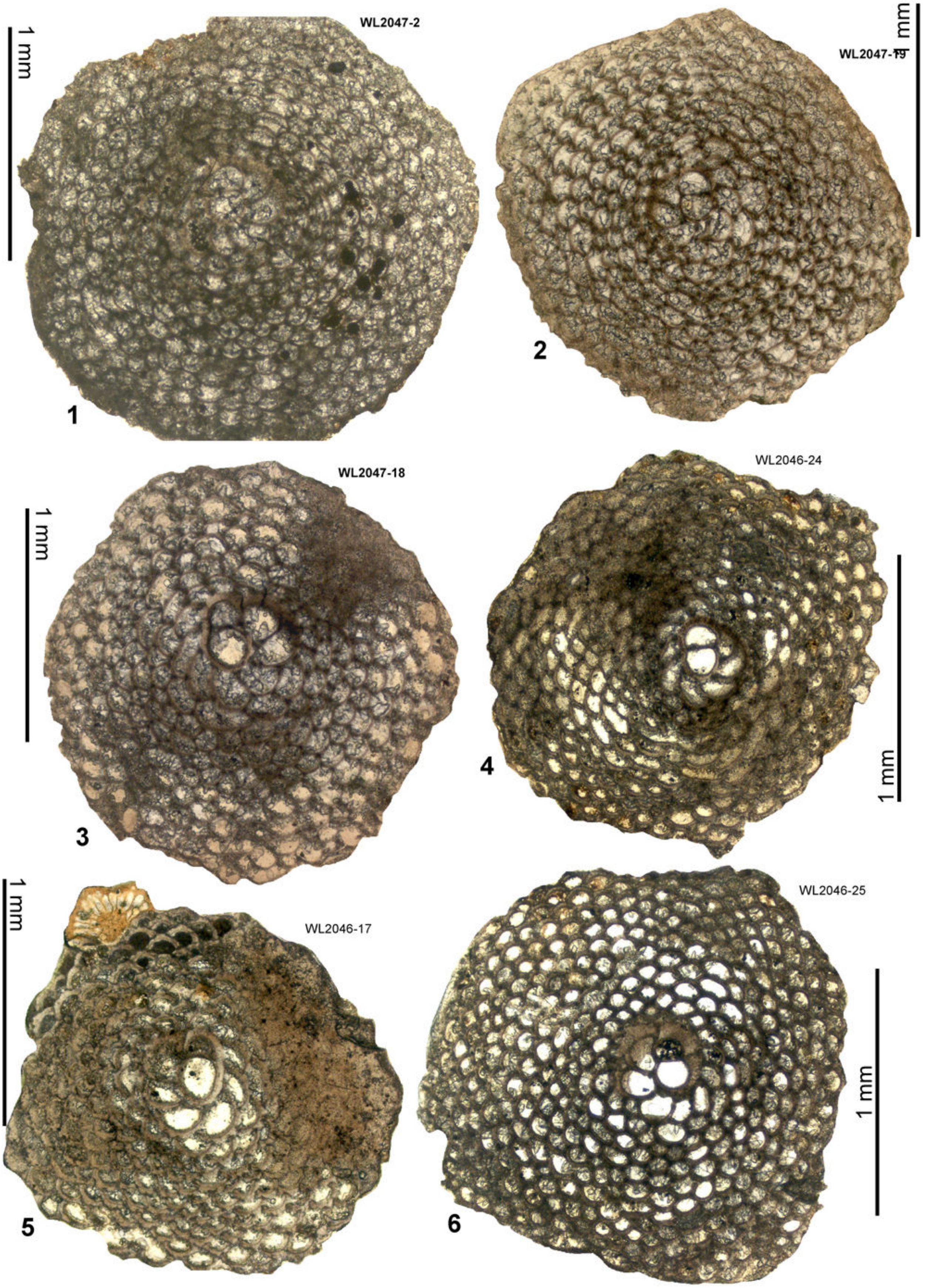


Figure 64: *Eolepidina antillea* (CUSHMAN, 1919), equatorial sections, megalospheric forms. **1** (EO.WL2047-2), R = 5. **2** (EO.WL2047-19), R = 5. **3** (EO.WL2047-18), R = 5. **4** (EO.WL2046-24), R = 5. **5** (EO.WL2046-17) R = 5. **6** (EO. WL2046-25), R = 5. Note differences in preservation between the two samples. Samples WL2046 and WL2047, Preston Hill Formation (ABZ8), Lilyfield, St Ann, Jamaica.

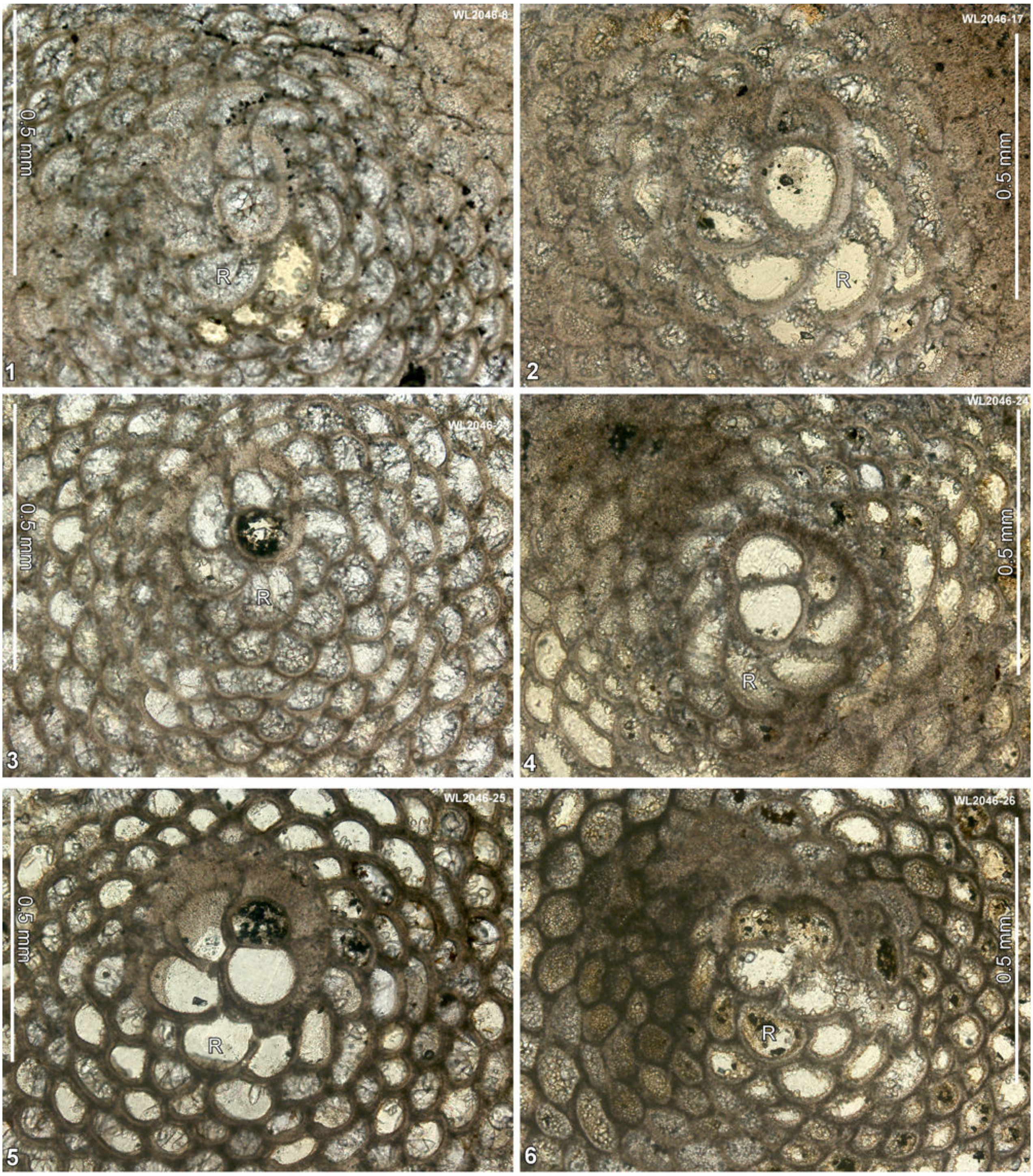


Figure 65: *Eolepidina antillea* (Cushman, 1919), details of equatorial sections, megalospheric forms. **1** (EO.WL2046-8), R = 5. **2** (EO.WL2046-17), R = 5. **3** (EO.WL2046-23), R = 5. **4** (EO.WL2046-24), R = 6. **5** (EO.WL2046-25), R = 5. **6** (EO.WL2046-26), R = 5. Sample WL2046, Preston Hill Formation (ABZ8), Lilyfield, St Ann, Jamaica.

Eolepidina subplana
(Barker & Grimsdale, 1936)
(Figs. 67 - 70)

Previous descriptions. Barker & Grimsdale, 1936, p. 241, Pl. 31, figs. 1-2; Pl. 32, figs. 12-13; Pl. 33, fig. 8; Pl. 35, fig. 6; Pl. 37, fig. 2.

Recognition. *Eo. subplana* is recognized by its low, lenticular test with lateral chambers and a primary spire consisting of typically 4 chambers. We place populations with R̄ = 4.5 - 3.5 in *Eo. subplana*.

Remarks. The ornament of *Eo. subplana* is variable. Some forms have an ornament consisting of regular pustules that extend across the entire surface, whereas other forms (Chapelton Formation at Lilyfield) have an ornament that consists of a central crown of pustules with radiating furrows in the marginal zone. These ornament types are also seen in *Eo. antillea*. *Eo. subplana* is the nominate species for ABZ9. The species has been recorded from Mexico (Veracruz), Jamaica, Florida, and St Bartholomew.

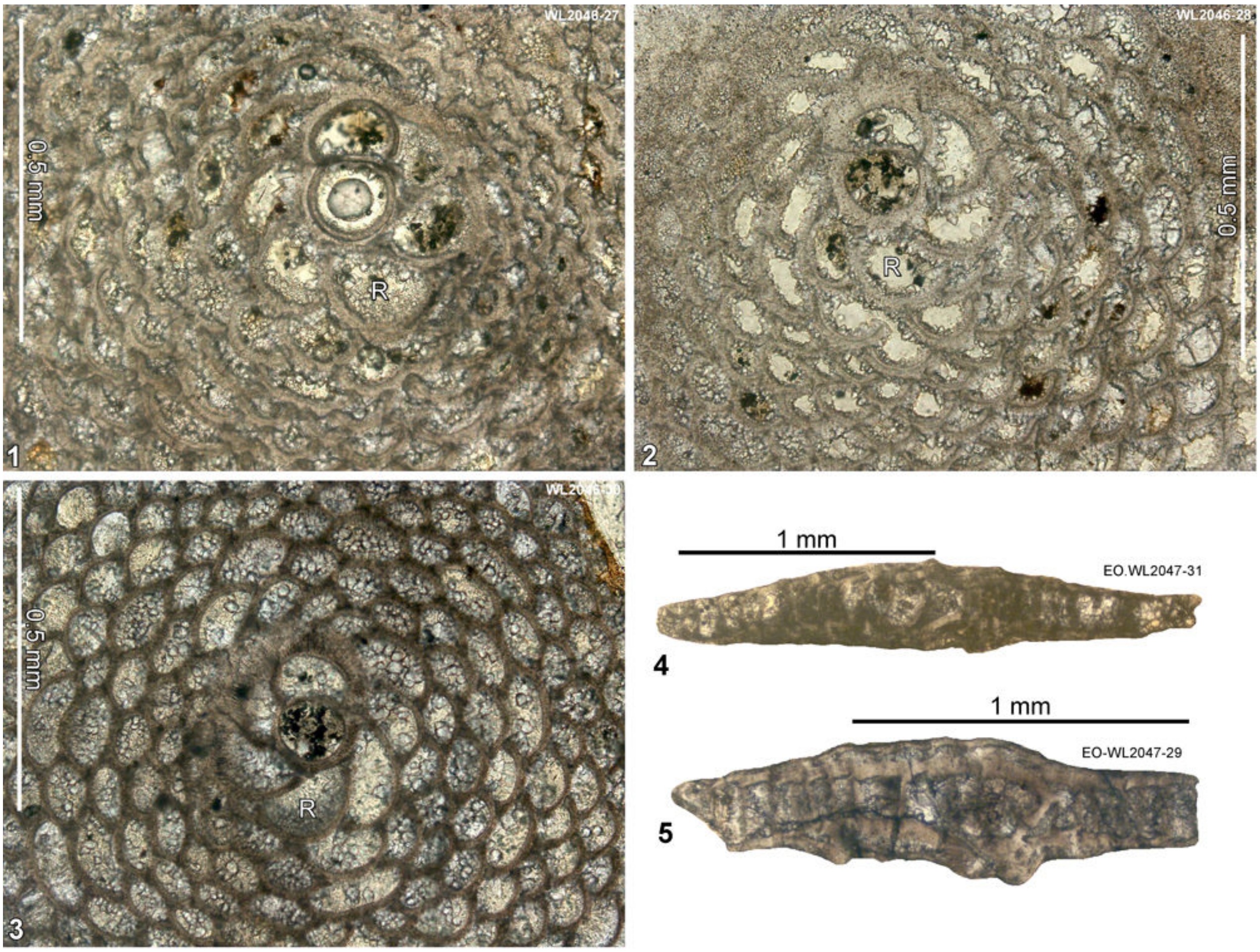


Figure 66: *Eolepidina antillea* (Cushman, 1919), megalospheric forms. **1** (EO.WL2046-27), equatorial section, R = 5. **2** (EO.WL2046-28), equatorial section, R = 5. **3** (EO.WL2046-30), equatorial section, R = 5. **4** (EO.WL2047-31), axial section. **5** (EO.WL2047-29), axial section. Preston Hill Formation (ABZ8), Lilyfield, St Ann, Jamaica.

Eolepidina gardnerae (Cole, 1929)

(Figs. 71 - 74)

Previous descriptions and figures. Cole, 1929, p. 60-62, Pl. 1, figs. 1-6; Pl. 2, figs. 1-2.

Recognition. *Eo. gardnerae* has one PAC and two subequal spires. This is clearly visible in material from the type series (Cole, 1929, Pl. 1, fig. 5; Pl. 2, fig. 2). We define $\bar{R}$ as ranging from 2.2 - 3.5. If a second PAC is present (*e.g.*, Figs. 26.3, 26.6) it either produces no spires or very short ones.

Remarks. We place the species *gardnerae* in the genus *Eolepidina* as we regard the development of two PACs as being of generic value. *Eo. gardnerae* is distinctive and easily distinguished from *P. chiapasensis*, based on the number of PACs, when several specimens are available for study. Although there is undoubtedly a graduation from *Eo. gardnerae* to *P. chiapasensis* to *Lepidocyclina ariana*, the separation of *Eo. gardnerae* from *P. chiapasensis* is useful biostratigraphically. *Eo. gardnerae* is the nominate species for ABZ10. The species has been recorded from Florida/Alabama (as *Polylepidina*: Robinson & Jiang, 1995), Jamaica and Veracruz (as *Polylepidina chiapasensis* by Barker & Grimsdale, 1936, Pl. 35, figs. 7-8) and Chiapas (as *Polylepidina antillea* by Frost & Langenheim, 1974, Pls. 30-31), Mexico.

Genus *Polylepidina* Vaughan, 1924

Type species. *Polylepidina chiapasensis* Vaughan from the Middle Eocene of Chiapas, Mexico.

Diagnosis. A lepidocyclininid with two PACs and three or four asymmetrical primary spires of periequatorial chambers. Lateral chamberlets developed on both sides, with low numbers (usually 3 to 5, but up to 6 or 7) of tiers and with vacuole-like chamberlets.

Discussion. We follow Robinson (1997) in regarding the presence of two PACs and asymmetrical primary spires as the diagnostic criterion for discrimination at the generic level.

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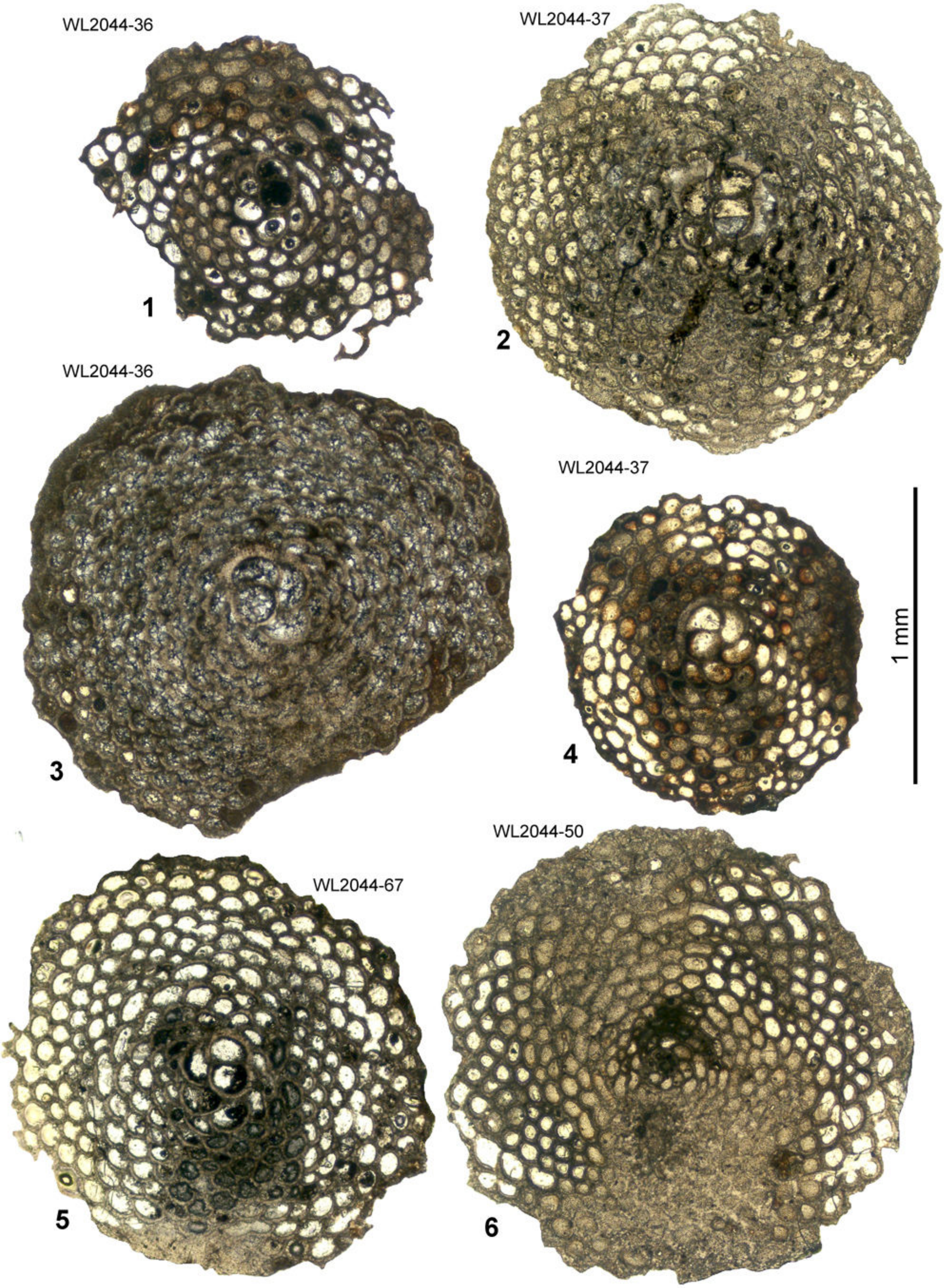

Figure 67: *Eolepidina subplana* (Barker & Grimsdale, 1936). **1** (EO.WL2044-36), equatorial section. **2** (EO.WL2044-37), equatorial section. **3** (EO.WL2044-36), equatorial section. **4** (EO.WL2044-37), equatorial section. **5** (EO.WL 2044-67), equatorial section. **6** (EO.WL2044-50), equatorial section. Chapelton Formation (ABZ9), Lilyfield, St Ann, Jamaica.

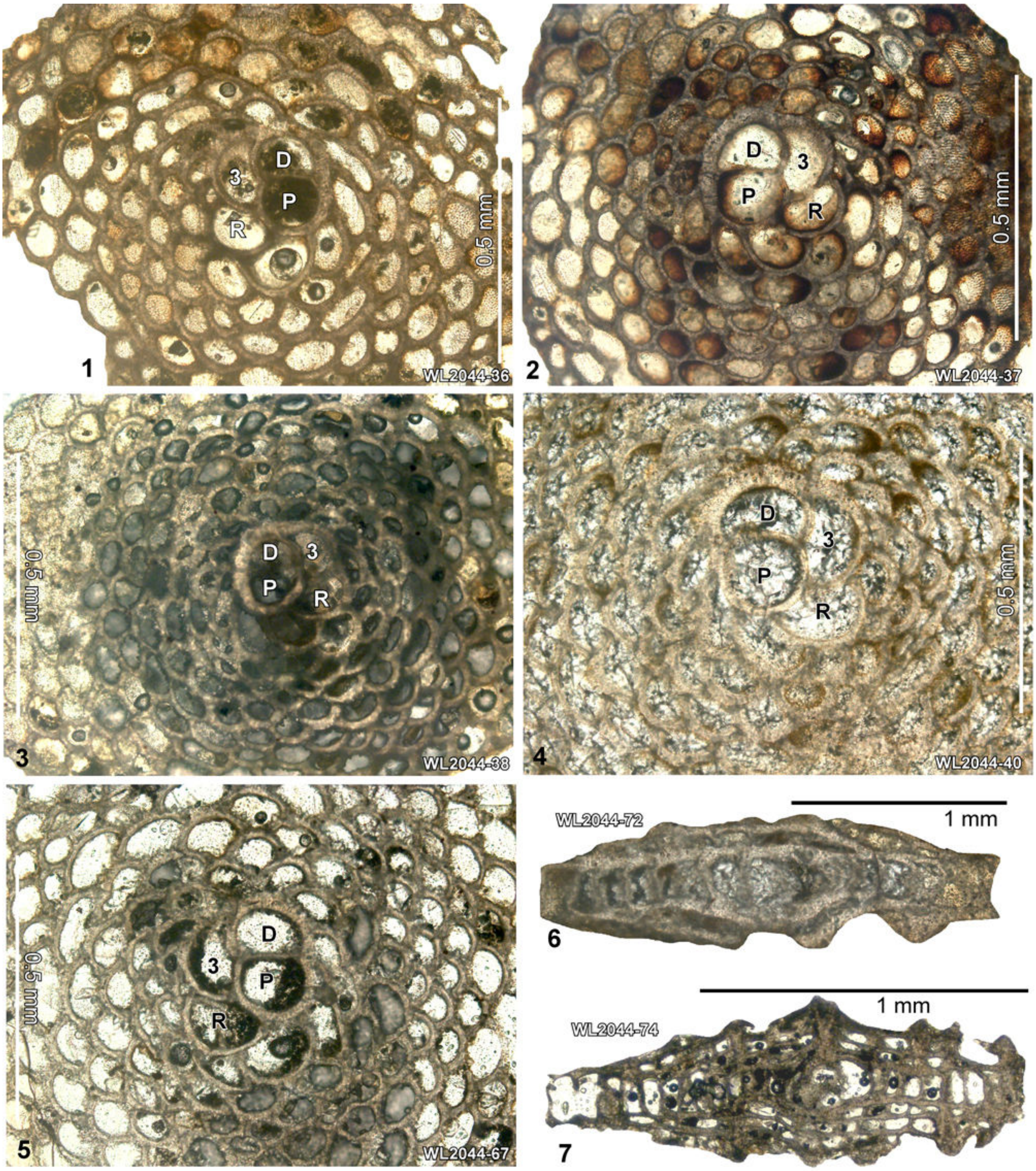

Figure 68: *Eolepidina subplana* (Barker & Grimsdale, 1936). **1** (EO.WL2044-36), equatorial section, R = 4. **2** (EO. WL2044-37), equatorial section, R = 4. **3** (EO.WL2044-38), equatorial section, R = 4. **4** (EO.WL2044-40), equatorial section, R = 4. **5** (EO.WL2044-67), equatorial section, R = 4. **6** (EO.WL2044-72), axial section. **7** (EO.WL2044-74), axial section. Chapelton Formation (ABZ9), Lilyfield, St Ann, Jamaica.

Polylepidina chiapasensis
VAUGHAN, 1924

(Figs. 75 - 80)

Previous descriptions and figures. Vaughan, 1924, p. 807-808, Fig. 4; 1929a, p. 288-289, Fig. 3.

Recognition. *Po. chiapasensis* is flat discoidal and has numerous small to large pustules extending across most, or all, of the surface, yet sometimes it has a marginal band with radial striations formed from very-fine granules (as in *Eo. semiradiata* (Barker & Grimsdale, 1936) = *Eo. antillea* (Cushman, 1919)). Here, we define Ṝ as ranging from 2.0 - 2.2, and typically three or four asymmetrical peri-embryonic spirals develop from the two PACs.

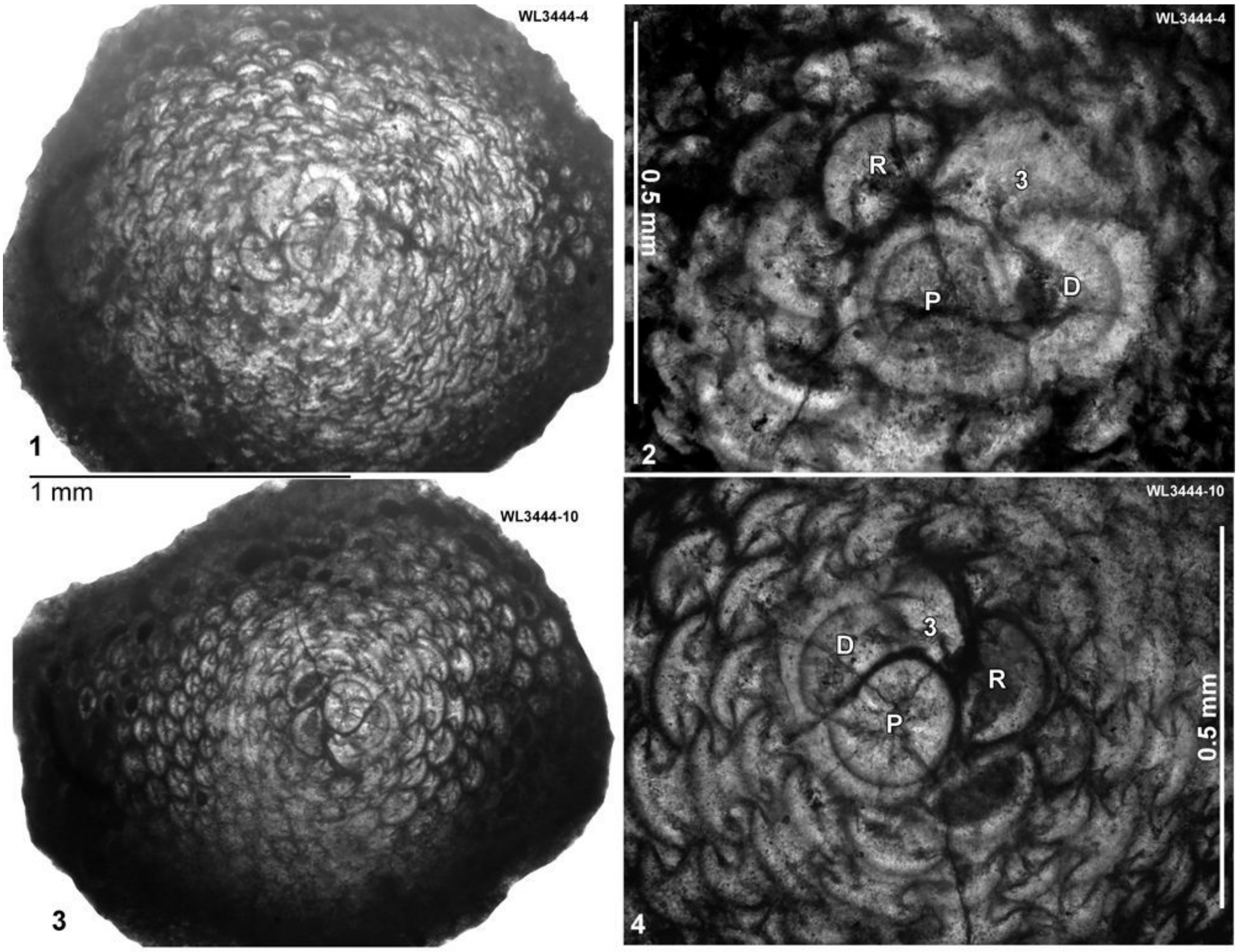

Figure 69: *Eolepidina subplana* (Barker & Grimsdale, 1936). Equatorial sections, megalospheric forms. **1-2** (UWIGM.WL3444-4), **3-4** (UWIGM.WL3444-10): Chapelton Formation (ABZ9), Albert Town, Trelawny, Jamaica.

Remarks. *P. chiapasensis* is externally similar to *Lepidocyclina ariana* and can only be distinguished in equatorial sections (*P. chiapasensis* is characterised by Ṝ = 2.0 - 2.2 with three or four asymmetrical peri-embryonic spirals, whereas *L. ariana* has Ṝ = 2 with two sets of two symmetrical peri-embryonic spirals). In most specimens, the three or four peri-embryonic spirals are markedly differently developed, with one spiral usually being dominant and having larger chambers. In a few specimens (*e.g.*, Fig. 80.3-4) the spirals have chambers of equal sizes and on first glance the spirals appear symmetrical; yet a closer inspection reveals the spirals are asymmetric as the closing chambers (c) lie closer to one PAC (P) that the other.

Polylepidina chiapasensis is the nominal species for ABZ11, and its presence indicates a level in the lower Bartonian. The species is widespread in Jamaica in the Chapelton Formation at Albert Town and Litchfield, and in the Preston Hill Formation at Salt Spring.

Genus *Lepidocyclina* Gümbel, 1868

Type species. *Nummulites mantelli* Morton, 1833 from the Marianna limestone (lower Oligocene), near Claiborne, Alabama, USA (Morton, 1833; Vaughan, 1927).

Synonyms. *Isolepidina* Douvillé, 1915 (type species *Nummulites mantelli* Morton, 1833) [objective synonym]; *Amphilepidina* Douvillé, 1922 (type species *Orbitoides sumatrensis* Brady, 1875) [junior synonym]; *Polyorbitoina* Geyn & Vlerk, 1935 (type species *Lepidocyclina (Polylepidina) proteiformis* Vaughan, 1924) [junior synonym]; *Multilepidina* Hanzawa, 1932 (*non* Silvestri, 1937) (type species *Lepidocyclina (Multilepidina) irregularis* Hanzawa, 1932) [junior synonym].

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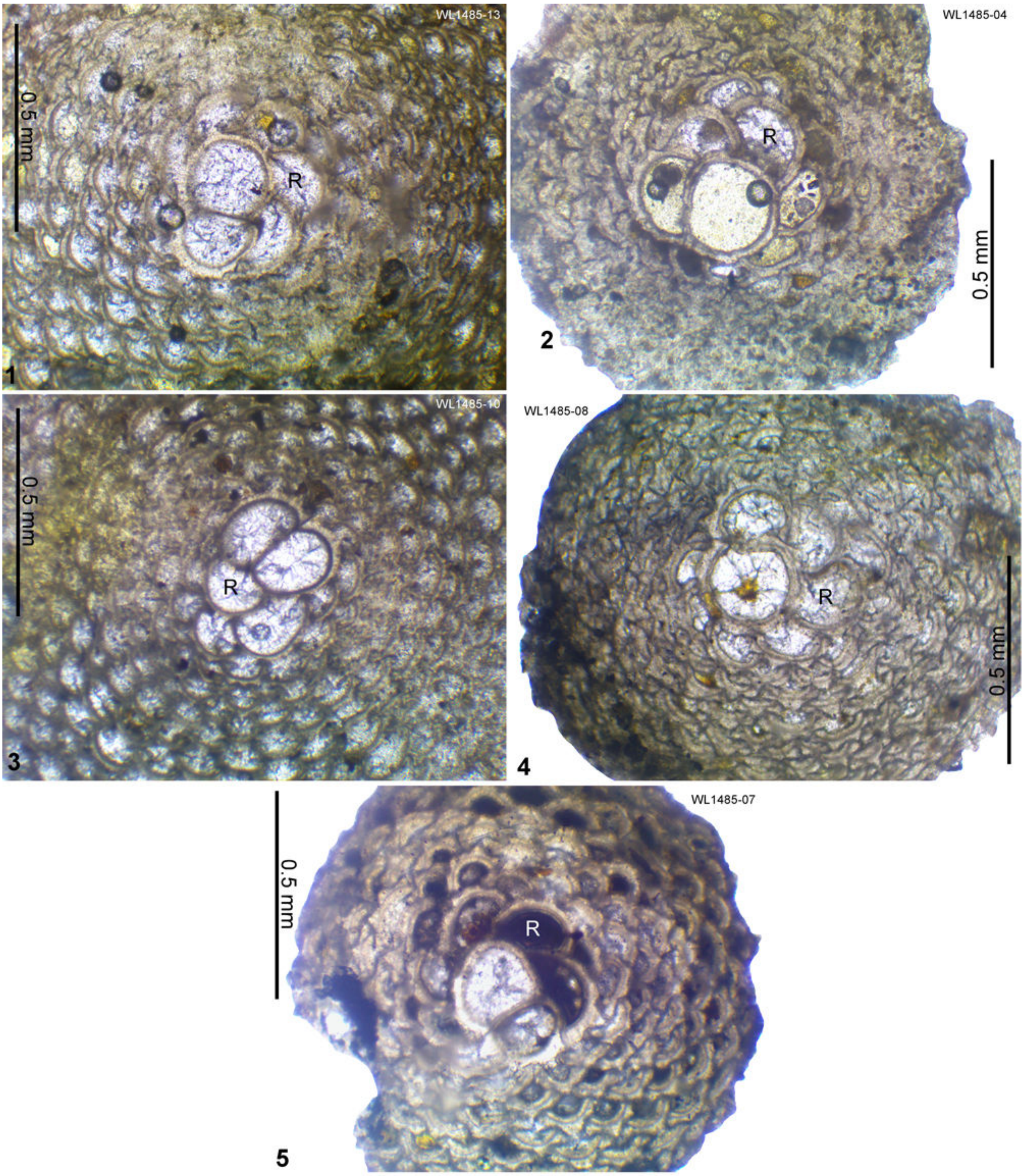


Figure 70: *Eolepidina subplana* (Barker & Grimsdale, 1936). **1** (ER1485-13), **2** (ER1485-04), **3** (ER1485-10), **4** (ER 1485-08), **5** (ER1485-07): megalospheric specimens, equatorial sections. Locality ER1485 of Robinson (1996), ABZ9, St Bartholomew.

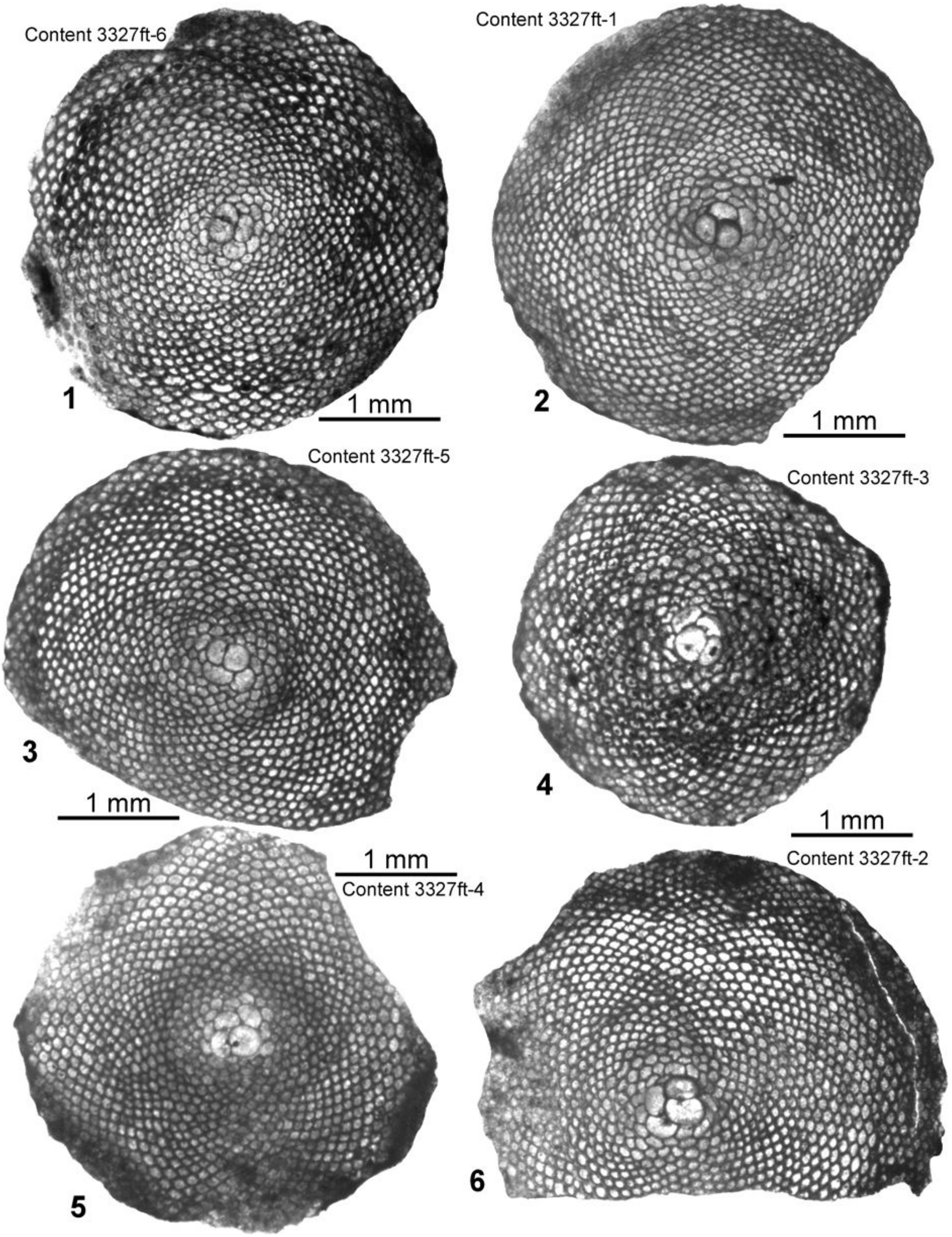


Figure 71: *Eolepidina gardnerae* (Cole, 1929). Megalospheric forms, equatorial sections. **1** (UWIGM.Content 3327ft-6), **2** (UWIGM.Content 3327ft-1), **3** UWIGM.Content 3327ft-5), **4** (UWIGM.Content 3327ft-3), **5** (UWIGM.Content 3327ft-4), **6** UWIGM.Content 3327ft-2): Content Well (depth 3327ft = 1014 m), ABZ10, Content, Westmoreland, Jamaica.

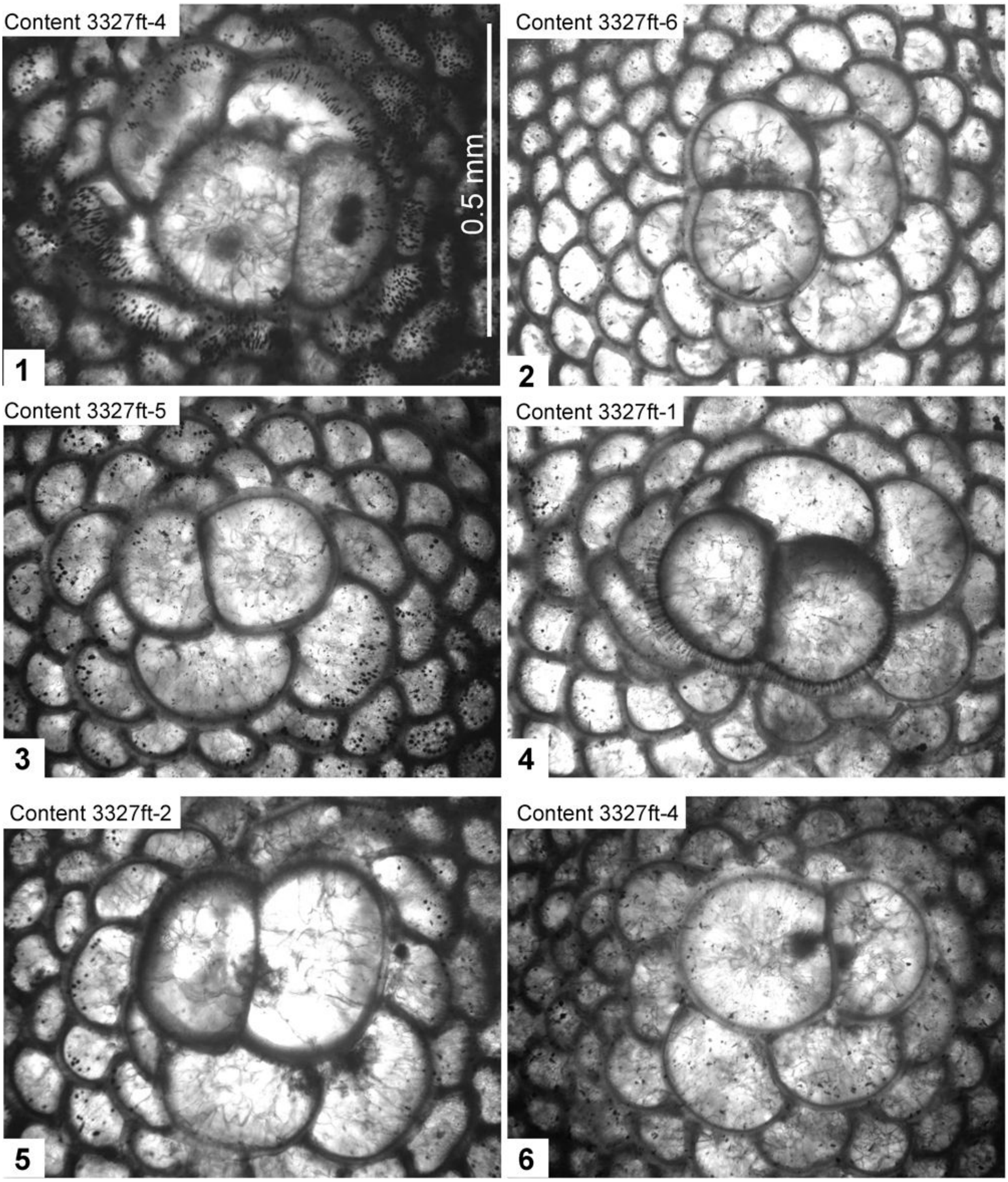


Figure 72: *Eolepidina gardnerae* (COLE, 1929). Megalospheric forms, equatorial sections (details). **1** (UWIGM. Content 3327ft-4), **2** (UWIGM.Content 3327ft-6), **3** UWIGM.Content 3327ft-5), **4** (UWIGM.Content 3327ft-1), **5** (UWIGM.Content 3327ft-2), **6** UWIGM. Content 3327ft-4): Content Well (depth 3327ft = 1014 m), ABZ10, Content, Westmoreland, Jamaica.

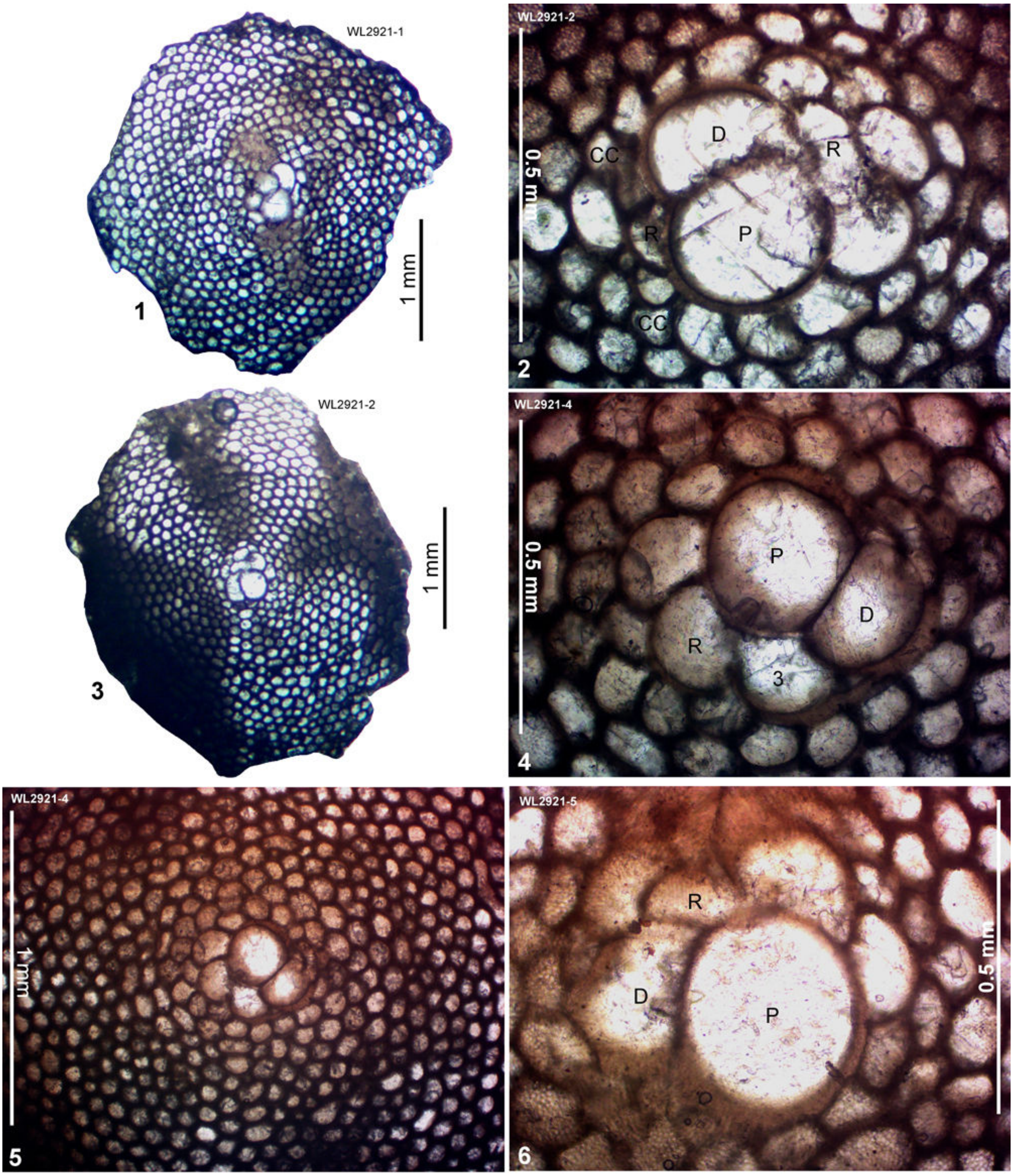


Figure 73: *Eolepidina gardnerae* (Cole, 1929). Megalospheric forms, equatorial sections. **1** (UWIGM.WL2921-1), specimen with R = 3. **2-3** (UWIGM.WL2921-2), specimen with R = 2. **4-5** (UWIGM.WL2921-4), specimen with R = 4). **6** (UWIGM.WL2921-5), specimen with R = 3. This population yields specimens that can be attributed on a typological approach to *Eo. subplana*, *Eo. gardnerae* and *Po. chiapasensis*, but to *Eo. gardnerae* using a statistical approach. Chapelton Formation (ABZ10), north of Elderslie, St James, Jamaica.

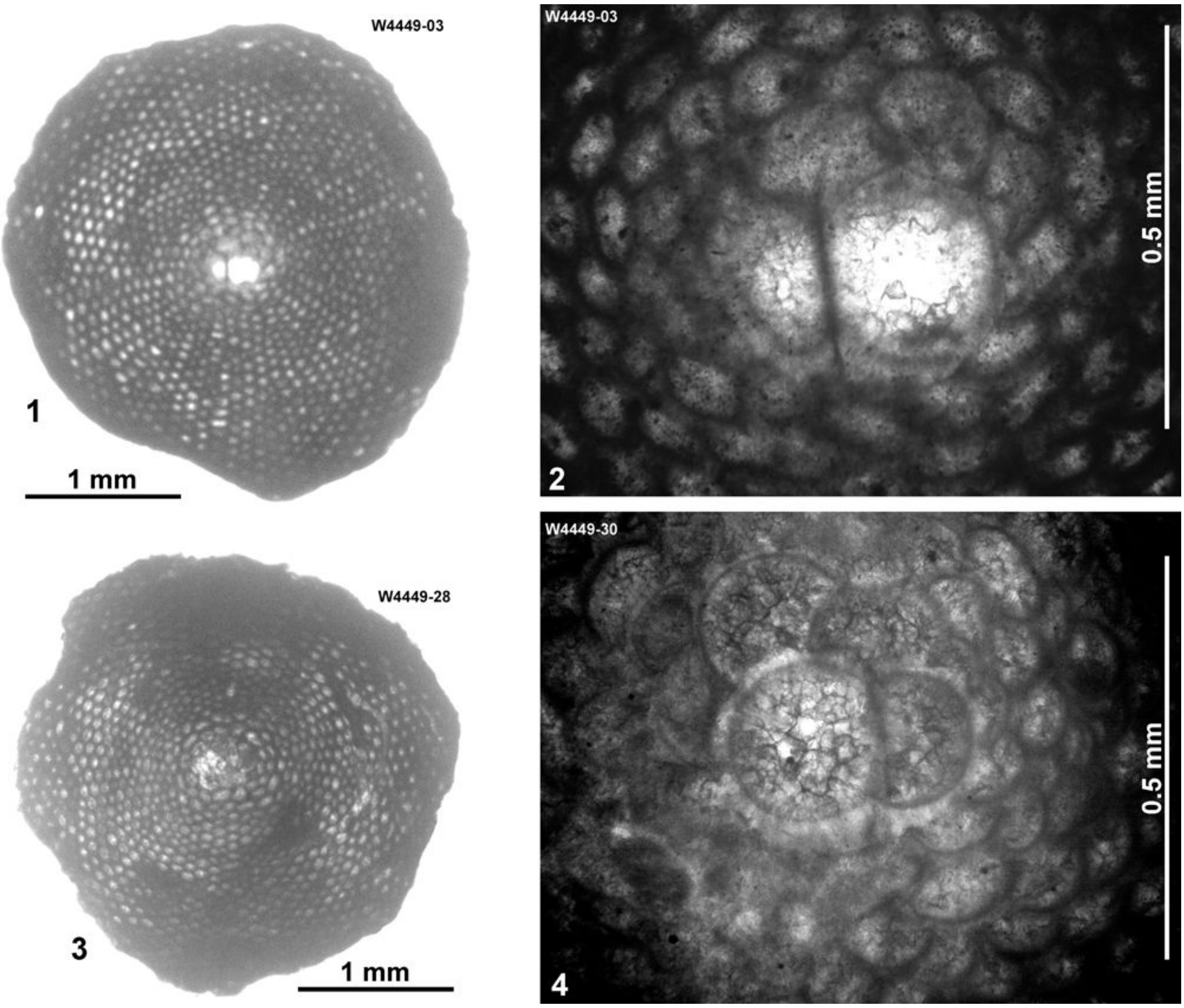


Figure 74: *Eolepidina gardnerae* (Cole, 1929). Megalospheric forms, equatorial sections. **1-2** (UWIGM.WL4449-03), R = 3. **3-4** (UWIGM.WL4449-30). Specimens of typical *Eo. gardnerae* that we regard as reworked in ABZ14 sediments (with *Plio. tobleri*), chalk without cherts, Cold Spring, Westmoreland, Jamaica.

Remarks. We restrict *Lepidocyclina* here to forms which have two PACs and an embryo with the protoconch and deuteroconch divided by a more-or-less straight to gently curved wall. The more 'primitive' forms lack adauxiliary chambers and include *Lep. ariana* Cole & Ponton. The more 'advanced' forms have adauxiliary chambers and include *Lep. ocalana* Cushman and *Lep. macdonaldi* Cushman. We do not think that separating these forms into separate subgenera (or genera) is useful as we are probably dealing with several distinct lineages that show a progression from forms lacking adauxiliary chambers to forms bearing adauxiliary chambers. The relationships with other 'simple' lepidocyclinids, such as *Lep. canellei* Lemoine & R. Douvillé from the Oligocene, are also unclear at the present time and we provisionally include all these forms in *Lepidocyclina* pending further work.

Lepidocyclina ariana
Cole & Ponton, 1934
(Figs. 81 - 84)

Previous description and figures. Cole & Ponton, 1934, p. 142-143, Pl. 2, figs. 1-5; Cole, 1944, p. 61-62, Pl. 1, fig. 14; Pl. 13, fig. 3; Pl. 14, figs. 1-7; Pl. 16, figs. 11-13; Pl.17, fig. 13.

Remarks. In equatorial view *L. ariana* is characterised by a typical four-spiral peri-embryonic chamber plan developed from two PACs; it lacks adauxilary chamberlets and has semi-circular equatorial chamberlets. In axial section, it possesses relatively few lateral chamberlets that have thick walls with small irregular vacuoles.

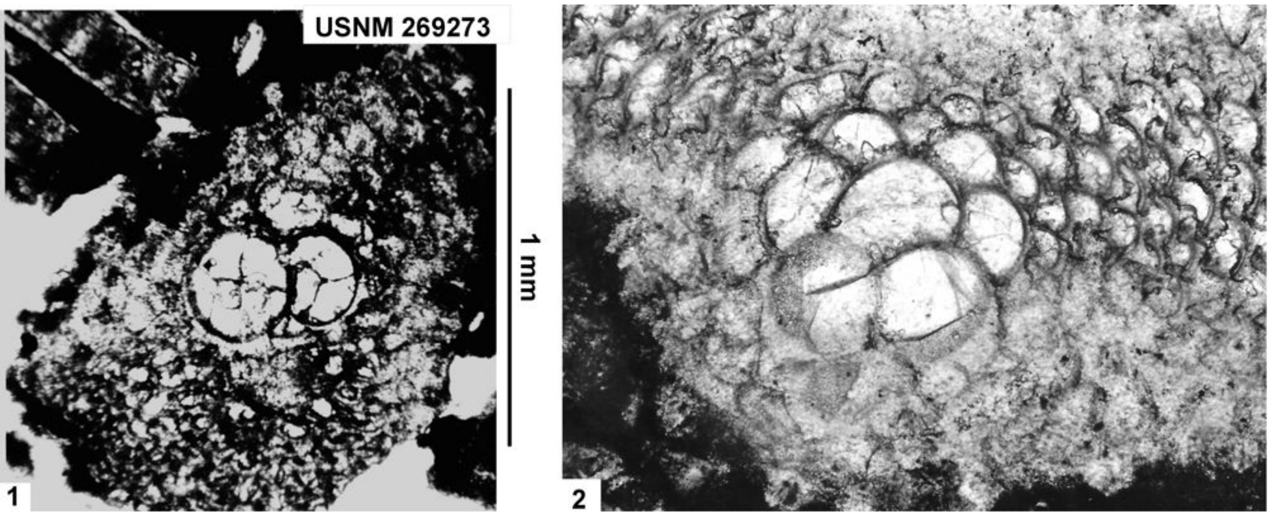


Figure 75: Specimens from the type material of *Polylepidina chiapasensis* VAUGHAN, 1923. **1**, off-centre equatorial section (USNM 269273), cut from same block as type specimens. **2**, off-centre equatorial section (USNM 324726), figured by VAUGHAN, 1929a, Fig. 3. Note that both have two PACs (although difficult to see in 1) and that the PACs are of similar size in 2; note two spirals with asymmetrical closing chamber (cc) in 2. Since these are off-centre sections we do not see all the peri-embryonic spires that are developed; 2 clearly shows two spires developing from two large PACs and a closing chamber (cc) that is asymmetrical to the spire development.

Occurrence. In Jamaica, *L. ariana* occurs during a strongly regressive interval, linked either to a major sea-level fall, or to local tectonics, and has only been found in deposits within basins; equivalent deposits on the platforms are either lacking, or represented by platform interior facies without lepidocyclinids. In Florida and Alabama the species is common at some localities (*e.g.*, COLE, 1944, 1945; ROBINSON & JIANG, 1995; ROBINSON, 1997). The species, with its distinctive lateral chamberlets is restricted to ABZ12.

Lepidocyclina macdonaldi
CUSHMAN, 1919

(Figs. 85 - 86)

Previous description and figures. CUSHMAN, 1919, p. 94, Pl. 40, figs. 1-6; CUSHMAN, 1920, p. 77, Pl. 34, figs. 1-3; COLE, 1952, p. 16, Pl. 7, figs. 1-19; Pl. 8, figs. 1-4; Pl. 14, fig. 11.

Remarks. COLE's (1952) material from Panama includes several species which show differences in the form of the lateral chambers. In 1956, COLE (p. 221) stated that three species of *Lepidocyclina*, namely *Lep. ariana*, *Lep. proteiformis* and *Lep. macdonaldi* could be separated on the basis of their lateral chamberlets: the first (*Lep. ariana*) had relatively thick but straight floors and roofs of the lateral chamberlets, and the chamberlet cavities were rather low; the second (*Lep. proteiformis*) had relatively thin and straight lateral floors and the cavities of the lateral chamberlets were open; the third (*Lep. macdonaldi*) had much thicker and curved floors and roofs of the lateral chamberlets and the cavities of the chamberlets were more appressed. *Lep. ariana* as figured here is relatively distinct, because of its basic four-spiral arrangement of peri-embryonic chambers and its thick walls to the lateral chamberlets that have thin spaced vacuole-like chambers. *Lep. macdonaldi* is also relatively distinct, in the form of its lateral chamberlets (thin) and thick curved roofs and floors; it is very distinctive in thin section. COLE (1956, Pl. 27, figs. 4-5) shows equatorial sections of *Lep. macdonaldi* from Jamaica, which appear to show the dark lines (cavities) above the equatorial layer, with the thick curved floors showing a bright area inside the cavities. Yet, the embryo is relatively similar to *Lep. proteiformis* and forms such as *Lep. ocalana*. The equatorial section of *Lep. proteiformis* illustrated by COLE (1956, Pl. 27, fig. 6) has an embryonic length of about 675 µm (as measured from his illustration), and therefore falls well outside the range of forms such as *Lep. ariana* and within the range of forms such as *Lep. montgomeriensis* and *Lep. ocalana*, although it has a simple four-spiral plan of peri-embryonic chambers. In fact, the lateral chamberlets of forms attributed to *Lep. proteiformis* from Jamaica and Mexico by COLE (1956) have lateral chambers similar to *Lep. ocalana*. We therefore tentatively attribute *Lep. proteiformis* of COLE, 1956 to the *Lep. ocalana* group.

COLE (1956, Pl. 27, figs. 3-5) illustrated three equatorial sections he referred to *Lep. macdonaldi*; these had embryo lengths of 520, 720 and 620 µm, respectively (as determined by measurement of the figures with the scale given). Four equatorial sections from sample WL4449 (ABZ14) from Cold Spring have an embryo length ranging from 488 µm to 766 µm (mean 660 µm, standard deviation 124.1 µm) and show the development of one or two adauxilary chambers. Both COLE's (1956) illustrations and our sectioned specimens have larger embryos than typical of *Lep. ariana*, and fall within the range of *Lep. ocalana*. It seems that *Lep. macdonaldi* and *Lep. ocalana* are parallel evolving lineages in the mid to late Eocene.

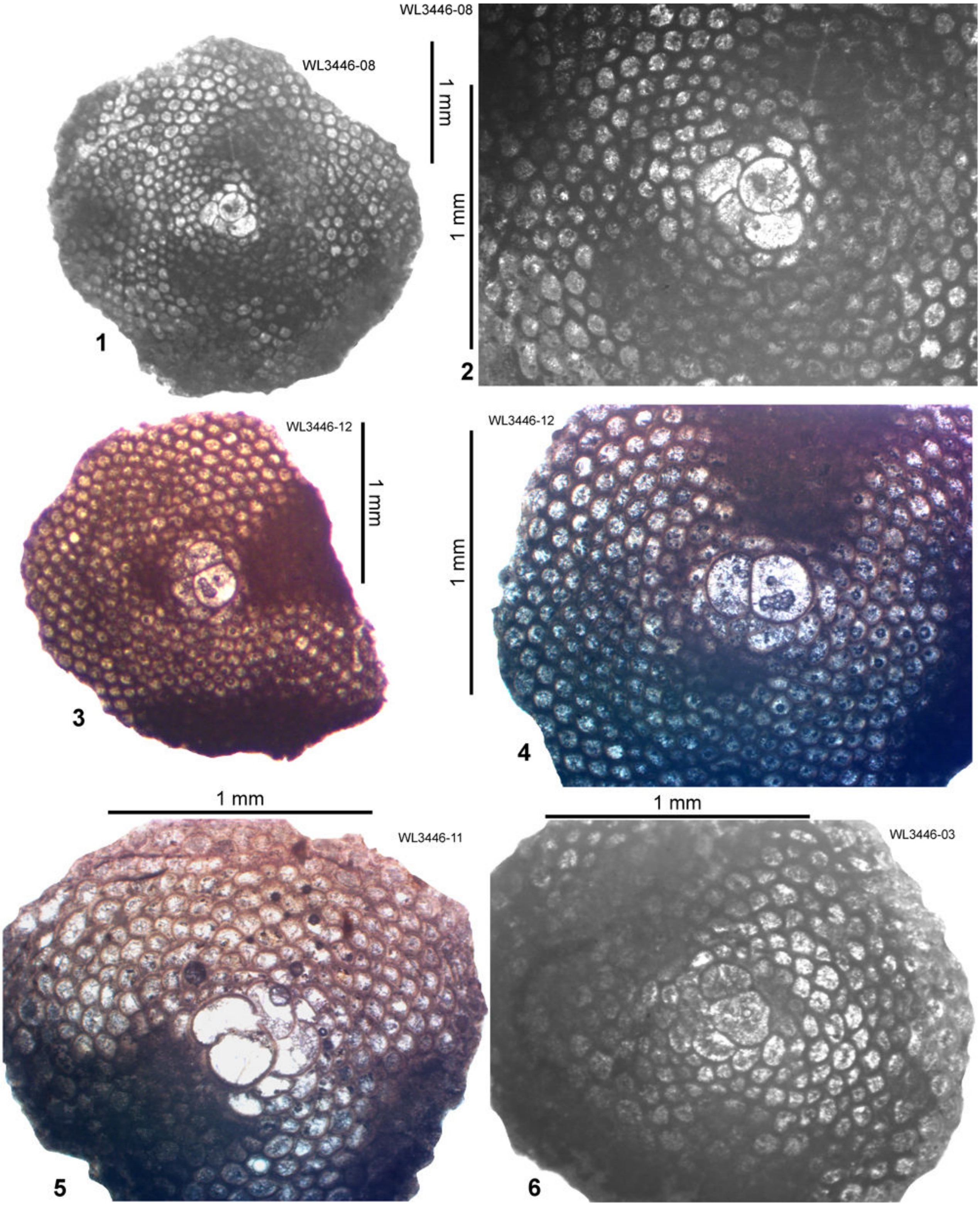


Figure 76: *Polylepidina chiapasensis* VAUGHAN, 1924 from Jamaica. **1-2** (UWIGM.WL3446-08), **3-4** (UWIGM.WL 3446-12), **5** (UWIGM. WL3446-11), **6** (UWIGM.WL3446-03): megalospheric specimens, equatorial sections. Sample WL3446 (ABZ11), Chapelton Formation (ABZ11), Albert Town, Trelawny, Jamaica.

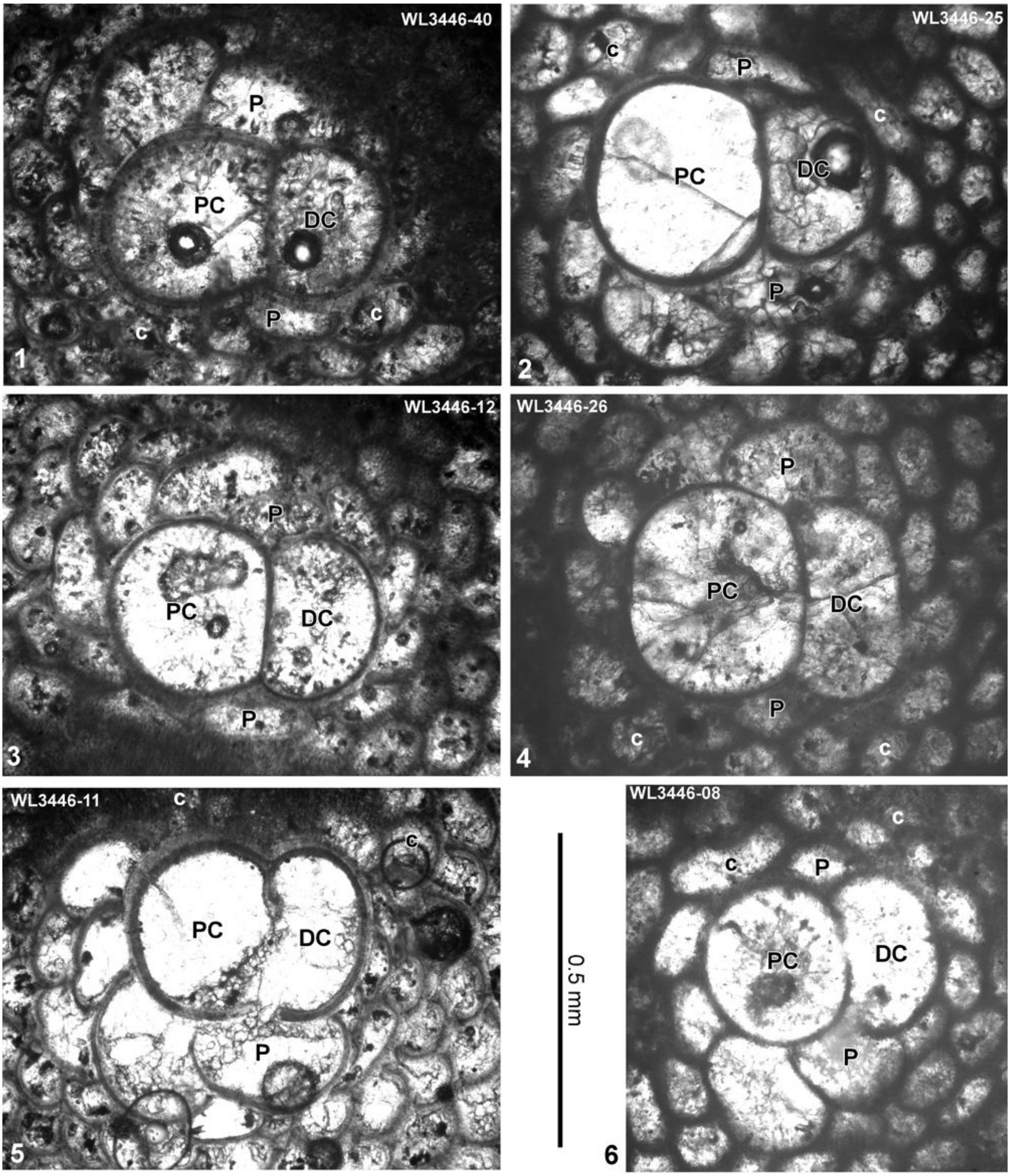


Figure 77: *Polylepidina chiapasensis* Vaughan, 1924 from Jamaica. **1** (UWIGM.WL3446-40), **2** (UWIGM.WL3446-25), **3** (UWIGM.WL3446-12), **4** (UWIGM.WL3446-26), **5** (UWIGM.WL3446-11), **6** (UWIGM.WL3446-08): megalospheric specimens, equatorial sections. Note all specimens have two PACs (P) (although difficult to see in 5) and two closing chambers (c). Sample WL3446 (ABZ11), Chapelton Formation (ABZ11), Albert Town, Trelawny, Jamaica.

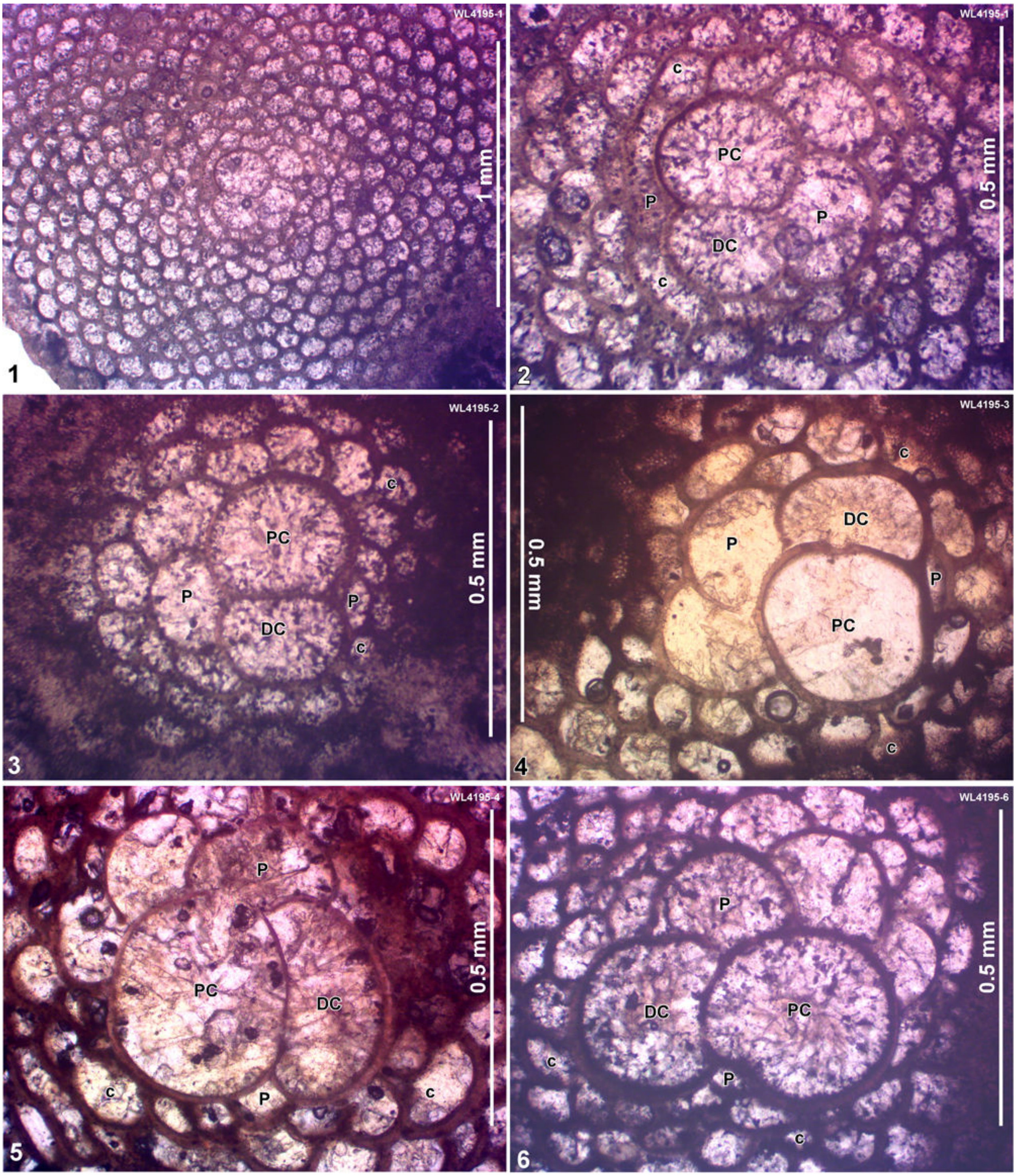


Figure 78: *Polylepidina chiapasensis* VAUGHAN, 1924. **1-2** (UWIGM.WL4195-01), **3** (UWIGM.WL4195-2), **4** (UWIGM.WL4195-03), **5** (UWIGM.WL4195-4), **6** (UWIGM.WL4195-6), megalospheric specimens, equatorial sections. Sample WL4195, Chapelton Formation (ABZ11), Litchfield, Trelawny, Jamaica.

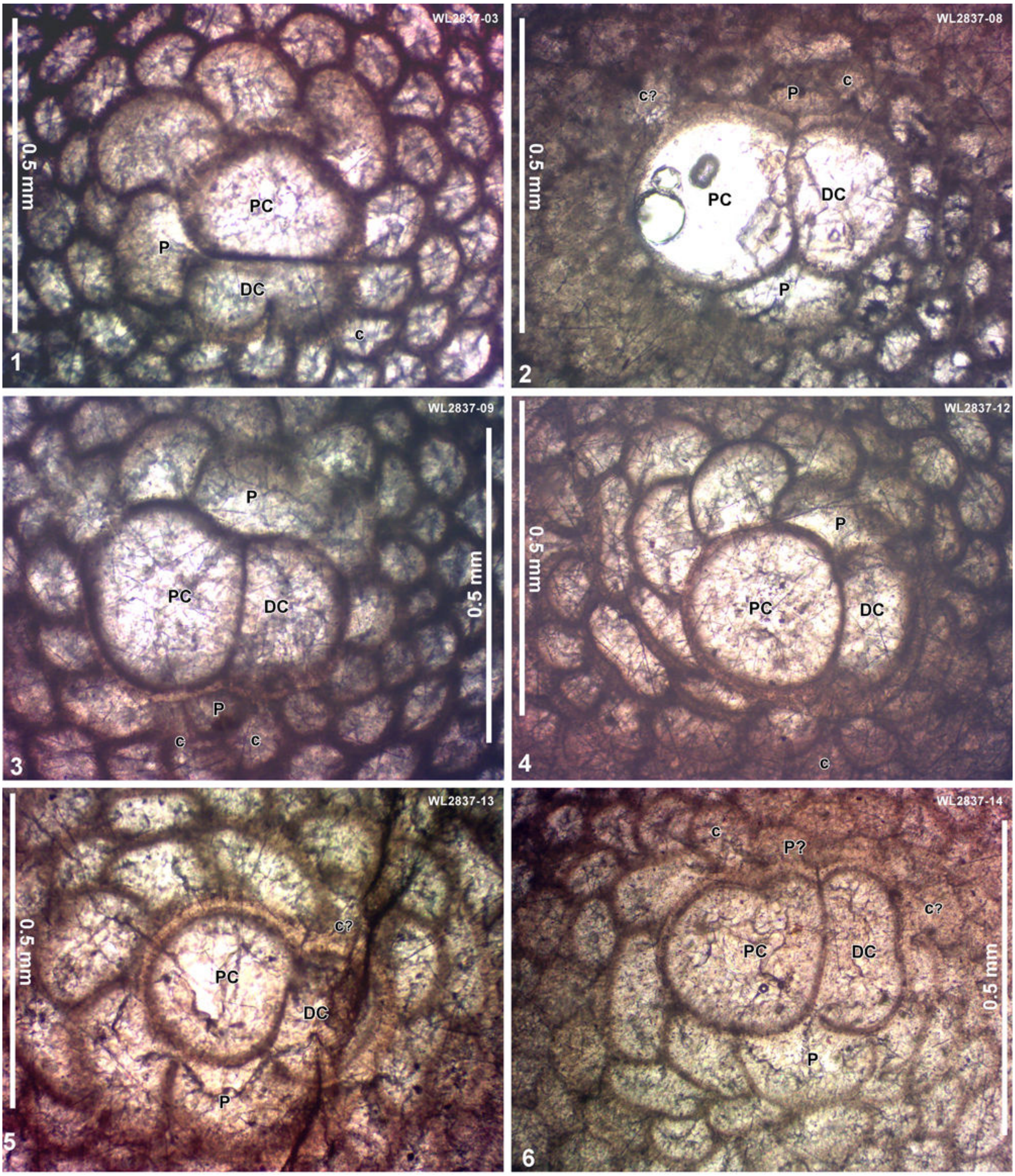


Figure 79: *Polylepidina chiapasensis* VAUGHAN, 1924. **1** (UWIGM.WL2837-03), **2** (UWIGM.WL2837-08), **3** (UWIGM.WL2837-09), **4** (UWIGM.WL2837-12), **5** (UWIGM.WL2837-13), **6** (UWIGM.WL2837-14): megalospheric specimens, equatorial sections. Sample WL2837 (ABZ11), Preston Hill Formation, Salt Spring, St James, Jamaica.

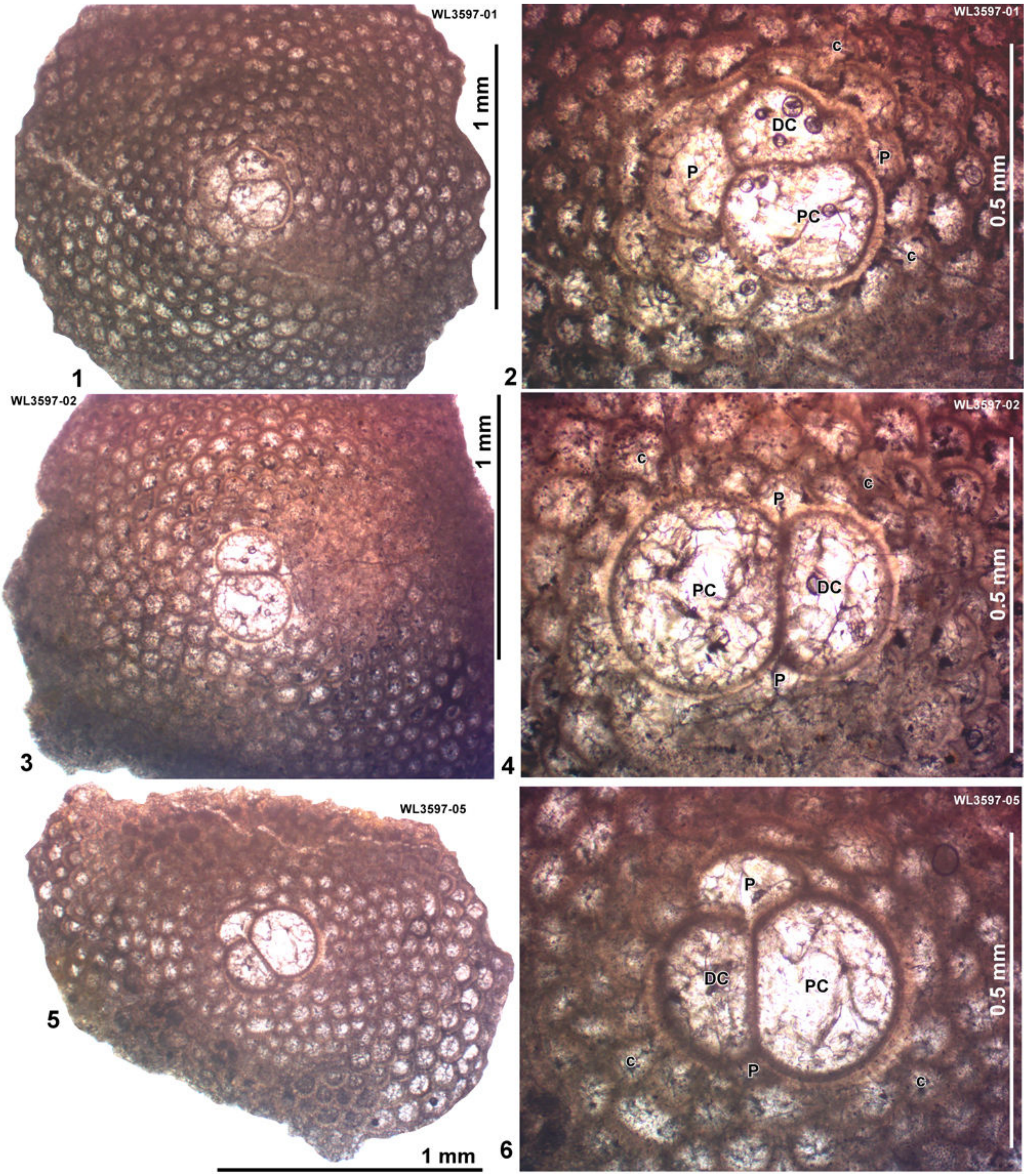


Figure 80: *Polylepidina chiapasensis* VAUGHAN, 1924. **1-2** (UWIGM.WL3597-01), **3-4** (UWIGM.WL3597-02), **5-6** (UWIGM.WL3597-05): megalospheric specimens, equatorial sections. Sample WL3597 (ABZ11), Preston Hill Formation, Salt Spring, St James, Jamaica.

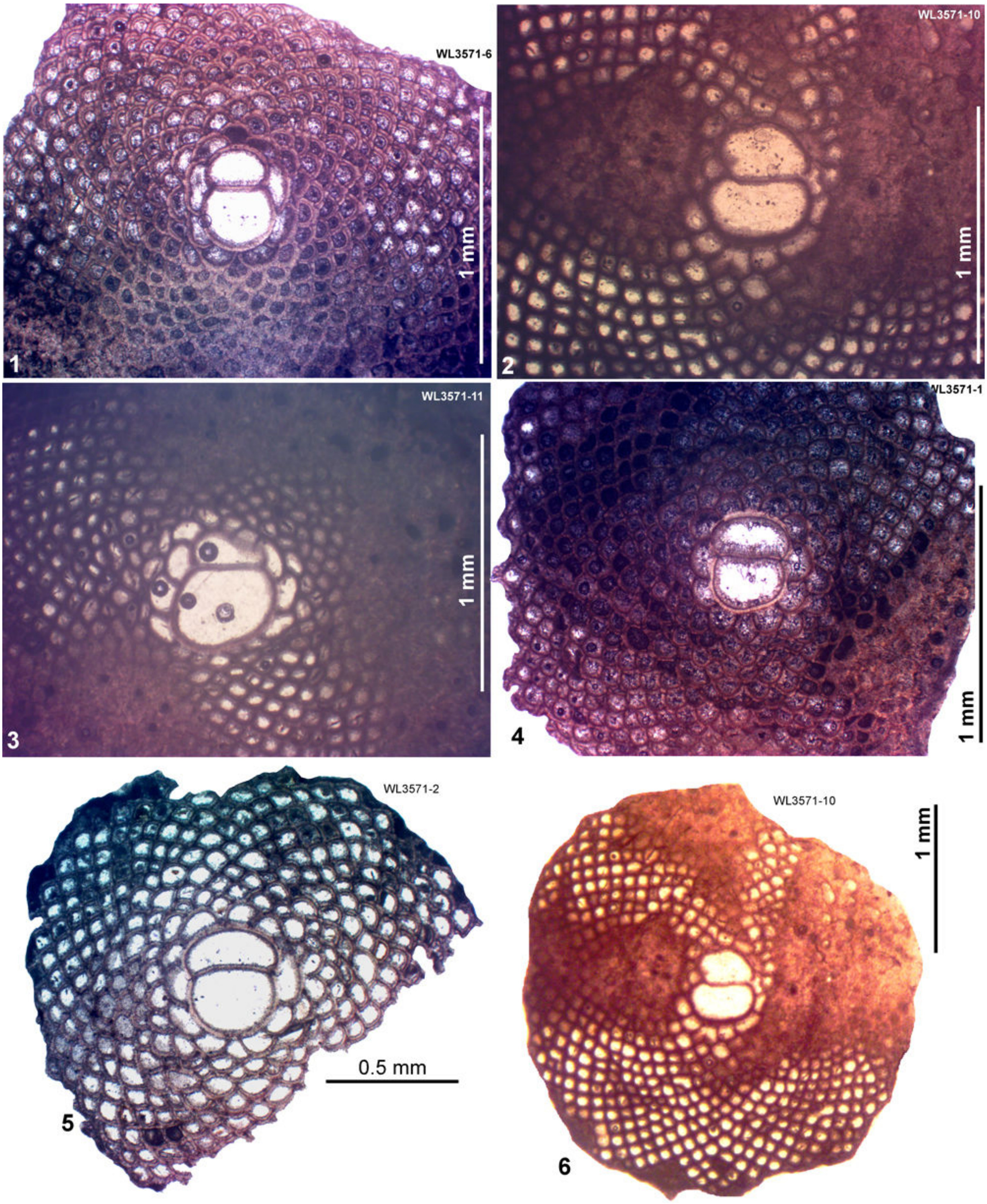


Figure 81: *Lepidocyclina ariana* Cole & Ponton, 1934, equatorial sections from the Yellow Limestone (ABZ12), Grants Pen, parish of St Thomas, Jamaica. **1** (UWIGM.WL3571-6); **2, 6** (UWIGM.WL3571-10); **3** (UWIGM.WL3571-11); **4** (UWIGM.WL3571-1); **5** (UWIGM.WL3571-2). Note the regular 4-spire plan in equatorial section.

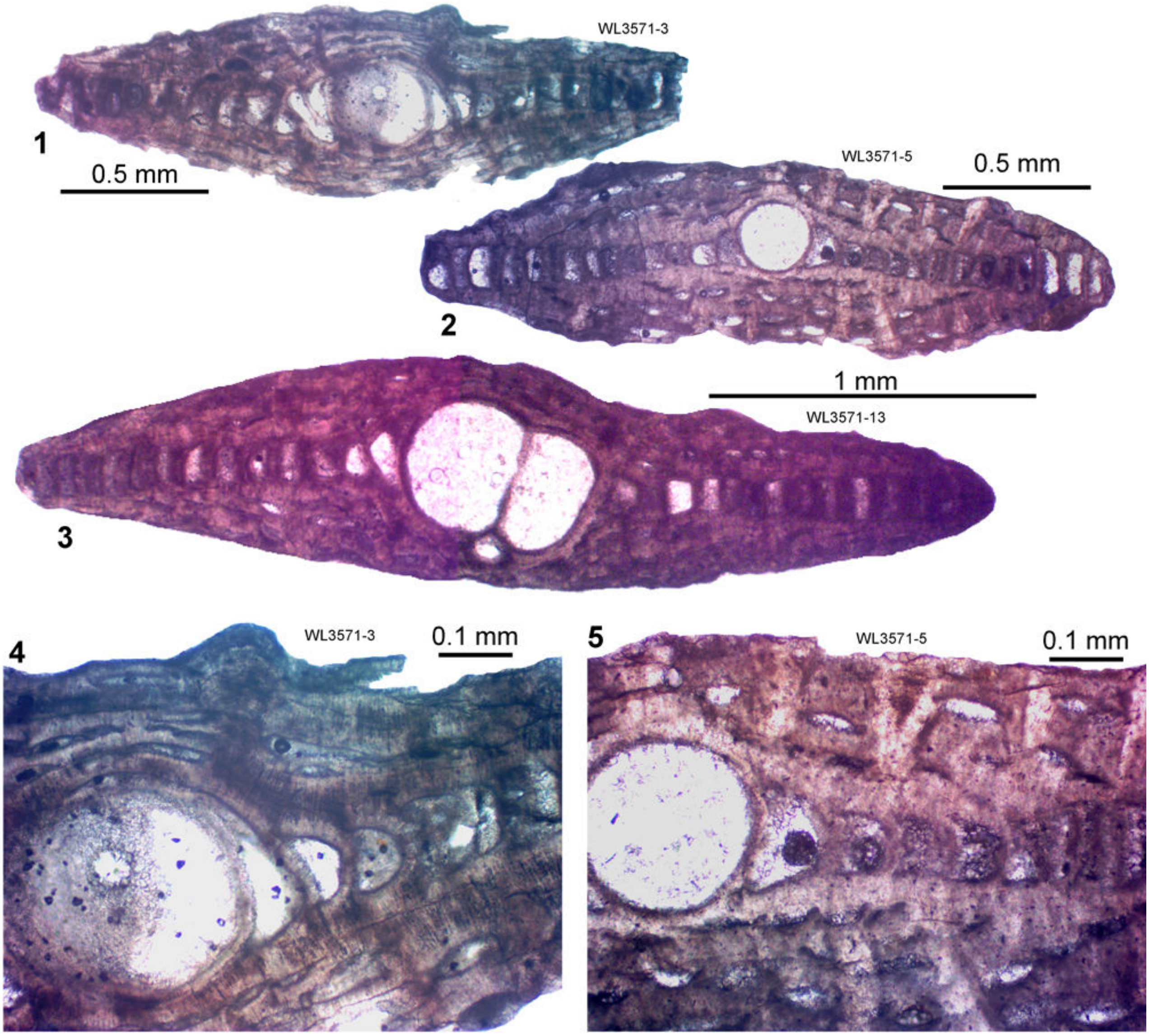


Figure 82: *Lepidocyclina ariana* COLE & PONTON, 1934, orientated axial sections from the Yellow Limestone (ABZ12), Grants Pen, parish of St Thomas, Jamaica. **1, 4** (UWIGM.WL3571-3), **2, 5** (UWIGM. WL3571-5), **3** (UWIGM.WL3571-13). Note the vacuolar appearance of the lateral chamberlets.

Our material shows the very distinctive features of the lateral chamberlets when seen in axial sections. The lateral chamberlets are strongly arcuate, offset in an en-echelon fashion, and do not show regular vertical tiers. Scattered piles (pillars) are also seen in the axial sections. This is consistent with material from the type locality in Mexico. Note that our specimens do not show an annular arrangement of equatorial chamberlets. This species resembles the arrangement seen in *Lep. ariana* in this respect rather than *Lep. ocalana*.

Range. Specimens of *Lep. macdonaldi* are common in ABZ14 (sample UWIGM.WL4449) at Cold Spring and Sherwood Content (samples UWIGM. R1068 and UWIGM.R1072) and sparingly so in the type Swanswick section at Swanswick House (ABZ16). In Panama, judging by a reinterpretation of the specimens illustrated by COLE (1952), the species ranges from zones ABZ14 to ABZ16.

Lepidocyclina ocalana CUSHMAN, 1920

(Figs. 87 - 89)

Previous description and figures. CUSHMAN, 1920, p. 70-71, Pl. 27, figs. 1-4; Pl. 28, figs. 1-3; COLE, 1941, p. 41-43, Pl. 13, figs. 1-7; Pl. 16, figs. 1-4, 6-10, 15. MOLINA *et al.* (2015, Pl. 1.5) and HOHENEGGER and TORRES SILVA (2020, Fig. 2) illustrated specimens of *Lep. ocalana* erroneously under the name *Lepidocyclina chaperi*.

Recognition. *Lep. ocalana* in equatorial section combines a relatively large embryo, with a straight boundary between the protoconch and deuteroconch, with adauxilary chambers on the protoconch and deuteroconch, a relatively large number of peri-embryonic chambers, and a generally annular arrangement of equatorial chamberlets. At any level, there is a gradation from forms with four peri-embryonic spires to forms with adauxilary chambers; we place all these forms in *Lep. ocalana* and consider them natural

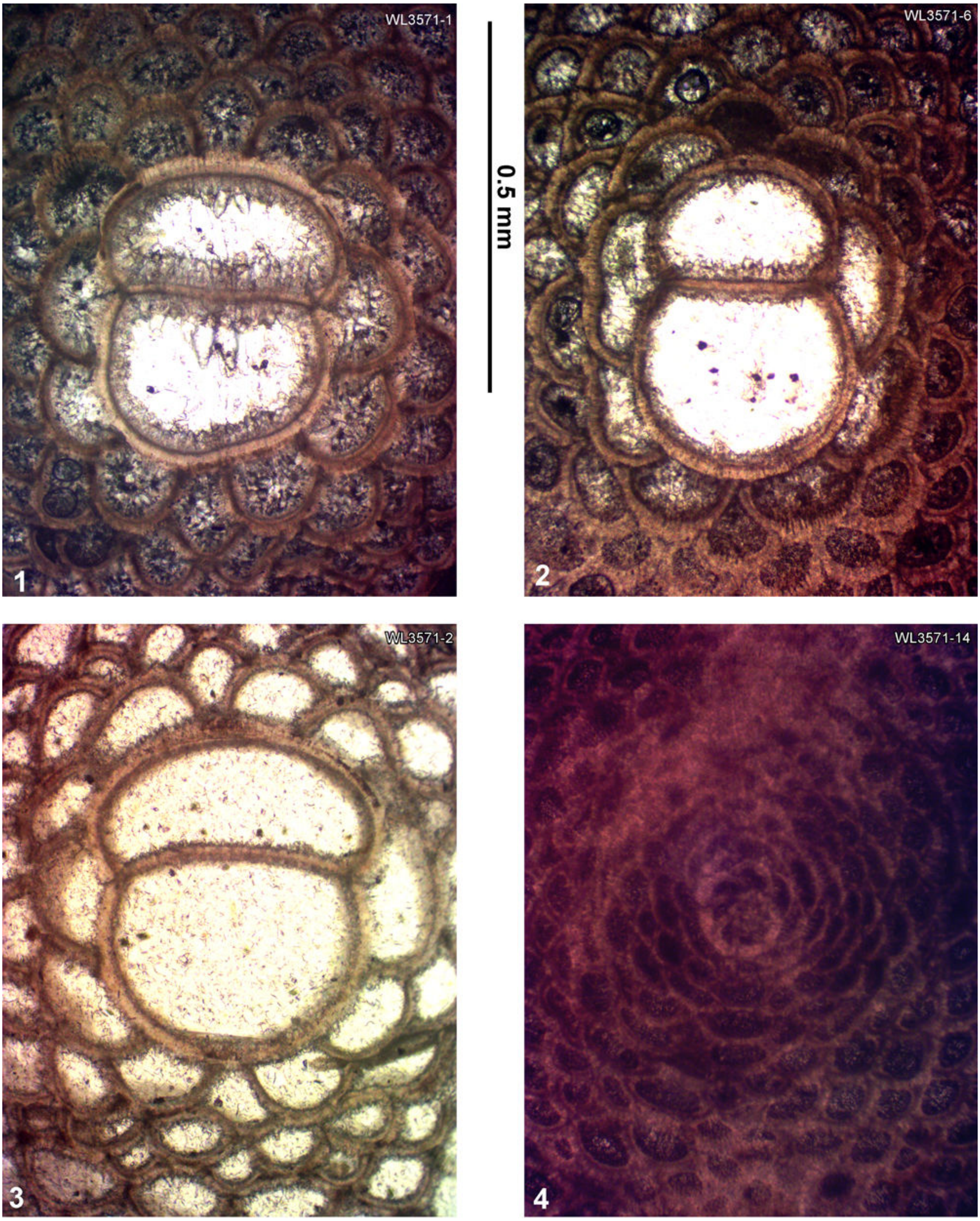


Figure 83: *Lepidocyclina ariana* Cole & Ponton, 1934, details of equatorial sections from the Yellow Limestone (ABZ12), Grants Pen, parish of St Thomas, Jamaica. **1** (UWIGM.WL3571-1), megalospheric form; **2** (UWIGM.WL 3571-6), megalospheric form; **3** (UWIGM.WL3571-2), megalospheric form; **4** (UWIGM.WL3571-14), microspheric form.

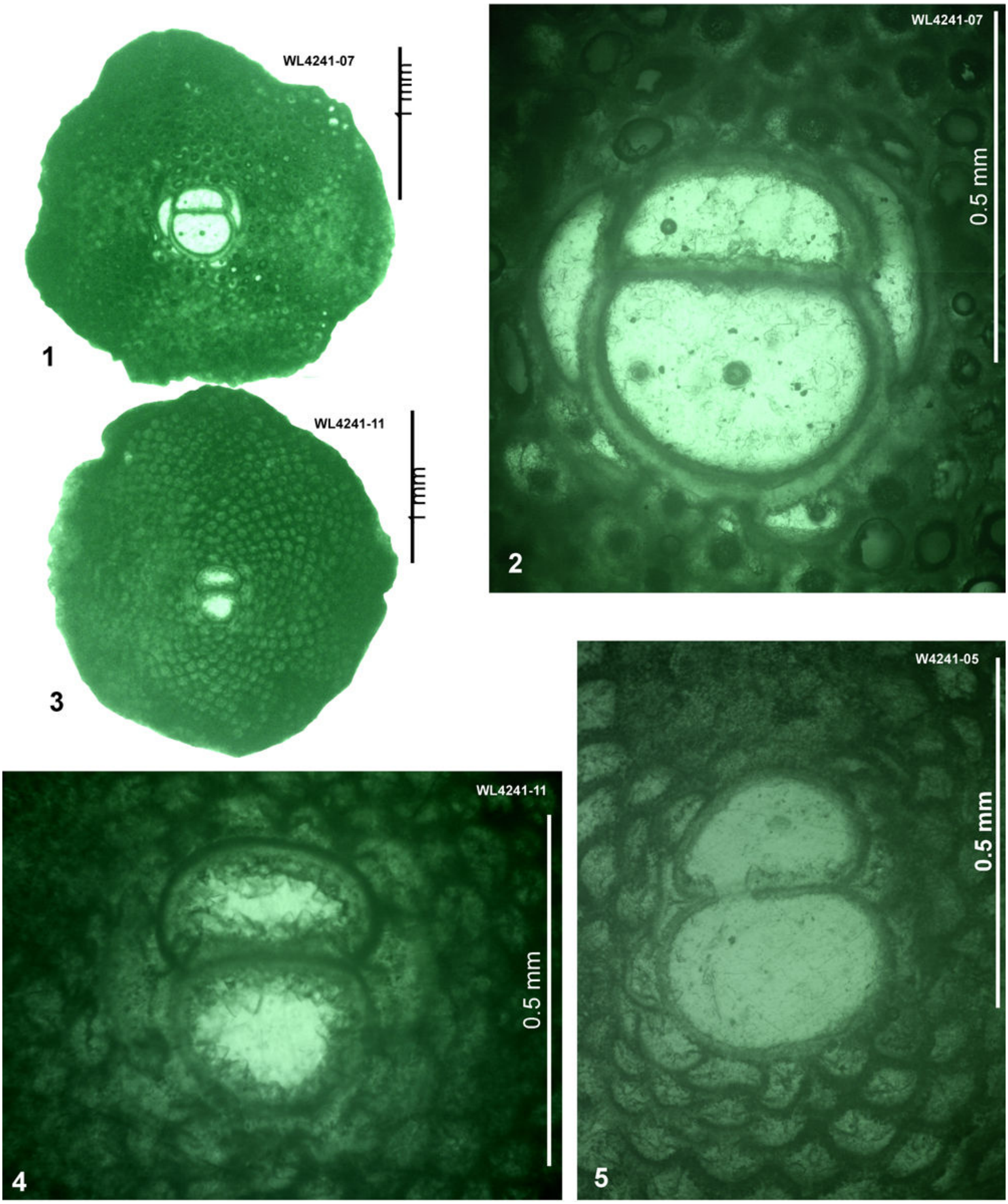


Figure 84: *Lepidocyclina ariana* COLE & PONTON, 1934. **1-2** (UWIGM.WL4241-07), **3-4** (UWIGM. WL4241-11), **5** (UWIGM.WL4241-05), megalospheric specimens, equatorial sections. Sample WL4241 (ABZ12), chalks with scattered cherts, Spot Valley, parish of St James, Jamaica.

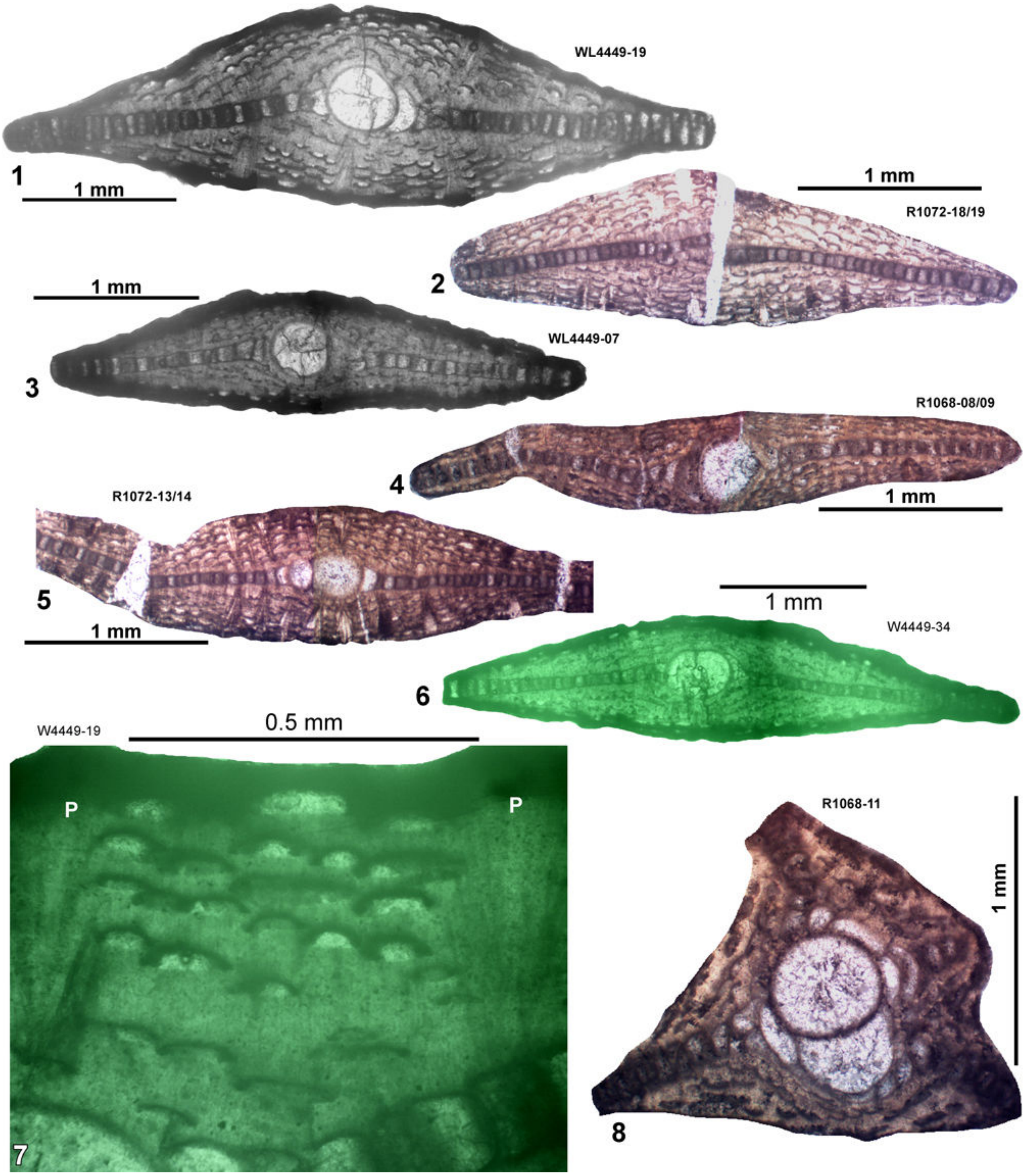


Figure 85: *Lepidocyclina macdonaldi* Cushman, 1920. **1** (WL4449-19), axial section, megalospheric form. **2** (R1072-18/19), off-centred, axial section, microspheric form. **3** (WL4449-07), axial section, megalospheric specimen. **4** (R1068-08/09), axial section, megalospheric form. **5** (R1072-13/14), axial section, megalospheric form. **6** (WL4449-34) axial section, megalospheric form. **7** (WL4449-19), detail of axial section (same as 82.1), showing form of lateral chamberlets at two pillars (P). **8** (R1068-11), equatorial section, slightly off centre, megalospheric form with selliform morphology. **1, 3, 6-7**: sample WL4449, Cold Spring, Hanover (ABZ14). **2, 4-5, 8**: samples R1068 and R1072, Sherwood Content, Trelawny (ABZ14).

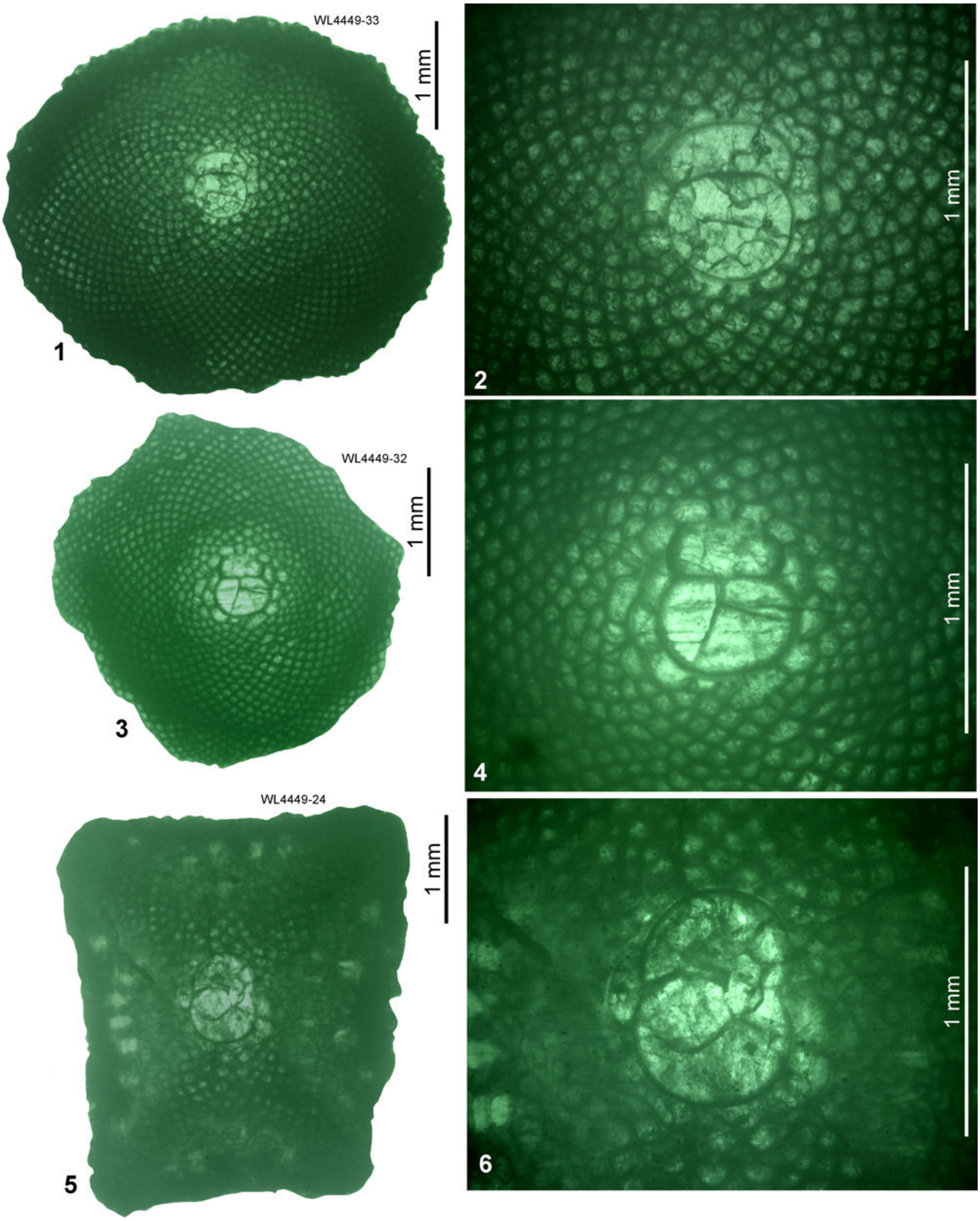


Figure 86: *Lepidocyclina macdonaldi* Cushman, 1920. **1-2** (WL4449-33), equatorial sections, megalospheric specimen. **3-4** (WL4449-32), equatorial sections, megalospheric specimen. **5-6** (WL4449-24), equatorial sections, weakly selliform megalospheric specimen. Sample WL4449, Cold Spring, Hanover (ABZ14).

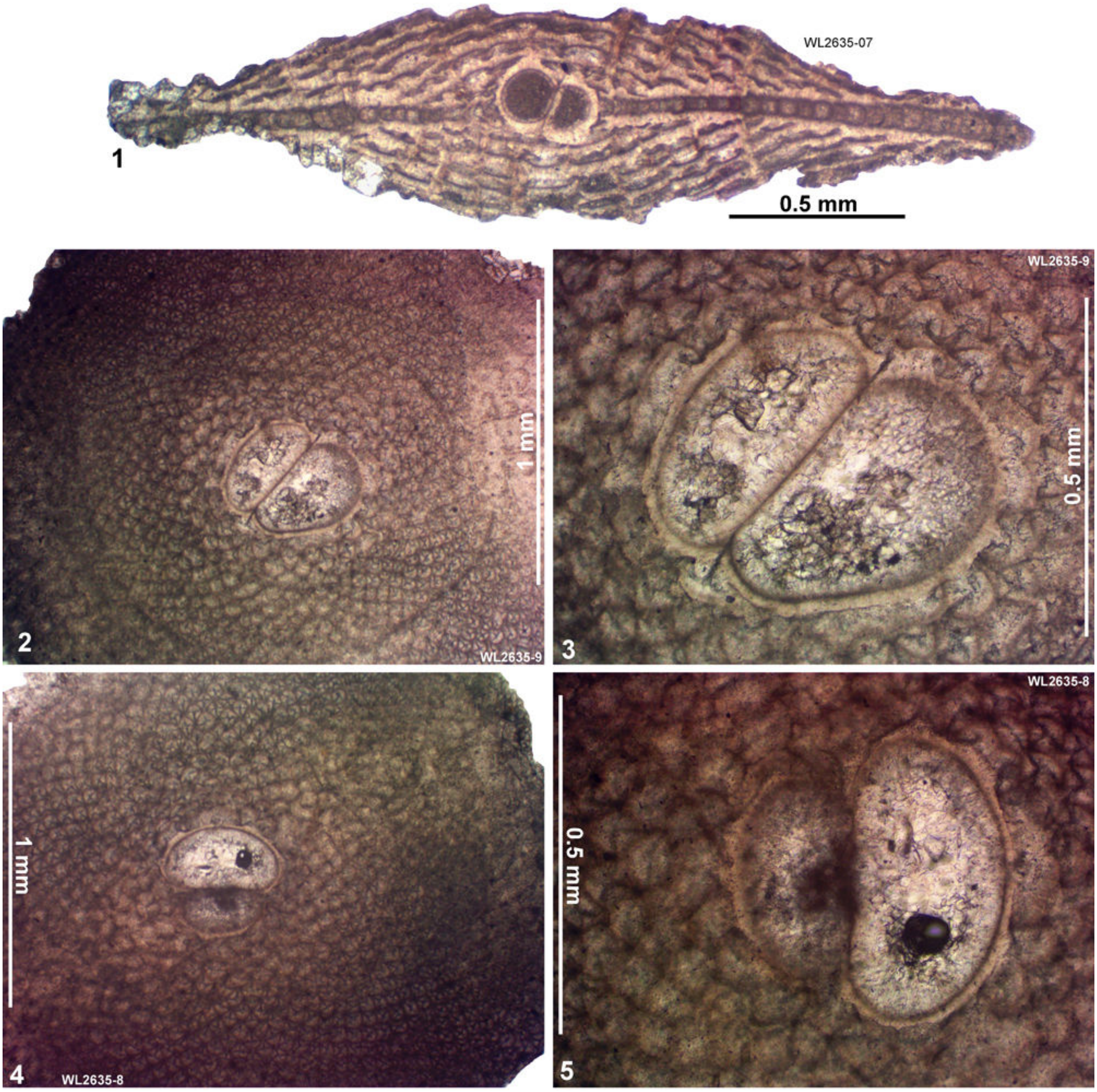


Figure 87: *Lepidocyclina ocalana* CUSHMAN, 1920, megalospheric specimens. **1** (UWIGM.WL2635-07), axial section, showing the embryo at an inclined angle to the equatorial plane. **2-3** (UWIGM.WL2635-9), equatorial section. **4-5** (UWIGM.WL2635-8), equatorial section; the difference in size between the first two chambers is probably due to the embryo being inclined as in 87.1. Ipswich Formation (ABZ13), Ipswich Railway Cutting, Ipswich, St Elizabeth, Jamaica.

variants of a single morphospecies. In axial section *Lep. ocalana* has a small number of layers of lateral chamberlets (up to about 7), which have open vacuoles, which are about as wide as the floors/roofs. Piles (pillars) are well developed.

Remarks. The species differs markedly from *Lep. macdonaldi* in axial section, with the later having arc-shaped, thin lateral chamberlets. Axial sections of the two species cannot be confused, but equatorial sections can. Equatorial sections sometimes show one larger and one smaller embryonic chamber (*e.g.*, Fig. 87.4-5), but this may be due to the embryo being tilted at an angle to the equatorial plane (*e.g.*, Fig. 87.1).

Range. In Florida *Lep. ocalana* occurs in the Ocala Limestone with *Eulepidina chaperi* and *Heterostegina ocalana* (COLE, 1941, 1943). In Panama, this species occurs with *Pliolepidina tobleri*, *Eulepidina chaperi* and *Heterostegina ocalana* (COLE, 1952). We have specimens in Jamaica from the middle unit of the Ipswich Formation (although these have a smaller embryo; Fig. 87), the Swanswick Formation *sensu lato*, the Claremont Formation and the Somerset Formation. The species therefore ranges through ABZ13 to ABZ16, and there is an increase in the size of the embryo passing from ABZ13 to ABZ14/ABZ15.

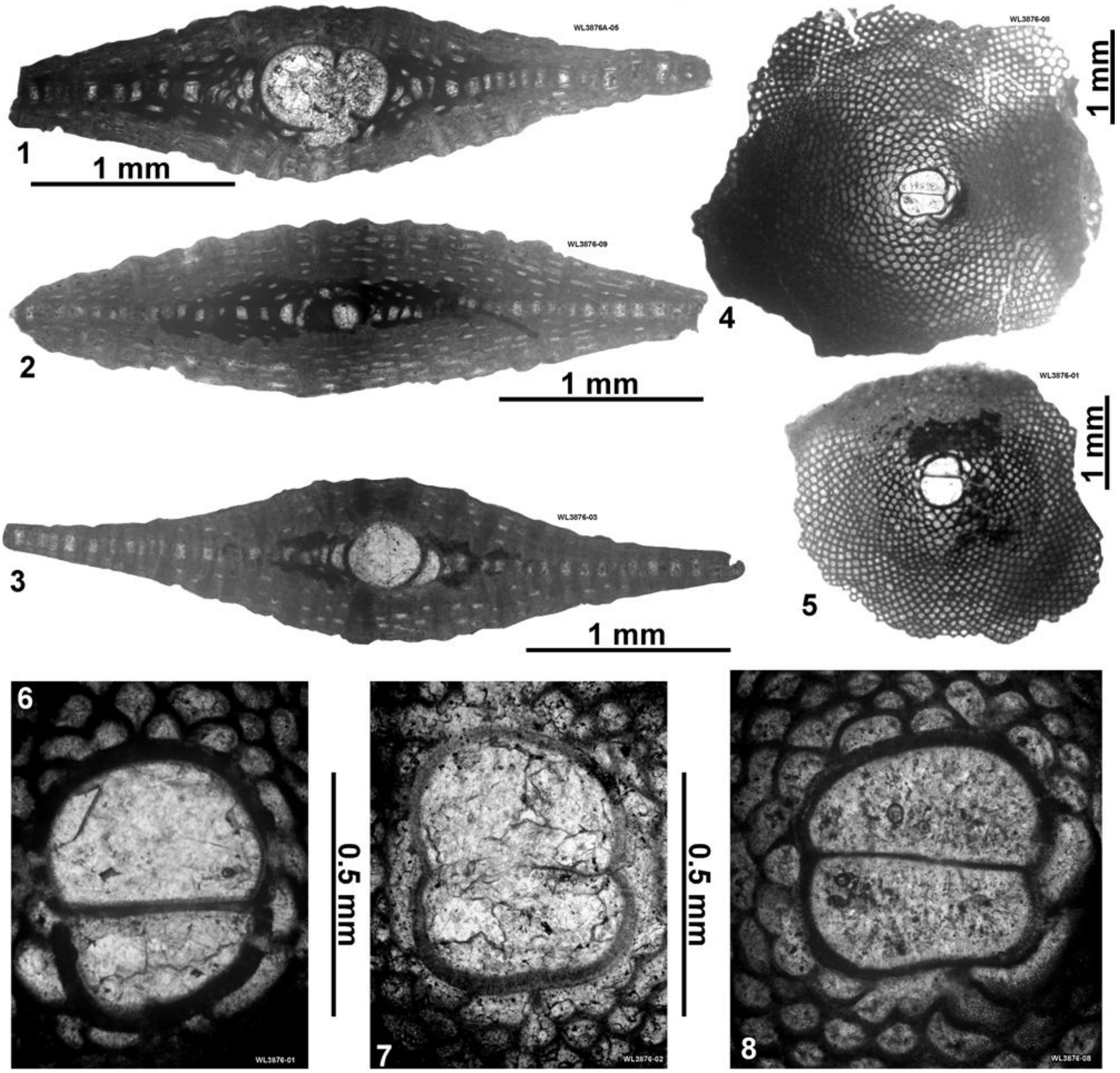


Figure 88: *Lepidocyclina ocalana* Cushman, 1920, megalospheric specimens. **1** (UWIGM.WL3876A-5), axial section. **2** (UWIGM.WL3876-09), axial section. **3** (UWIGM.WL3876-03), axial section. **4, 8** (UWIGM. WL3876-08), equatorial section. **5-6** (UWIGM.WL3876-01), equatorial section, note development of one adauxilary chamber on protoconch. **7** (UWIGM.WL3876-02), equatorial section. Swanswick Formation *s.l.* (ABZ15), Highway 2000, St Ann, Jamaica.

Genus *Eulepidina* Douvillé, 1911, p. 59

Type species. *Orbitoides dilatata* Michelotti, 1861 from the early Miocene of northern Italy (Michelotti, 1861).

Synonyms. *Trybliolepidina* ven der Vlerk, 1928 (type species *Orbitoides (Lepidocyclina) ephippioides* Jones & Chapman, 1900) [junior synonym].

Remarks. We follow Robinson (2004) in placing *Lepidocyclina chaperi* as the earliest species of *Eulepidina*.

Eulepidina chaperi
(Lemoine & R. Douvillé, 1904)

(Figs. 90 - 91)

Previous descriptions and figures. Cole, 1952, p. 23-27, Pl. 8, figs. 5-8; Pl. 9, figs. 3-19; Pl. 10, figs. 1-10; Pl. 11, figs. 1-8; Pl. 12, figs. 1-15; Pl. 20, figs. 8-10; Pl. 23, figs. 8, 11-12.

Recognition. The species is easily distinguished in equatorial section by the deuteroconch partially enveloping the protoconch, by the small

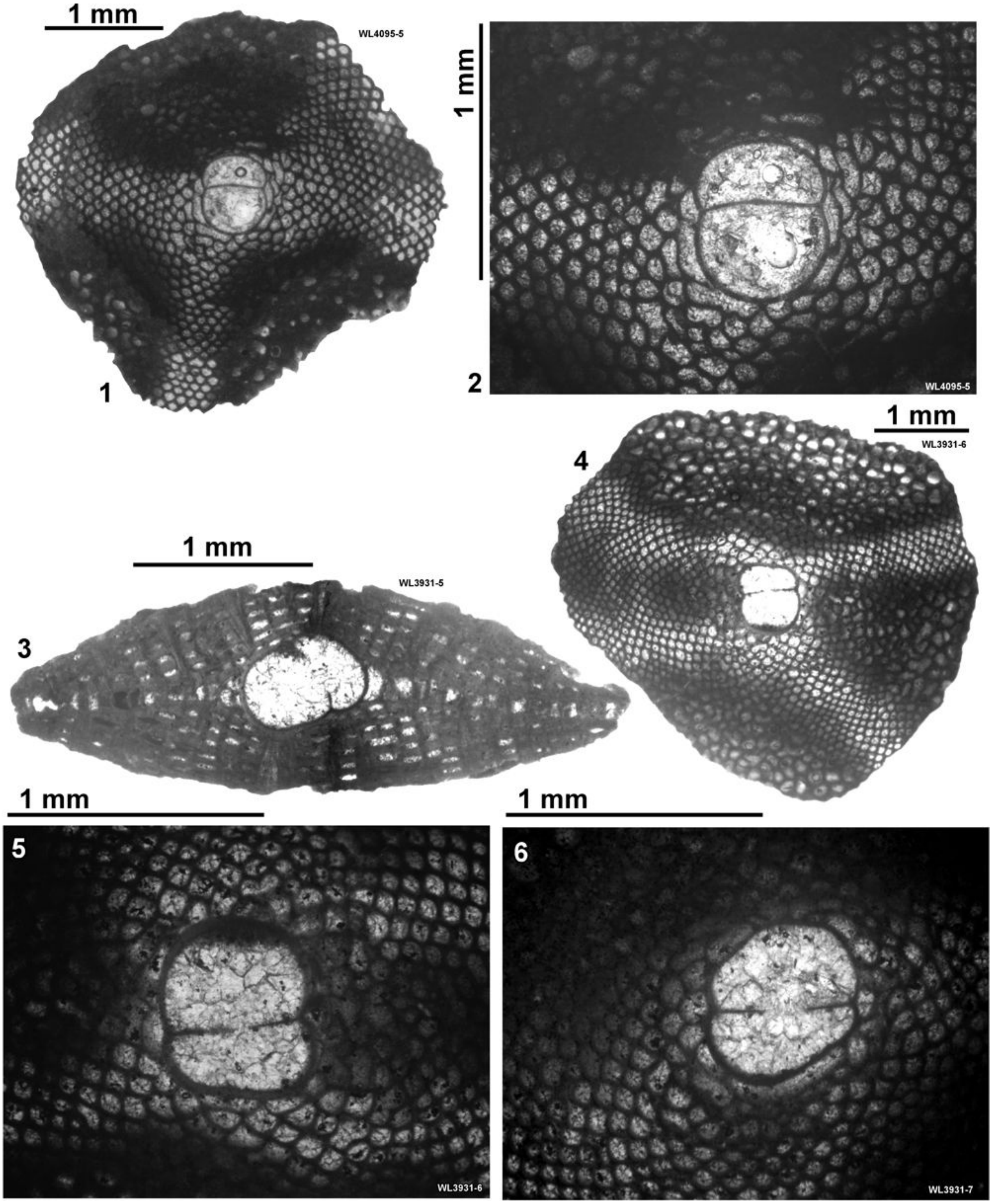


Figure 89: *Lepidocyclina ocalana* CUSHMAN, 1920, megalospheric specimens. **1-2** (UWIGM.WL4095-05), equatorial section, weakly selliform with equatorial chamberlets in annular rings. **3** (UWIGM.3931-5), axial section. **4-5** (UWIGM.3931-6), equatorial section, weakly selliform variety. 6 (UWIGM.3931-7), equatorial section. **1-2**, Claremont Formation (ABZ15); **3-6**, Somerset Formation (ABZ16); Highway 2000, St Ann, Jamaica.

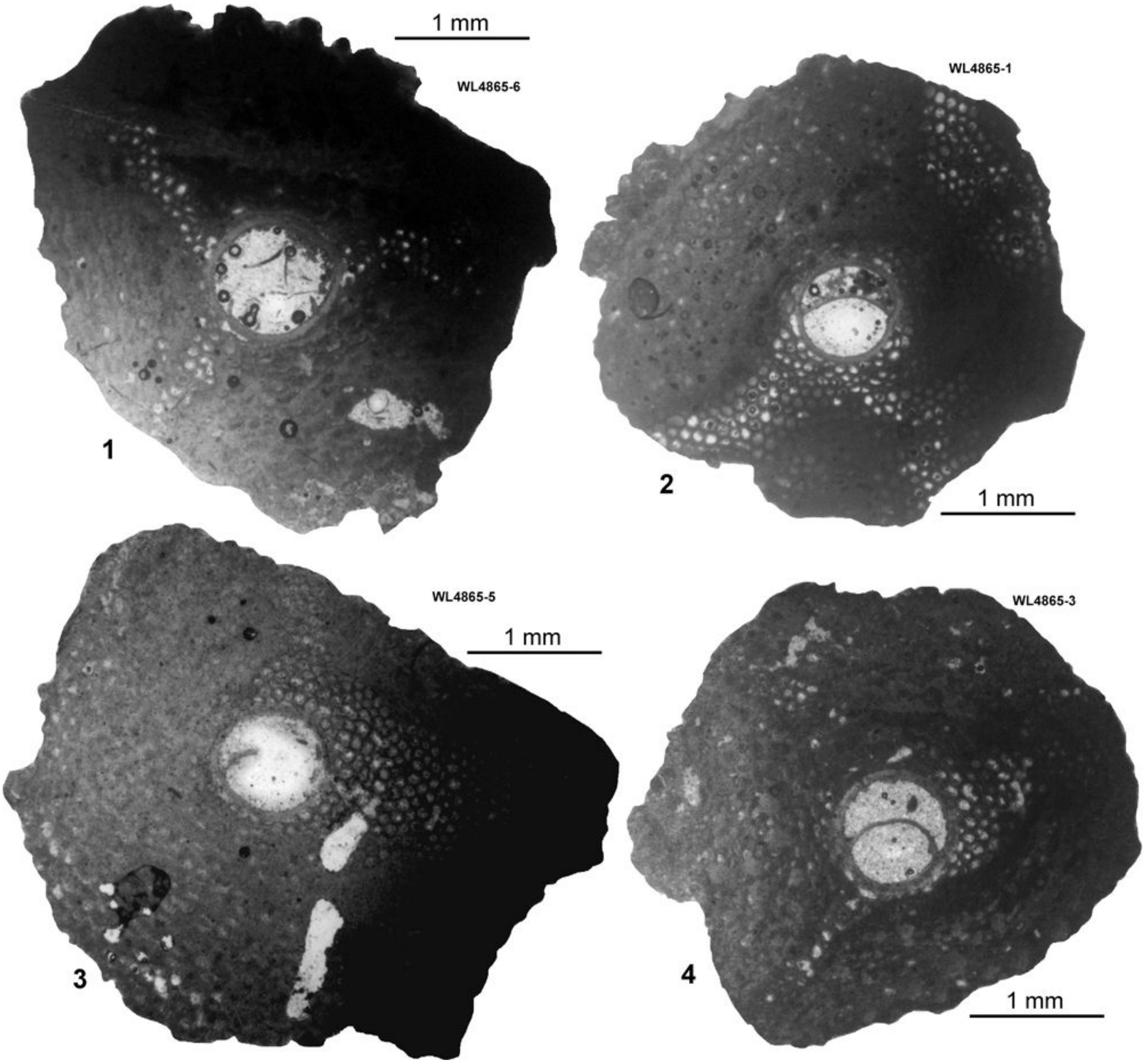


Figure 90: *Eulepidina chaperi* (Lemoine & R. Douvillé, 1904), rather poorly preserved. **1** (UWIGM.WL4865-6); **2** (UWIGM.WL4865-1); **3** (UWIGM.WL4865-5); **4** (UWIGM.WL4865-3): megalospheric specimens, equatorial sections. Sample WL4865, chalk (ABZ16), Dressikie, parish of St Mary, Jamaica.

and numerous peri-embryonic chambers and by the annular arrangement of the equatorial chamberlets. Specimens range from lenticular to weakly selliform (saddle-shaped). The species is distinguished from Oligocene species (such as, *Eu. undosa* and *Eu. favosa*) by its relatively similar diameters of the protoconch and deuteroconch, whereas in the Oligocene species the deuteroconch has a much greater diameter than the protoconch. The length of the embryo of *Eu. chaperi* is notably larger than that of co-occurring specimens of *Lep. ocalana*. *Eu. chaperi* occurs in upper ABZ15, ABZ16, and in the earliest Oligocene (ABZ17).

Subfamily ORBITOININAE
Mitchell, E. Robinson & Özcan
subfam. nov.

Diagnosis. The subfamily shows a parallel development to the Lepidocyclininae through eolepidine, unilepidine, polylepidine and lepidocycline forms to nephrolepidine forms. Early members of the subfamily have a relatively large number of well-developed lateral chamberlets in contrast to the early members of the Lepidocyclininae, which have none. The earliest member of the subfamily is *Planorbitoinella* gen. nov., which has well-developed lateral chamberlets. It is likely that the Orbitoinidae initially evolved in north-eastern South America during the Lutetian and subsequently spread across the American LBF bioprovince.

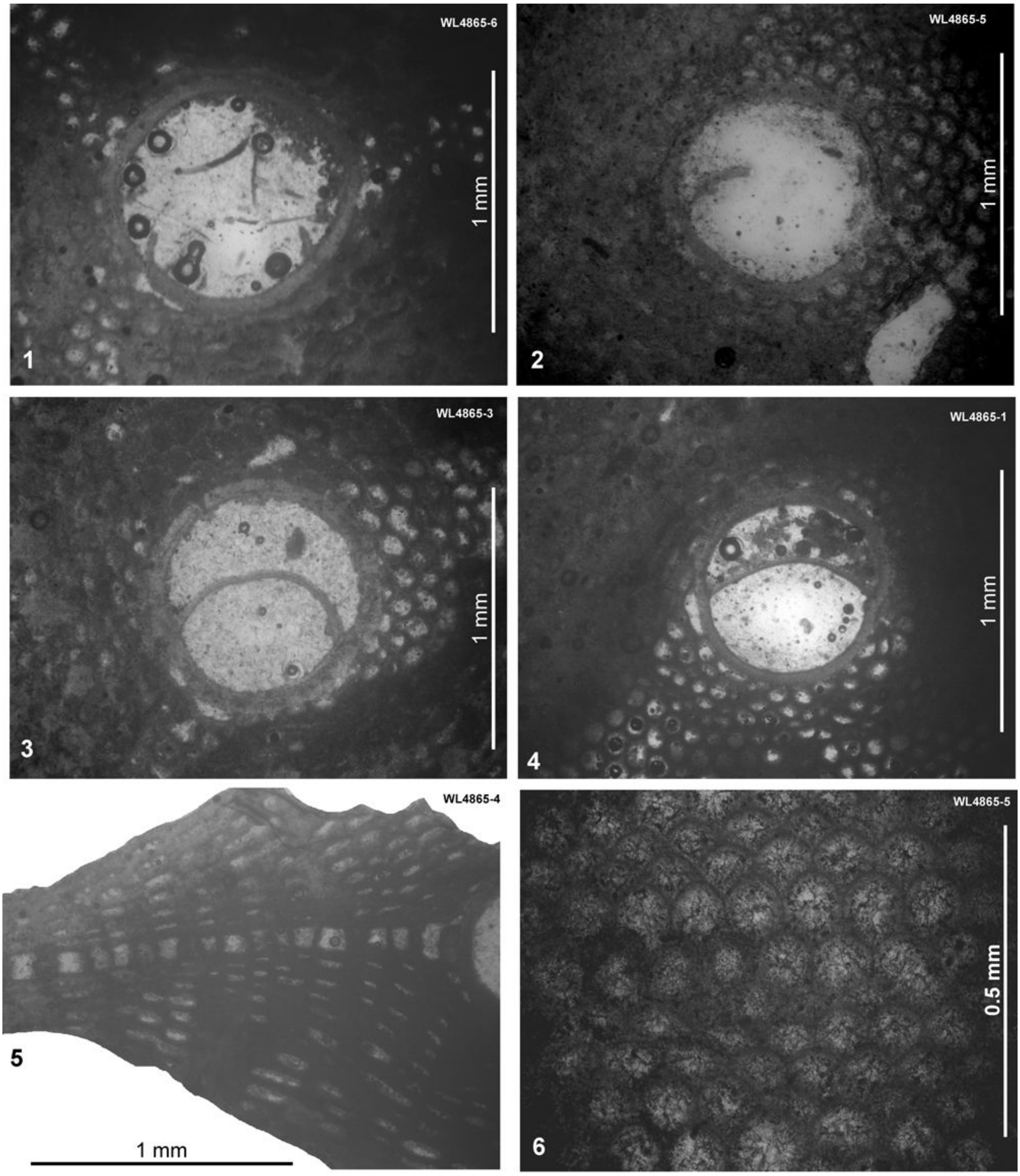


Figure 91: *Eulepidina chaperi* (LEMOINE & R. DOUVILLÉ, 1904), rather poorly preserved specimens. **1** (UWIGM.WL 4865-6); **2** (UWIGM.WL4865-5); **3** (UWIGM.WL4865-3); **4** (UWIGM.WL4865-1): details of embryo, with the walls of the protoconch partially broken away in 1 and 2 - note the thickened embryo wall. **5** (UWIGM.WL4865-4), axial section, showing lateral chamberlets. **6** (UWIGM.WL4865-5), details of equatorial chamberlets showing annular arrangement. Sample WL4865 (ABZ16), chalk, Dressikie, parish of St Mary, Jamaica.

Genera included. *Planorbitoinella* gen. nov., *Polyorbitoinella* gen. nov., *Orbitoina* SCHENCK & FRIZZELL, 1936, *Pliolepidina* DOUVILLÉ, 1915, *Nephrolepidina* DOUVILLÉ, 1911.

Remarks*.* The evolutionary development of this subfamily is parallel to that of the Lepidocyclininae and gives rise to homeomorphs. Details of the Orbitoininae are give in Tables 20-21 and Figs. 92 - 95. *Planorbitoinella* gen. nov. gives rise to *Polyorbitoinella* gen. nov., which in turn gives rise to *Orbitoina*, and *Orbitoina* gives rise to *Pliolepidina*. *Nephrolepidina* (not shown) with its small embryo, probably evolved from *Orbitoina*, but this requires further work. Here we describe the forms that have so far been found in Jamaica and comment on selected forms from the Ameri-

Table 20: Measurements of the length of the embryo (Ele) for species of Orbitoininae

Species	Sample	Zone	Length of nucleus (µm)				Source
			range	mean	SD	n	
Pl. nitida	Venezuela	ABZ7	150 - 195	-	-	2	*Raadshooven, 1951
Pl. ecuadorensis?	Venezuela	ABZ7	210 - 220	-	-	2	*Raadshooven, 1951
Pl. ecuadorensis	WL4869 Grants Town	ABZ7	-	206	-	1	Our measurements
Pl. ecuadorensis	WL3309 Farm Turn	ABZ7	-	118	-	1	Our measurements
Pl. ecuadorensis	WL3310 Farm Turn	ABZ7	89 - 166	135	29	7	Our measurements
Pl. ecuadorensis	WL3324 Kilancholly	ABZ7	-	162	-	1	Our measurements
Pl. ecuadorensis	Clay Pebble Bed, Ecuador	-	120 - 150	-	-	-	Hofker, 1956
Po. lilyfieldensis	WL2047 Jamaica	ABZ8	-	153	-	1	Our measurements
Po. lilyfieldensis	WL2046 Jamaica	ABZ8	215 - 310	149	23.5	12	Our measurements
Po. lilyfieldensis	WL2044 Jamaica	ABZ9	155 - 275	214	32.6	9	Our measurements
Po. lilyfieldensis	WL2041 Jamaica	ABZ9	210 - 215	213	3.5	2	Our measurements
O. cedarkeysensis	Florida	ABZ13?	160 - 200	-	-	-	Cole, 1944
O. wrighti	WL3876/3876A	ABZ15	239 - 330	2714	42.0	4	Our measurements
O. rdouvillei	Types (Peru)	-	265 - 295	-	-	-	Todd & Barker, 1932
O. rdouvillei	Borthworth's (Peru)	-	222 - 240	-	-	-	Todd & Barker, 1932
O. rdouvillei	Cardo Grits (Peru)	-	204 - 307	-	-	-	Todd & Barker, 1932
O. rdouvillei	Organos Grits (Peru)	-	207 - 307	-	-	-	Todd & Barker, 1932
O. rdouvillei	Yapato Grits (Peru)	-	248 - 315	-	-	-	Todd & Barker, 1932
O. rdouvillei	All specimens (Peru)	-	204 - 340	276	-	-	Todd & Barker, 1932
O. rdouvillei	Peru	-	145 - 260	195	-	9	Colletti *et al.*, 2019
O. rdouvillei	WL3446 Jamaica	ABZ11	238 - 378	310	45.5	12	Our measurements
O. rdouvillei	Florida	ABZ11	240 - 460	315	77.1	8	Cole, 1944
O. rdouvillei	WL4241 Jamaica	ABZ12	256 - 363	310	75.7	2	Our measurements
O. sherwoodensis	Jamaica	-	240 - 400	-	-	-	Vaughan, 1928
O. rdouvillei	WL4449 (reworked)	ABZ14	255 - 510	370	105.1	4	Our measurements
O. trinitatis	Trinidad	-	300 - 350	-	-	-	Douvillé, 1924
O. trinitatis	Trinidad	-	400 - 650	-	-	-	Eames *et al.*, 1962
O. trinitatis	WL3571 Jamaica	ABZ12	383 - 470	428	43.6	3	Our measurements
O. kugleri	Venezuela	-	350 - 400	-	-	-	Vlerk, 1932
O. trinitatis	WL2635 Jamaica	ABZ13	333 - 486	410	108.2	2	Our measurements

*Specimens measured from illustrations in publications (which is dependent on accuracy of plate reproduction when only magnifications were given). $^+$ Specimens considered reworked.

Table 21: Width of Proloculus/Protoconch (Pwi) for species of Orbitininae from Jamaica

Species	Sample	Zone	Width of Proloculus/Protoconch (µm)				Source
			range	mean	SD	n	
Pl. ecuadorensis	WL4869 Grants Town	ABZ7	-	107	-	1	Our measurements
Pl. ecuadorensis	WL3309 Farm Turn	ABZ7	-	79	-	1	Our measurements
Pl. ecuadorensis	WL3310 Farm Turn	ABZ7	51 - 118	95	24.7	7	Our measurements
Pl. ecuadorensis?	WL3324 Kilancholly	ABZ7	-	118	-	1	Our measurements
Pl. ecuadorensis?	WL2047 Jamaica	ABZ8	-	112	-	1	Our measurements
Po. lilyfieldensis	WL2046 Jamaica	ABZ8	160 - 205	179	15.2	12	Our measurements
Po. lilyfieldensis	WL2044 Jamaica	ABZ9	130 - 200	160	23.0	8	Our measurements
Po. lilyfieldensis	WL2041 Jamaica	ABZ9	130 - 170	150	28.3	2	Our measurements
Pa. wrighti	WL3876/3876A	ABZ15	110 - 214	150	56.2	3	Our measurements
O. rdouvillei	WL3446 Jamaica	ABZ11	142 - 264	201	31.9	12	Our measurements
O. rdouvillei	WL4241 Jamaica	ABZ12	128 - 187	158	41.7	2	Our measurements
O. rdouvillei	WL4449 Jamaica	ABZ14 $^+$	158 - 230	197	34.6	4	Our measurements
O. trinitatis	WL3571 Jamaica	ABZ12	277 - 292	282	8.4	3	Our measurements
O. trinitatis	WL2635 Jamaica	ABZ13	206 - 343	275	96.9	2	Our measurements

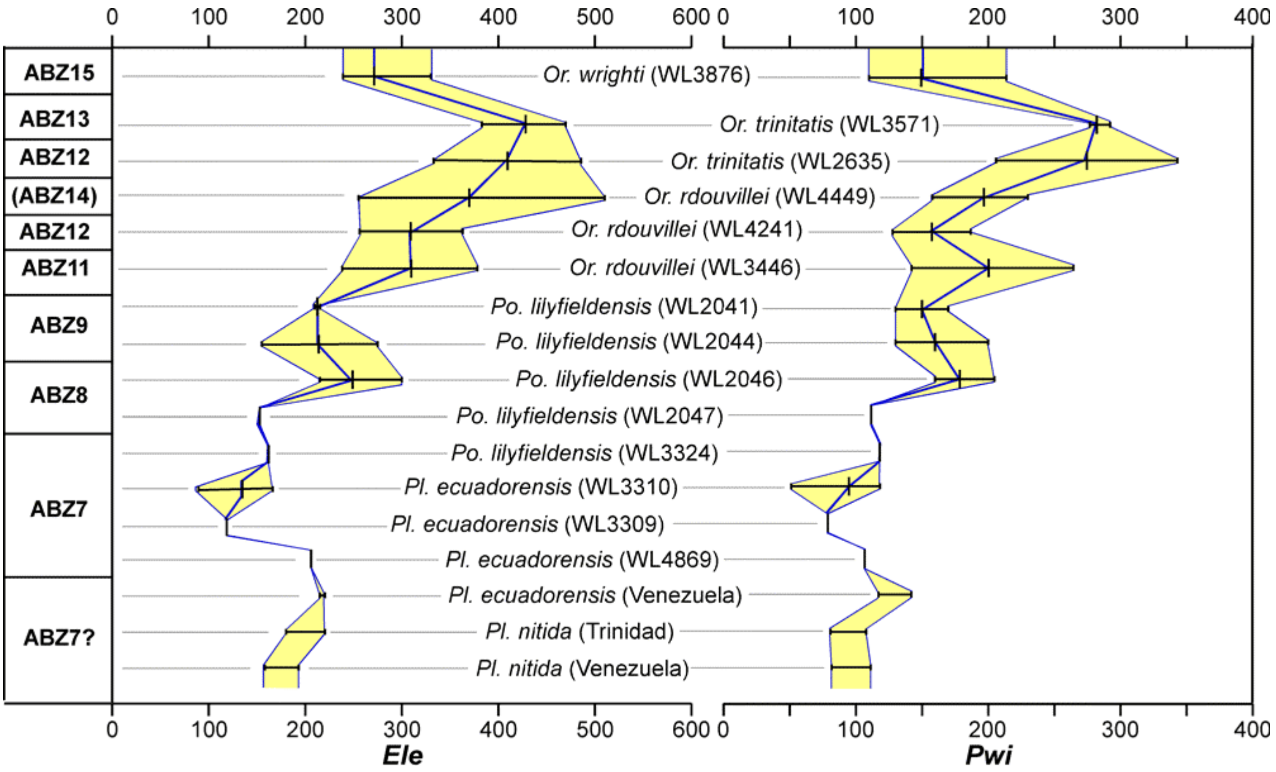


Figure 92: Length of embryo (Ele) and width of proloculus/protoconch (Pwi) for the evolution of the Orbitoininae plotted against zone.

can LBF bioprovince. Furthermore, as we get higher in the Eocene, the distinction between the Lepidocyclininae and the Orbitoininae becomes more difficult because of convergent morphologies, and assignment of specimens to a genus becomes more problematic. Table 20 provides measurements of the length of the embryo, including the walls (Ele) for different species belonging to the Orbitoininae. Table 21 provides measurements of the width of the proloculus/protoconch, excluding the walls (Pwi) for different species belonging to the Orbitoininae. Variations of the length of the embryo (Ele) and width of the proloculus/protoconch are shown in Fig. 92 and a plot of Ele versus Pwi is shown in Fig. 93.

Genus *Planorbitoinella* MITCHELL, E. ROBINSON & ÖZCAN gen. nov.

Type species. *Lepidocyclina ecuadorensis* HOFKER, 1956 from the Clay Pebble Beds of the sea cliffs at Ancon, Ecuador (HOFKER, 1956).

Diagnosis. An Orbitoininae with an eolepidine to unilepidine morphology, a small proloculus and many, well-developed tiers of lateral chambers.

Remarks. *Planorbitoinella* appears before *Eolepidina* or *Polylepidina*, and has lateral chamberlets, which are absent in early species of the Lepidocyclininae such as *Eulinderina* that occur at the same time. *Planorbitoinella* and *Eolepidina* are homeomorphs in the evolutionary development of different lineages (subfamilies) of the Lepidocyclinidae. These are the roots of GRIMSDALE's (1959) *Lepidocyclina* branches X and Y, respectively. We establish a parallel series of genera to those seen in the Lepidocyclininae and erect *Planorbitoinella* for populations with mean R = 3 and 4, and *Polyorbitoinella* for forms with mean R = 2 and asymmetrical spires of peri-embryonic chambers.

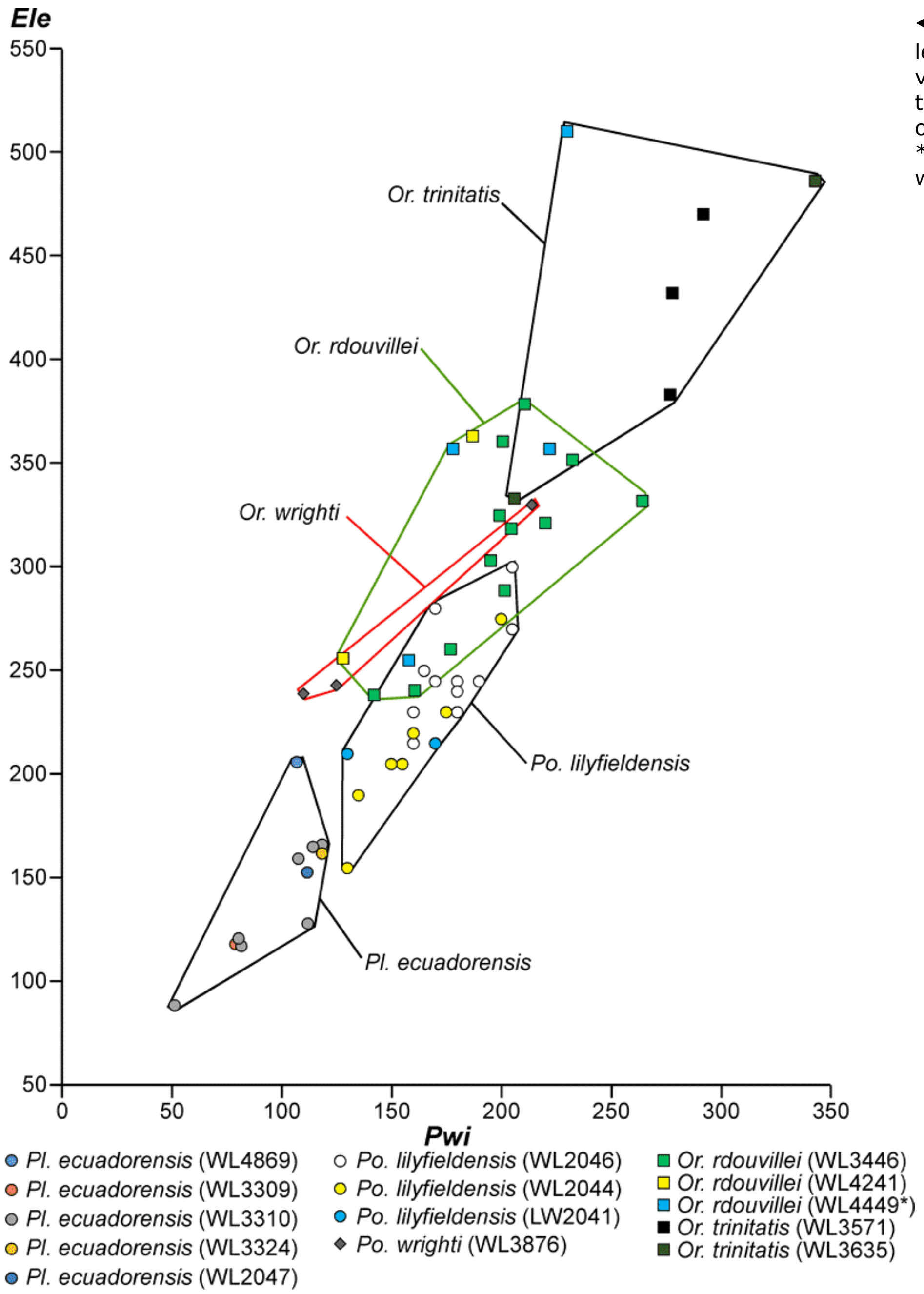
Planorbitoinella nitida (CAUDRI, 1996)

(Fig. 96.6-10)

Previous descriptions. *Lepidocyclina (Polylepidina) nitida*: CAUDRI, 1996, p. 1215-1216, Pl. 2.12-13, Pl. 14.3-8, Pl. 30.3; *Lepidocyclina* spec. A: RAADSHOOVEN, 1951, p. 482, Figs. k-l, Pl. I, fig. 6; Pl. II, figs. 1, 3-4.

Recognition. *Planorbitoinella nitida* can be recognized by having a mean R of 3.5 or more, in conjunction with the presence of multiple tiers of lateral chamberlets.

Discussion. *Planorbitoinella nitida* (CAUDRI, 1996) is the earliest species of *Planorbitoinella* that we are aware of. The species shows an eolepidine morphology combined with well-developed lateral chamberlets. In Venezuela, RAADSHOOVEN (1951) reported *Lepidocyclina* spec. A (= *Pl. nitida*) as occurring in the Quebrada Grande Limestone (Baralt District, State of Zulia, western Venezuela) with *Helic. gyralis* and *Operculinoides* cf. *oliveri*, but at a lower level than *Lep.* spec. B (= *Pl. ecuadorensis*). The associated foraminifers would suggest an assignment to a level low in ABZ7. This assemblage has not been seen by us in Jamaica. In Trinidad, *Pl. nitida* occurs with *Operculinoides* spp. (CAUDRI, 1996) and can therefore be assigned to ABZ7.



◀ **Figure 93:** Cross plot of length of embryo (Ele in µm) versus width of proloculus/protoconch (Pwi in µm) for species of Orbitoininae from Jamaica. *includes indigenous and reworked specimens.

The material illustrated by Caudri (1996; Fig. 96.10-12) shows an embryo succeeded by one chamber and then the chamber with the first retrovert aperture; thus mean R = 4. Three specimens of *Lep*. spec. A were illustrated by Raadshooven (1951); two have R = 4 (*e.g.*, Fig. 96.8) and one has R = 3 and the secondary spire from R has only one chamber (Fig. 96.9). This would suggest a provisional assignment to *Pl. nitida* pending the study of more specimens.

Planorbitoinella ecuadorensis (Hofker, 1956)

(Figs. 96.1-5, 97 - 99)

Synonymy. *Lepidocyclina* spec. B: Raadshooven, 1951, p. 481, Figs. m-n, Pl. 1, fig. 7; Pl. 2, figs. 2, 5-6; *Lepidocyclina ecuadorensis* Hofker, 1956, p. 938-939, Figs. 71-73.

Previous descriptions and figures. Hofker, 1956, p. 938-939, Figs. 71-73.

Type specimens. Hofker (1956, p. 940) stated there were four syntypes placed in the U.S. National Museum (Smithsonian). Online, the Smithsonian indicates that the holotype is USNM PR 4811, which is an uncut free specimen. Only one additional entry is present (USNM PR 4811A). The species must be interpreted based on Hofker's (1956) illustrations of an axial section (Hofker, 1956, Fig. 73b) and its arrangement of peri-embryonic chamberlets as seen in equatorial section (Hofker, 1956, Fig. 72); this shows a unilepidine arrangement (Fig. 96.6).

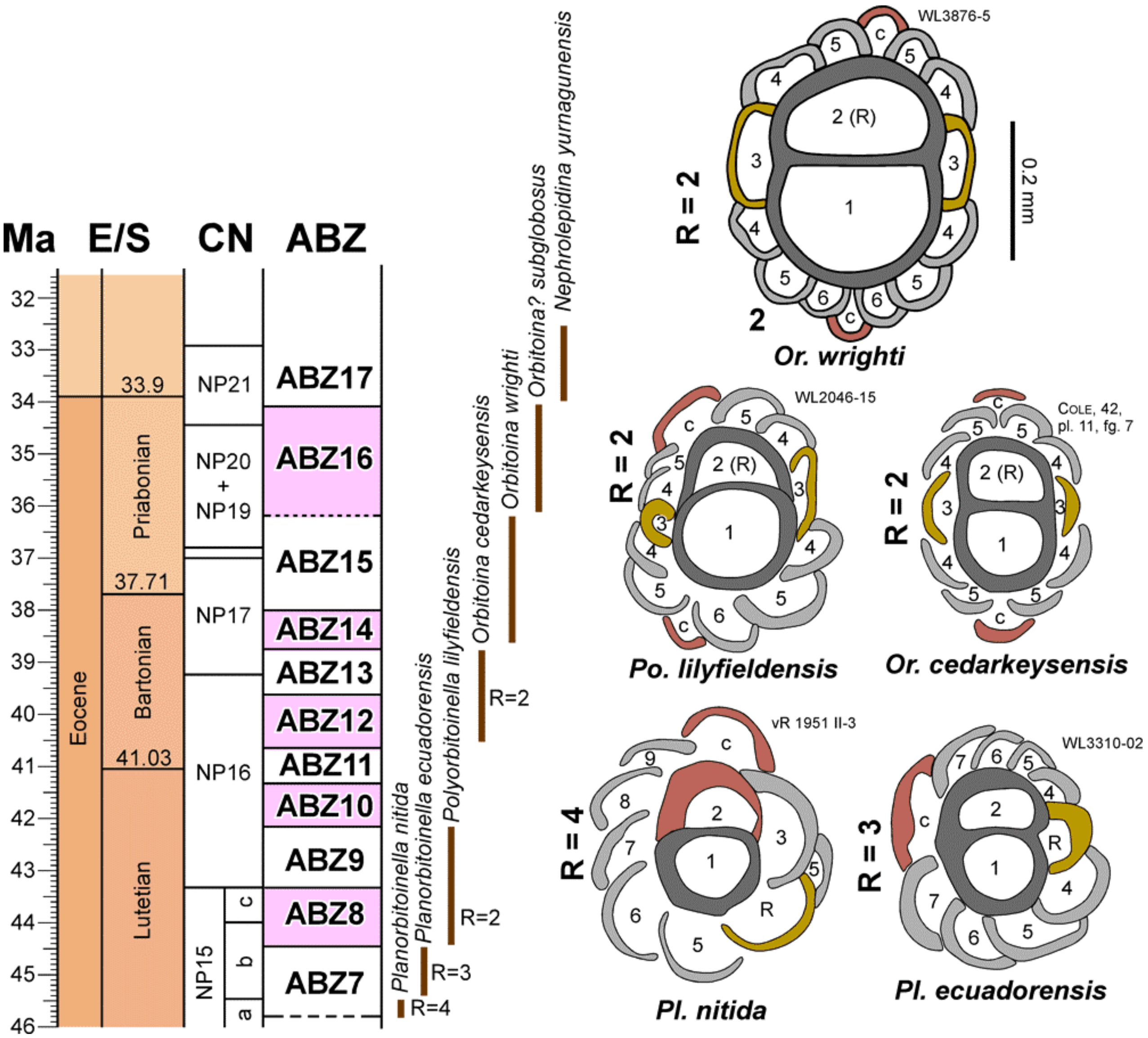


Figure 94: Evolution of the Orbitoininae with small embryos. vR = van Raadshooven.

Recognition. The species is recognised by its unilepidine arrangement (mean R = 2.2 to 3.5) of equatorial chambers in combination with a large number of lateral chamberlets with well-developed, open vacuoles. The equatorial chamberlets tend to be arranged in short radial rows. Unfortunately, Jamaican specimens are not easy to photograph, so we present a series of drawings showing the arrangements of equatorial chambers (Fig. 97) to complement the photomicrographs.

Remarks. Hofker (1956) illustrated additional specimens in his Fig. 73, but these illustrations are difficult to interpret, and our interpretation has been made based on Hofker's (1956) Fig. 72. Raadshooven (1951) illustrated three specimens of *Lep.* spec. B; two of these show a unilepidine morphology (*e.g.*, Fig. 96.3) and one shows a polylepidine morphology (Fig. 96.4); given the dominance of unilepidine forms (even with only three specimens), this material is assigned to *Pl. ecuadorensis*; this population may be a little younger than the Jamaican material assigned to *Pl. ecuadorensis*, since the latter only includes unilepidine forms (Figs. 96 - 99).

Hofker (1956) and Cushman and Stainforth (1951) attributed the occurrence of *Pl. ecuadorensis* in the Clay Pebble Beds in Ecuador to the upper middle Eocene, but placed it before the appearance of the planktic foraminifer *Hantkenina* (which they took to mark the base of the upper Eocene). *Hantkenina* appears in planktic foraminifer zone E10 (P12) and suggests that the occurrence of *Pl. ecuadorensis* is older than this. This is consistent with the occurrence of *Pl. ecuadorensis* in Jamaica which is correlated with planktic foraminifer zone E8 (upper P9).

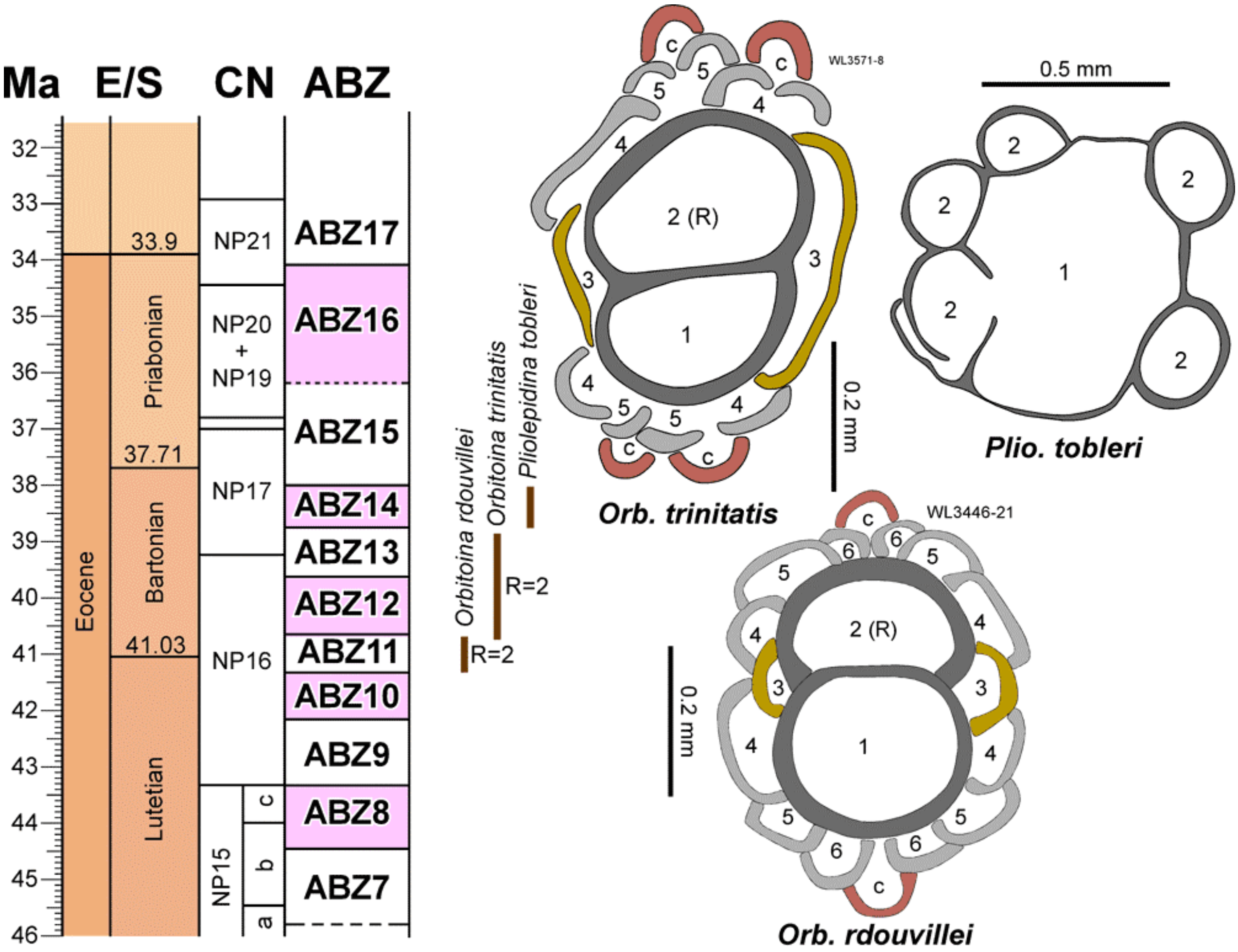


Figure 95: Evolution of the *Orbitoina* with large embryos.

In Jamaica, *Pl. ecuadorensis* occurs with *Operculinoides* spp. in the Preston Hill Formation (ABZ7) at Grants Town (St Mary), Farm Turn (St Ann) and Kilancholly (St Ann). In Venezuela, *Pl. ecuadorensis* occurs in the early middle Eocene San Juan Limestone in the Baralt District, State of Zulia, western Venezuela, where it is also associated with *Operculinoides* spp. (cited as *O. jennyi* by Raadshooven, 1951); it can therefore also be assigned to ABZ7. We therefore suspect that *Pl. ecuadorensis* is a characteristic species of upper ABZ7 (whereas *Pl. nitida* is probably a lower ABZ7 species). The lack of *Pl. nitida* in Jamaica may be due to the hiatus between ABZ6 and ABZ7 (with NP15a not being recognized).

Cole (1960) regarded *Lep. ecuadorensis* as a synonym of *Helicolepidina spirals* Tobler; whereas Adams (1987, p. 293) stated that *Lep. ecuadorensis* was a problematic species which is neither a true *Lepidocyclina*, nor a typical *Polylepidina*, while the absence of an extended primary spire prevented assignment to *Helicolepidina*. As shown here, *Pl. ecuadorensis* is close to the origin of the Orbitoininae, and is unrelated to either *Helicolepidina* or *Polylepidina*.

Genus *Polyorbitoinella*

Mitchell, E. Robinson & Özcan gen. nov.

Type species. *Polyorbitoinella lilyfieldensis* sp. nov. from the Chapelton Formation (zones ABZ7 and ABZ8) at Lilyfield, St Mary, Jamaica.

Diagnosis. An Orbitoininae with a polylepidine morphology (mean R = 2.0 - 2.2 with asymmetrical spires of epiembryonic chamberlets), a small proloculus and many, well-developed tiers of lateral chambers.

Remarks. *Polyorbitoinella* shares the same relationship with *Planorbitoinella* as *Polylepidina* does to *Eolepidina*. We regard the presence of two PACS in combination with asymmetrical spires of peri-embryonic chambers as being of generic significance by analogy with the Lepidocyclininae.

◆

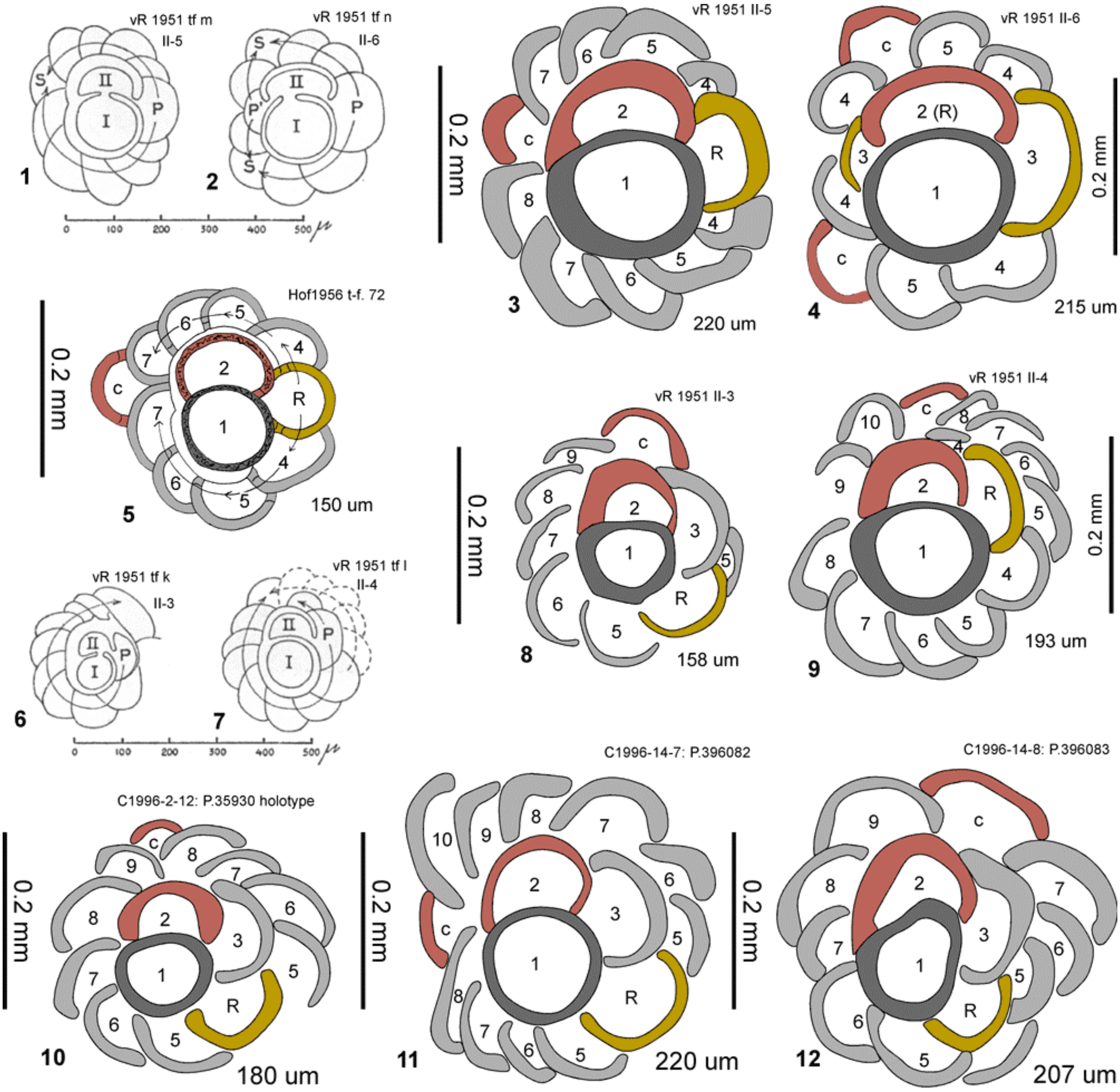


Figure 96: Drawings from published photomicrographs of the equatorial chamber arrangements of previously illustrated specimens of *Planorbitoinella nitida* and *Pl. ecuadorensis* from Venezuela, Ecuador, and Trinidad. **1-2**, original interpretations of *Lep.* spec. B (= *Pl. ecuadorensis*) as given by RAADSHOOVEN, 1951, Fig. 1 m-n. **3-4**, our interpretation of the illustrations of the same specimens of *Pl. ecuadorensis* draw from figures in RAADSHOOVEN (1951), Pl. II, figs. 5-6 (same as 95.1-2, respectively). **5**, specimen of *Pl. ecuadorensis* figured by HOFKER, 1956, from Venezuela. **6-7**, original interpretations of *Lep.* spec. A (= *Pl. nitida*) as given by RAADSHOOVEN, 1951, Fig. 1 k-l. **8-9**, our interpretation of the illustrations of the same specimens of *Pl. nitida* drawn from figures in RAADSHOOVEN (1951), Pl. II, figs. 3-4 (same as 95.8-9, respectively). **10-12**, drawings from specimens of *Pl. nitida* figured by CAUDRI (1996): holotype - Pl. 2, fig. 12; other specimens: Pl. 14, fig. 7; Pl. 14, fig. 8, respectively. See text for locations of specimens and discussion. vR = RAADSHOOVEN; Hof = HOFKER; C = CAUDRI.

Polyorbitoinella lilyfieldensis
MITCHELL, E. ROBINSON & ÖZCAN sp. nov.
(Figs. 100 - 105)

Diagnosis. As for genus.

Type specimens. Holotype: OE.WL2046-11 (Figs. 100.6, 101.3, 105.1); Paratypes: EO.WL 2046.5, WL2046.6, WL2046.10, WL2046.15, WL 2046.19, WL2046.21, WL2046.29, WL2046.31-34 (Figs. 100 - 102, 105); sample WL2046, Preston Hill Formation, Lilyfield area, St Ann (ABZ8).

Origin of name. From the district of Lilyfield in the parish of St Ann, Jamaica, where the species is found.

Description. Megalospheric specimens predominate, whereas microspheric specimens are relatively rare. Specimens are typically lenticular with a rounded umbo and a gradual thinning towards the relatively acute periphery. The ornament consists of a series of fine pustules extending across the surface of the test. Megalospheric

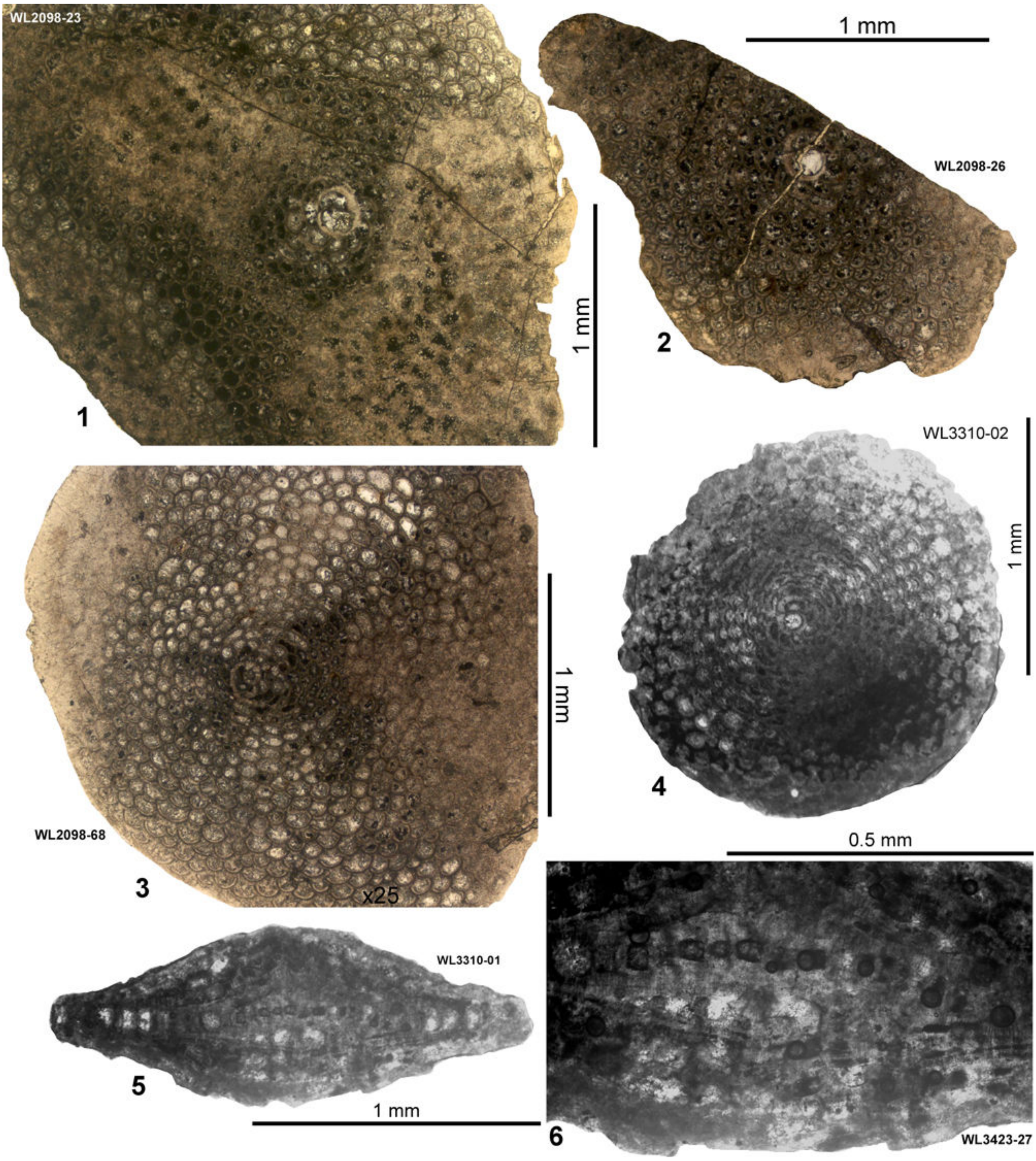


Figure 97: *Planorbitoinella ecuadorensis* (HOFKER, 1956). **1** (EO.WL2098-23), equatorial section, megalospheric specimen. **2** (EO.WL2098-26), equatorial section, megalospheric specimen. **3** (EO.WL2098-48), equatorial section, microspheric specimen. **4** (UWIGM.WL3310-02), equatorial section, megalospheric specimen. **5-6** (UWIGM.WL3310-01), axial section (slightly off-center), megalospheric specimen. Preston Hill Formation, Farm Turn, St Mary, Jamaica.

specimens have diameters of up to 2.8 mm and thicknesses of up to 0.6 mm. Orientated equatorial sections show the nepiont in detail (Figs. 100 - 101, 103 - 104). The embryo consists of two chambers and has a mean length of 213 - 249 µm with the embryo of individual specimens ranging from 155 - 310 µm. The deuteroconch is slightly smaller than the protoconch; the protoconch is circular and the deuteroconch weakly arcuate (*i.e.*, the wall is convex towards the deuteroconch). There are two PACs, one is often larger, or they may be of similar sizes. Two peri-embryonic spires develop from each PAC. At least one pair of asymmetrical spires is developed in most specimens, usually with one more chamber than the opposite spire (Fig. 105.2, .5-9, .11, .16). Spires consist of from 1 to 4 chambers excluding the closing chambers, but usually consist

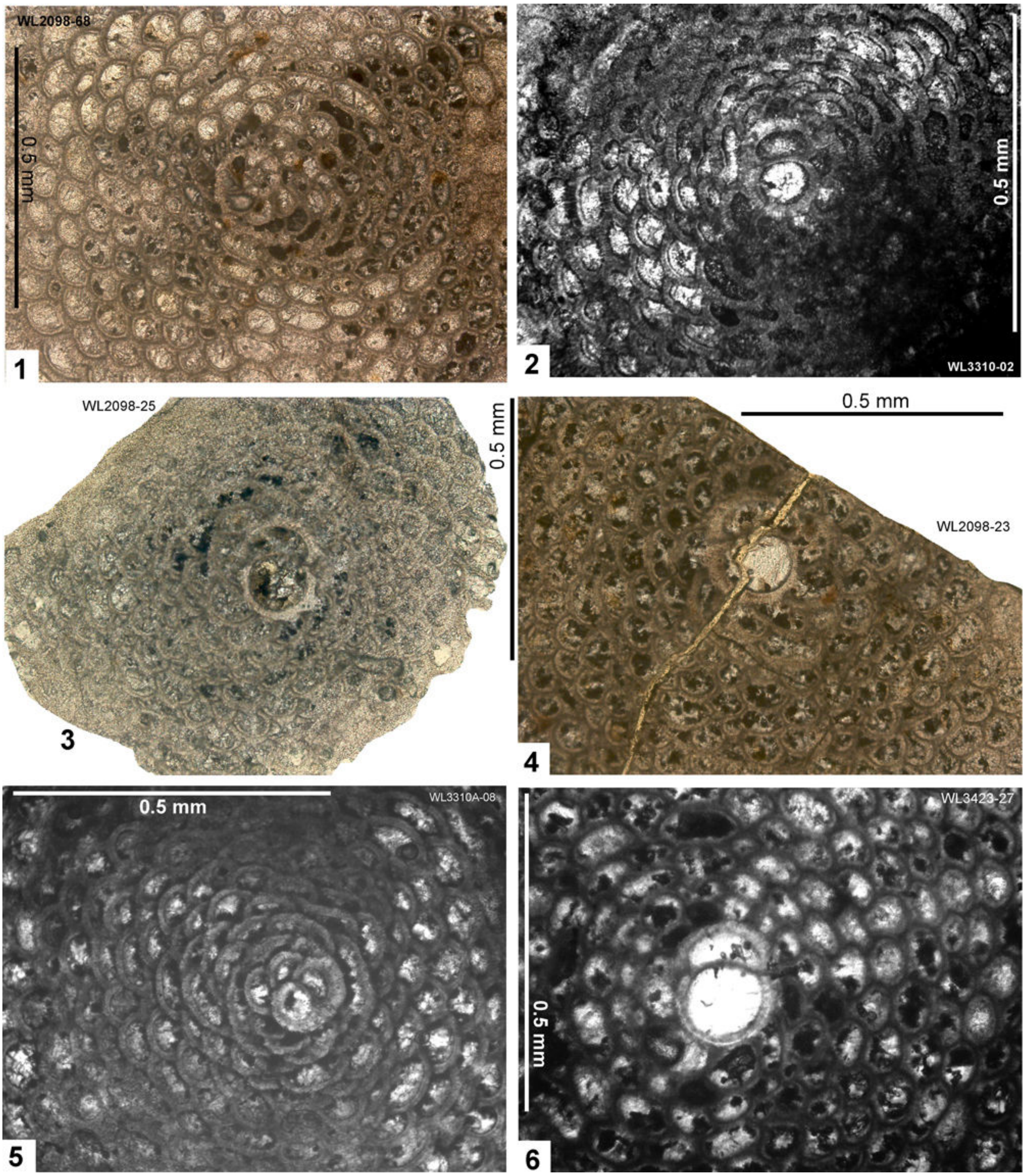


Figure 98: *Planorbitoinella ecuadorensis* (Hofker, 1956) from the Preton Hill Formation of Jamaica. **1** (EO.WL2098-68), equatorial section, microspheric form. **2** (UWIGM.WL3310-02), equatorial section, megalospheric form. **3** (EO. WL2098-25), equatorial section, megalospheric form. **4** (EO.WL2098-23), equatorial section, megalospheric form. **5** (UWIGM.WL3310A-08), equatorial section, megalospheric form with a very small embryo. **6** (UWIGM.WL3423-27), equatorial section, megalospheric form. WL2098, WL3010 and WL3010A from the Preston Hill Formation (ABZ7), Farm Turn, St Mary, Jamaica. WL3423 from the Preston Hill Formation (ABZ7), Kilancholly, St Mary, Jamaica.

of 1, 2 or 3 chambers. In a few specimens, the spires have symmetrical numbers of chambers (typically 2 to 3 chambers), but have the closing chambers arranged asymmetrically with respect to the protoconch-deuteroconch axis (*e.g.*, Fig. 105.1, .3, .10, .14-15). In a few cases (Fig. 105.4, 105.13) the peri-embryonic spires are symmetrical around the protoconch-deuteroconch axis. The three samples (WL2041, WL.2044, WL 2046) are interpreted to represent natural populations dominated by forms with two PACs and predominantly asymmetrically developed spires

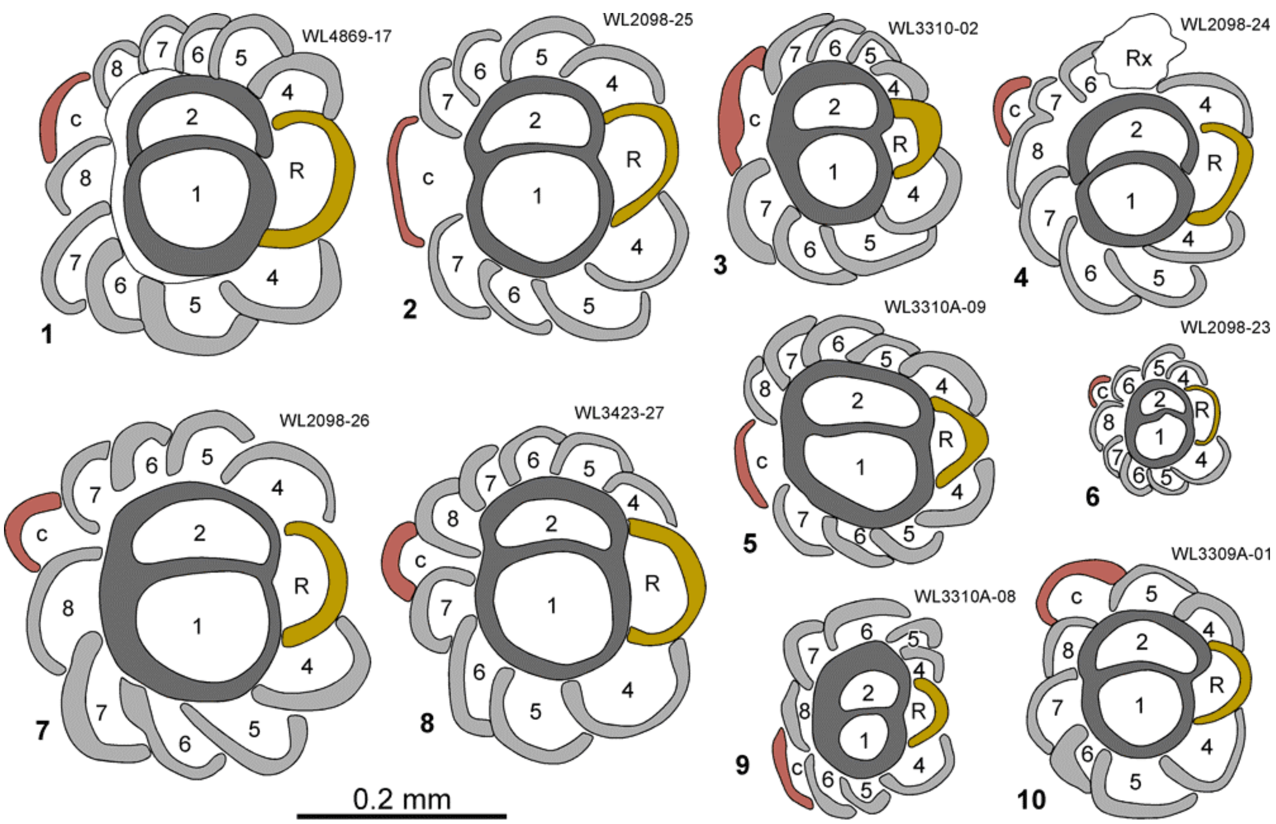


Figure 99: Line drawings of the equatorial chamber arrangement as seen in specimens of *Planorbitoinella ecuadorensis* (Hofker, 1956) from Jamaica. All specimens show a unilepidine morphology. **1** (UWIGM.WL4869-17), **2** (EO.WL2098-25), **3** (UWIGM.WL3310-02), **4** (EO.WL2098-24), **5** (UWIGM.WL3310A-09), **6** (EO.WL2098-23), **7** (EO.WL2098-26), **8** (UWIGM.WL3423-27), **9** (UWIGM.WL3310A-08), **10** (UWIGM.WL3309A-01). Preston Hill Formation (ABZ7): WL4869 from Grants Town; WL2098, WL3309A, WL3310 and WL3310A from Farm Turn; WL3423 from Kilancholly, St Mary, Jamaica. Rx, recrystallized area.

of peri-embryonic chambers or closing chambers. Orbitoidiform growth follows from the peri-embryonic spires and the equatorial chamberlets are arcuate. Axial sections are regularly elliptical (Figs. 102.6, 104.6) and have 4 to 6 layers of lateral chamberlets. The lateral chamberlets range from relatively narrow to moderately wide and overlap chamberlets of the previous layer. Piles (pillars) can be seen developed in the axial sections. Microspheric forms are rare (Figs. 101.5, 103.3, 104.5). The nepionic stage consists of 2-3 whorls of uniserial equatorial chambers, with a thickened wall which terminates in a chamber with a retrovert aperture. From this chamber a primary spiral of equatorial chambers encircles the thickened wall and terminates in a closing chamber of the short counter spiral. Orbitoidiform growth consisting of equatorial chamberlets in microspheric forms is similar to megalospheric specimens.

Distribution. Zones ABZ8 - ABZ9, Lilyfield, parish of St Ann, Jamaica, where it occurs with *Eolepidina antillea* (ABZ8) and *Eo. subplana* (ABZ9).

Remarks. *Polyorbitoinella lilyfieldensis* gen. nov., sp. nov. occurs in Jamaica through zones ABZ8-ABZ9 in the Preston Hill and Chapelton formations at Lilyfield, parish of St Ann; all levels are characterised by specimens that have predominantly asymmetrical spires or asymmetrical closing chambers (specimens with symmetrical spires and closing chambers are rare and considered part of the normal populations). The species shows a similar nepionic development to *Polylepidina chiapasensis* (ABZ11), but occurs with more primitive species of the Lepidocyclininae (*Eo. antillea* and *Eo. subplana*). *Po. lilyfieldensis* can be distinguished from *Polylepidina* by its smaller embryo and its greater number of layers of lateral chamberlets.

Genus *Orbitoina*

SCHENCK & FRIZZELL, 1936

Type species. *Isolepidina trinitatis* Douvillé, 1924 from the middle or late Eocene of Trinidad (by original designation).

Synonymy. *Orbitoina* Geyn & Vlerk, 1935 [*nomen nudum*]; *Isorbitoina* Geyn & Vlerk, 1935 [*nomen nudum*]; *Isorbitoina* Schenck & Frizzell, 1936 (type species *Isolepidina trinitatis* Douvillé, 1924) [objective synonym]; *Isorbitoina* Thalmann, 1938 (type species *Isolepidina trinitatis* Douvillé, 1924) [junior objective synonym]; *Neolepidina* Brönnimann, 1947 (type species *Isolepidina trinitatis* Douvillé, 1924) [subjective junior synonym].

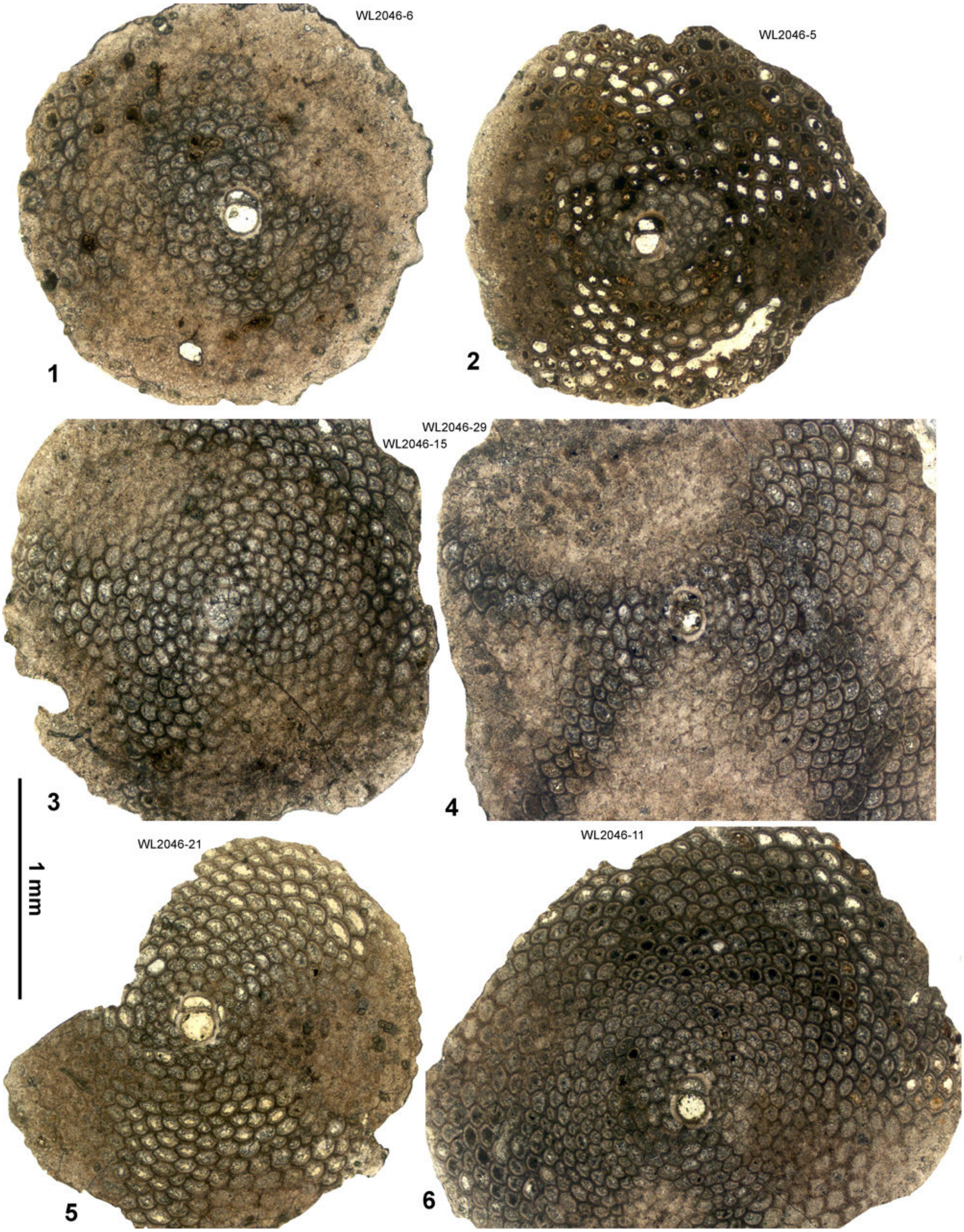


Figure 100: *Polyorbitoinella lilyfieldensis* sp. nov. **1** (EO.WL2046-6), **2** (EO.WL2046-5), **3** (EO.WL2046-15), **4** (EO. WL 2046-29), **5** (EO.WL2046-21), **6** (EO.WL2046-11): equatorial sections. Preston Hill Formation (ABZ8), Lilyfield, parish of St Ann, Jamaica.

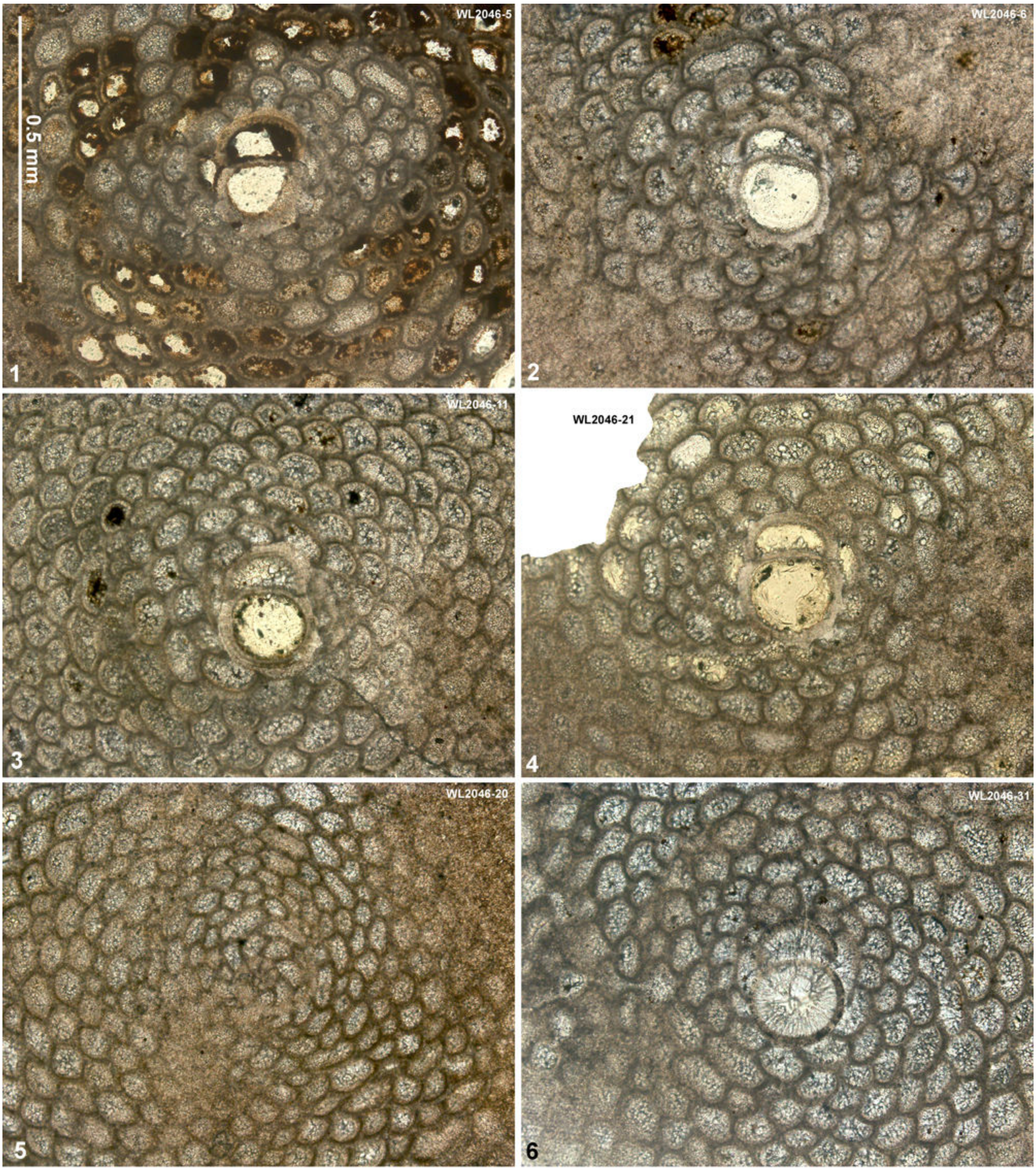


Figure 101: *Polyorbitoinella lilyfieldensis* sp. nov. Details of equatorial sections. **1** (EO.WL2046-5), **2** (EO.WL2046-4), **3** (EO.WL2046-11), **4** (EO.WL2046-21), 5 (EO.WL2046-20), **6** (EO.WL2046-31). **1-5**, megalospheric specimens, **6**, microspheric specimen. Preston Hill Formation (ABZ8), Lilyfield, parish of St Ann, Jamaica.

Remarks. Numerous species have been described that can be assigned to *Orbitoina*, but many of these need to be synonymised; this is beyond the scope of this paper. Here we describe some of the species that occur in the Middle and Upper Eocene that have biostratigraphic value. The main characters of importance in the recognition of species are: the size of the embryo, the form of the peri-embryonic chambers, the distribution of pillars and the form of the axial section.

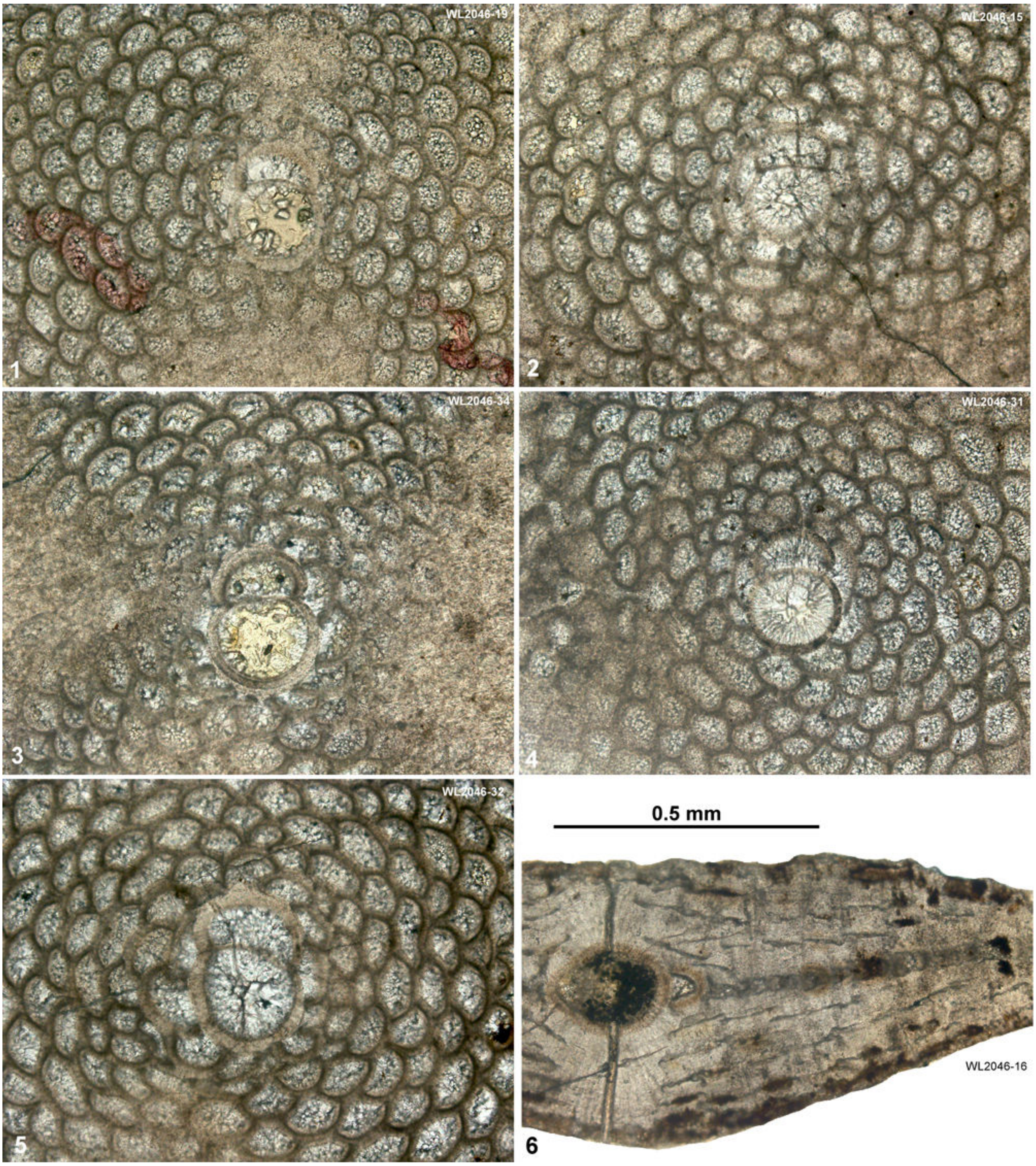


Figure 102: *Polyorbitoinella lilyfieldensis* sp. nov. **1** (EO.WL2046-19), **2** (EO.WL2046-15), **3** (EO.WL2046-34), **4** (EO.WL2046-31), **5** (EO.WL2046-32), **6** (EO.WL2046-16). **1-5**, equatorial sections; **6**, axial section. Preston Hill Formation (ABZ8), Lilyfield, parish of St Ann, Jamaica.

Orbitoina cedarkeysensis (Cole, 1942)

(Fig. 94)

Previous descriptions and figures. Cole, 1942, p. 43-45, Pl. 3, figs. 1-2; Pl. 8, fig. 11; Pl. 11, figs. 6-7; Pl. 12, figs. 1-7; Cole, 1944, p. 62, Pl. 7, figs. 16-17, 22.

Recognition. This species was described by Cole (1942, 1944) from wells in Florida, and is distinguished from species of *Orbitoina* from similar stratigraphic levels by its small embryo (160 to 200 µm).

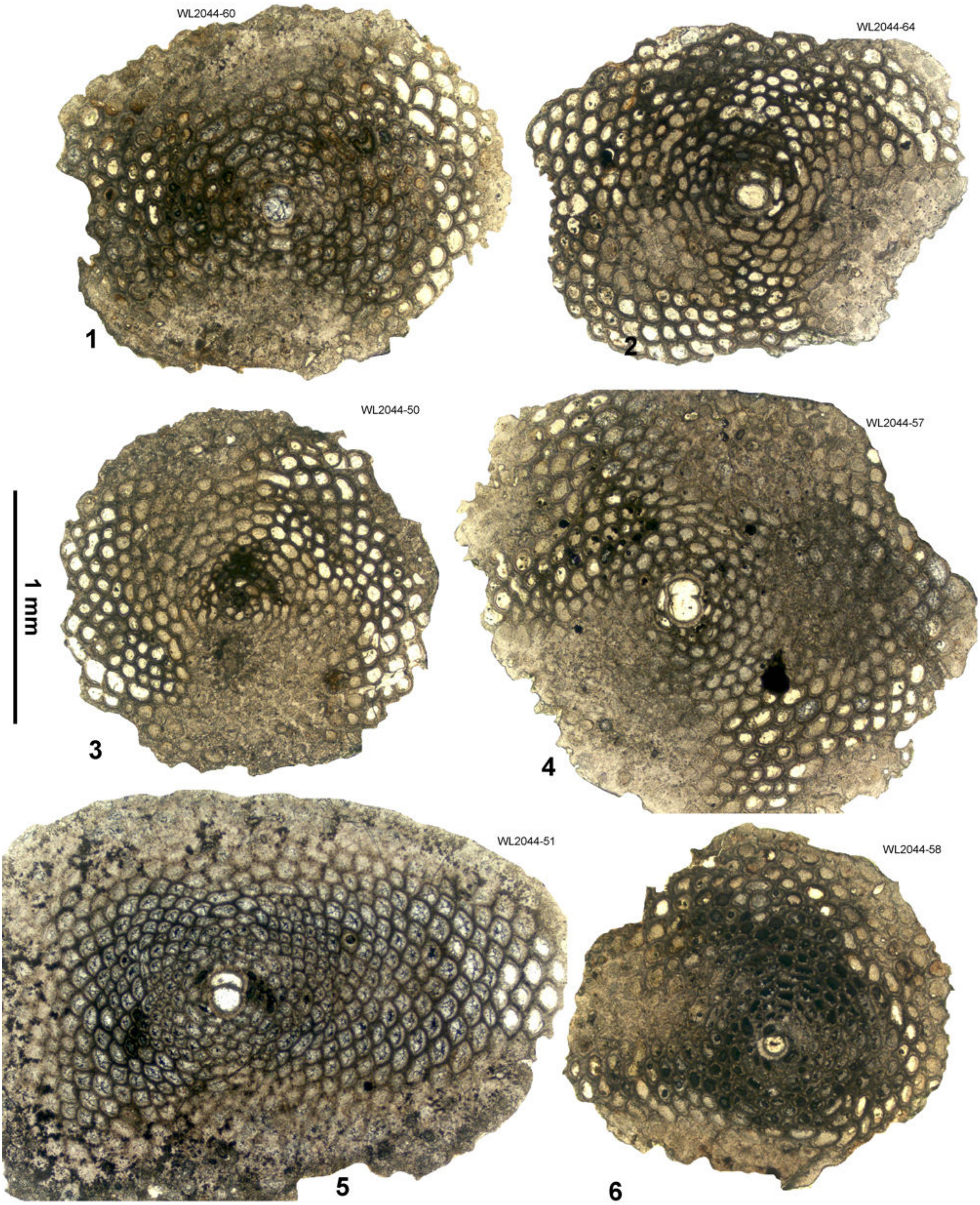


Figure 103: *Polyorbitoinella lilyfieldensis* sp. nov. Equatorial sections. **1** (EO.WL2044-60), **2** (EO.WL2044-64), **3** (EO.WL2044-50), **4** (EO.WL2044-57), **5** (EO.WL2044-51), **6** (EO.WL2044-58). **1-2, 4-6**, megalospheric specimens; **3**, microspheric specimen. Preston Hill Formation (ABZ9), Lilyfield, parish of St Ann, Jamaica.

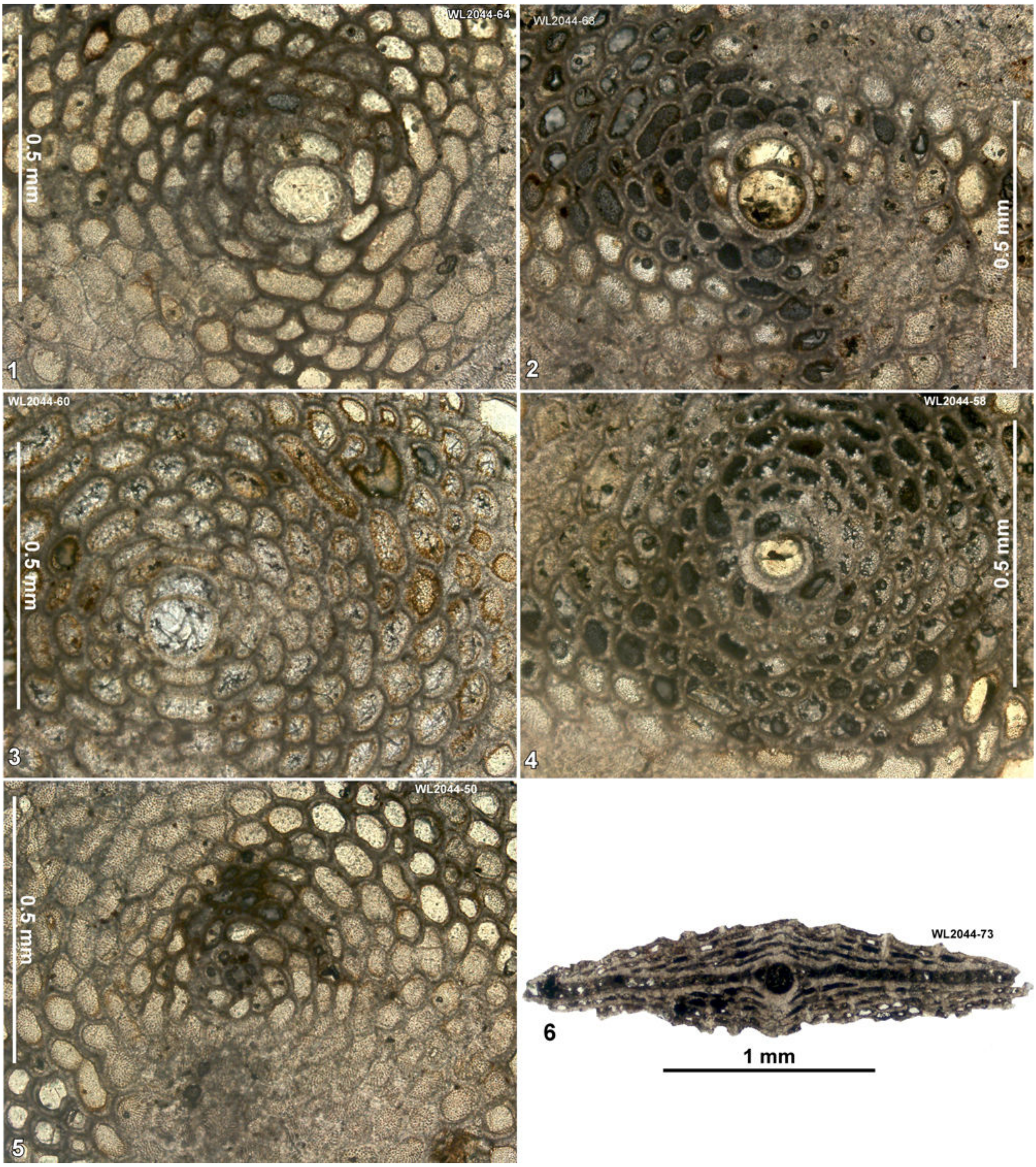


Figure 104: *Polyorbitoinella lilyfieldensis* sp. nov. **1** (EO.WL2044-64), **2** (EO.WL2044-63), **3** (EO.WL2044-60), **4** (EO.WL2044-68), **5** (EO.WL2044-50), **6** (EO.WL2044-73). **1-4**, megalospheric specimens, equatorial section; **5**, microspheric specimen, equatorial section; **6**, axial section of megalospheric specimen. Preston Hill Formation (ABZ9), Lilyfield, parish of St Ann, Jamaica.

Remarks. Cole (1942, 1944) described this species from three wells in Florida, the Sholtz No.1, the Cedar Key No. 2, and the St Mary's Oil Company, Hillard Turpentine Company No. 1. It seems to occur in a distinct stratigraphic interval in Florida, which is best interpreted in the St Mary's Oil Company well. Here it occurs above *Lepidocyclina ariana*, but below the more restricted foraminiferal facies with dictyoconids and *Fabularia vaughani* (*i.e.*, Avon Park Formation). This would suggest a likely assignment to zones ABZ12 or ABZ13. The species has not been recorded in Jamaica.

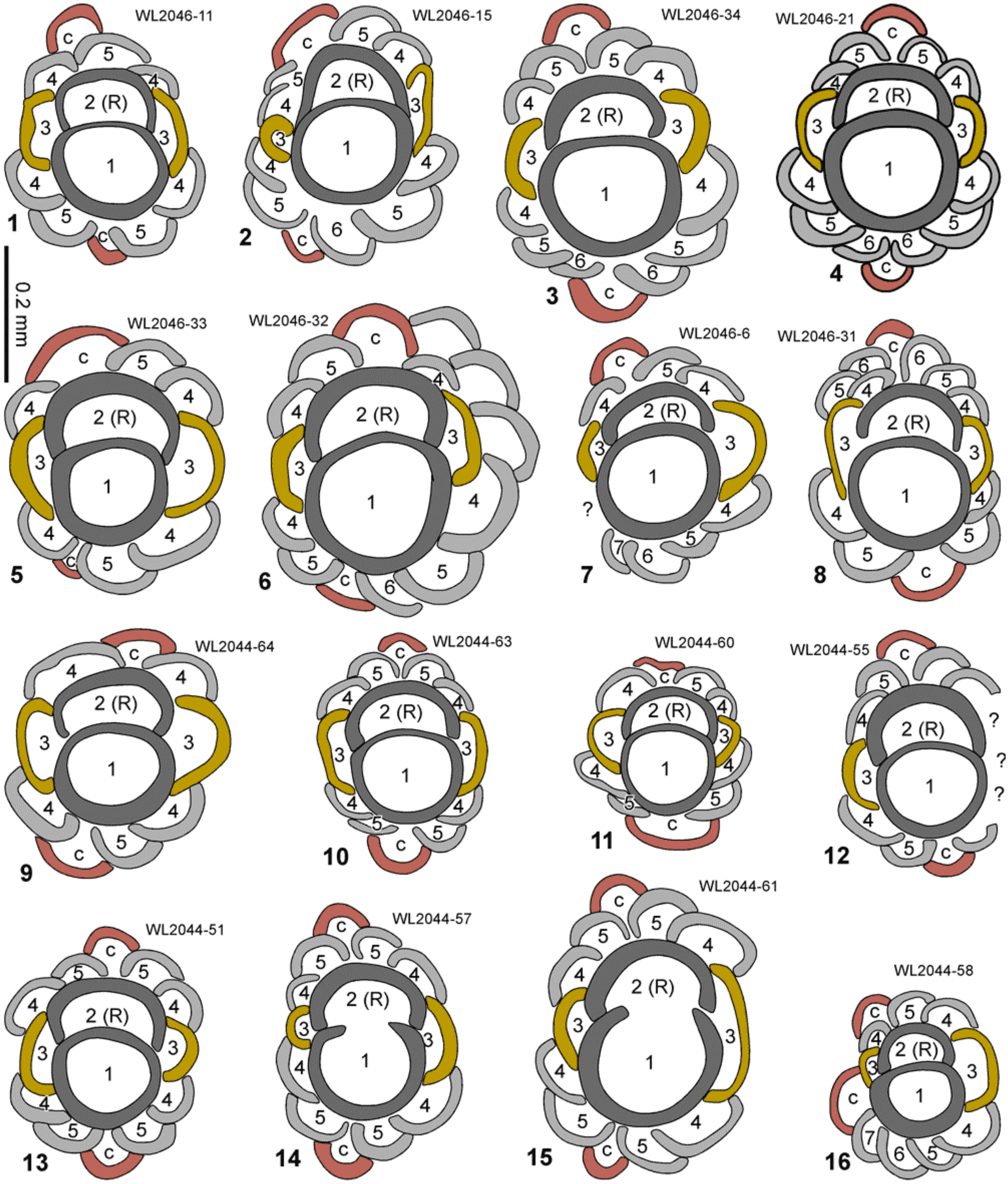


Figure 105: *Polyorbitoinella lilyfieldensis* sp. nov. Line drawings showing coiling of peri-embryonic equatorial chambers in equatorial section; note presence of two PACs and generally asymmetrical coiling. **1** (EO.WL2046-11), **2** (EO.WL2046-15), **3** (EO.WL2046-34), **4** (EO.WL2046-21), **5** (EO.WL2046-33), **6** (EO.WL2046-32), **7** (EO.WL2046-6), **8** (EO.WL2046-31): ABZ8. **9** (EO.WL2044-64), **10** (EO.WL2044-63), **11** (EO.WL2044-60), **12** (EO.WL2044-55), **13** (EO.WL2044-51), **14** (EO.WL2044-57), **15** (EO.WL2044-61), **16** (EO.WL2044-58): ABZ9. Preston Hill Formation, Lilyfield, parish of St Ann, Jamaica.

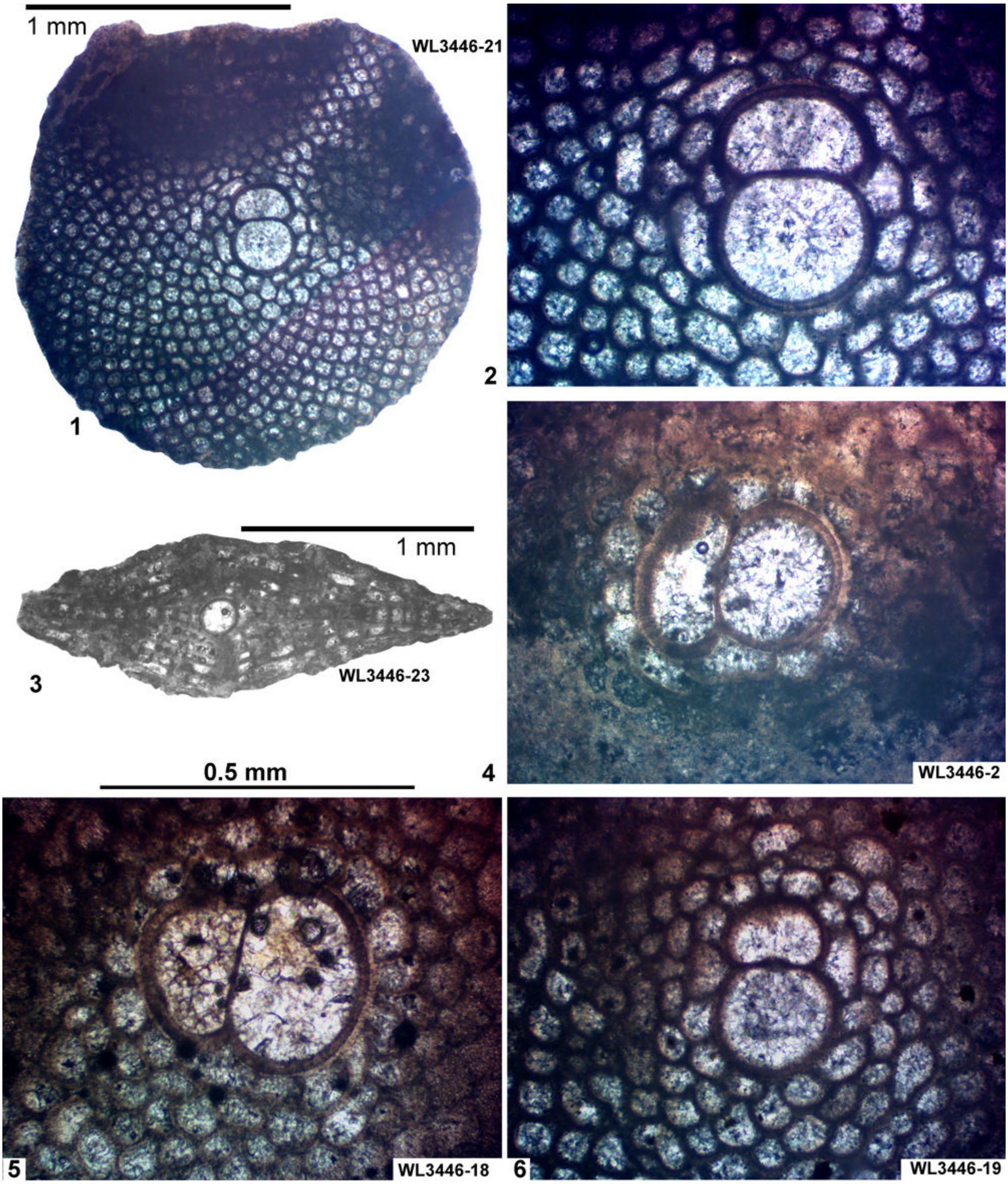


Figure 106: *Orbitoina rdouvillei* (Lisson, 1921). **1-2**, equatorial section (UWIGM.WL3446-21); **3**, axial section (UWIGM.WL3446-23); **4**, equatorial section (UWIGM.WL3446-2); **5**, equatorial section (UWIGM.WL3446-18); **6**, equatorial section (UWIGM.WL3446-19). Scale bar for **2, 4-6** is the 0.5 mm scale above 5. Chapelton Formation, Albert Town, Jamaica, ABZ11.

Orbitoina rdouvillei (Lisson, 1921)

(Fig. 106)

Synonyms. *Lepidocyclina rdouvillei* Lisson, 1921, p. 53-55, Pls. 4-5; *Lepidocyclina peruviana* Cushman (in Bosworth, 1922), p. 138, Pl. XXIV, fig. 1; *Lepidocyclina antillea* Cushman (in Bosworth, 1922) (non *Lepidocyclina antillea* Cushman, 1919), p. 137-138, Pl. XXIV, fig. 2; *Lepidocyclina rdouvillei* var. *armata* L. Rutten, 1928, p. 944-945, Figs. 24l-m, 29a-d, Pl. II, figs. 27-28; *Lepidocyclina pervuviana* Todd & Wright, 1932, p. 535-537, Pl. XLI, figs. 1-4; Pl. XLII, figs. 2-3, 5-7; *Lepidocyclina sherwoodensis* Vaughan, 1928, p. 287-288, Pl. 48, figs. 4-8.

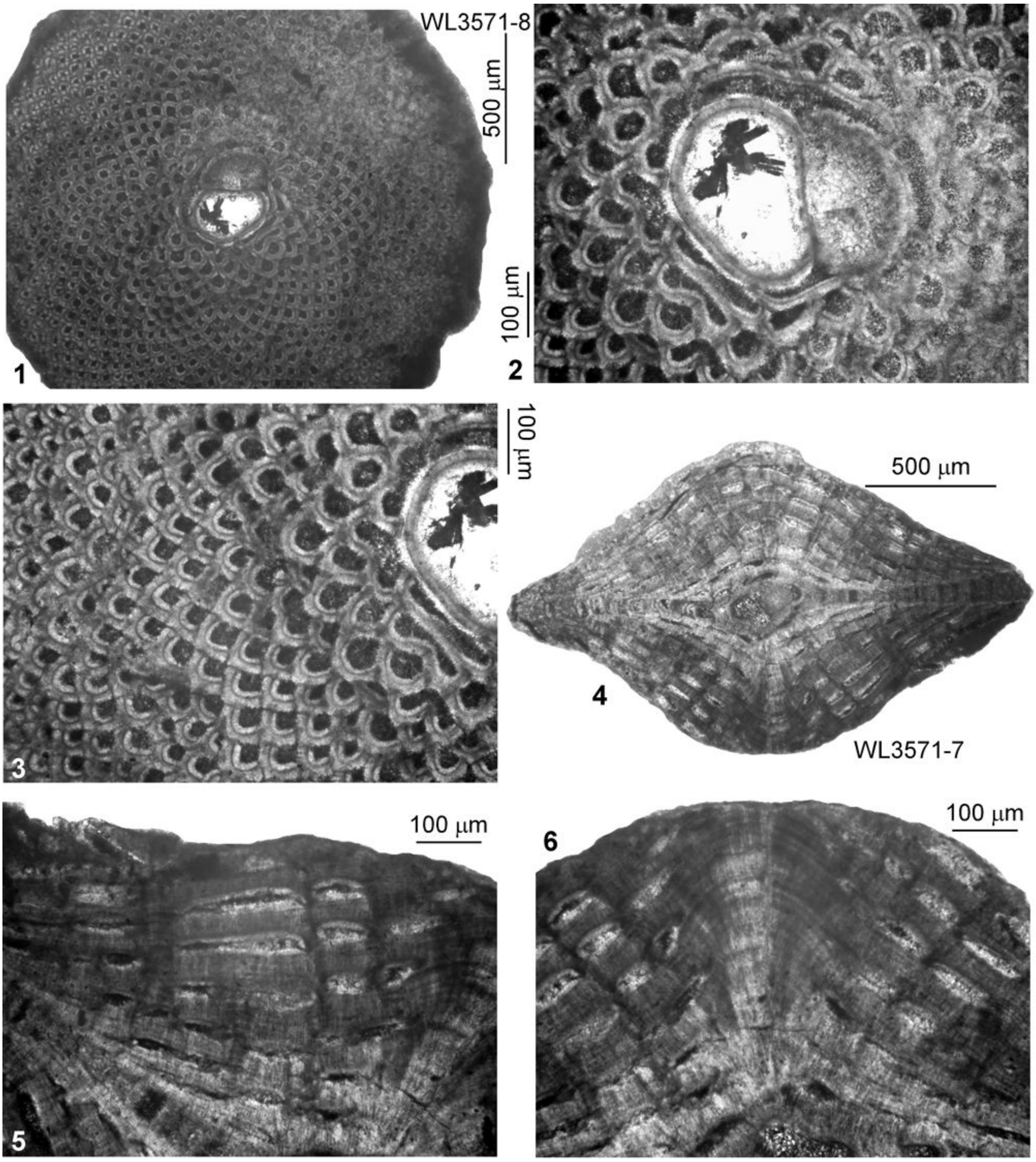


Figure 107: *Orbitoina trinitatis* Douvillé, 1924. **1-3**, equatorial section (WL3571-8), note the narrow PACs and the elongate two-humped chamberlets that for the spirals. **4-6**, axial section (WL3571-7), note the pillars and regular tiers of chamberlets. Limestones above the Grants Pen Clay (Yellow Limestone), Grants Pen, St Thomas, Jamaica (ABZ12).

Previous descriptions and figures. Lisson, 1921, p. 53-55, Pls. 4-5; Todd & Wright, 1932, p. 535-537, Pl. XLI, figs. 1-4; Pl. XLII, figs. 2-3, 5-7; Coletti *et al.*, 2019, Fig. 10.

Recognition. An *Orbitoina* with an embryo with a length of 204 to 340 µm, with a relatively thick wall, two PACs and four symmetrical spirals of peri-embryonic chambers. Equatorial sections often show a radial arrangement of chamberlets. Axial sections show well-developed lateral chamberlets with up to 10 layers presents; the pillars are well developed.

Remarks. *Lepidocyclina peruviana* was described by Cushman (in Bosworth, 1922), but only external details were given. Todd and Barker (1932) provided the details of the interior based on some of the type series together with additional material. They stated (Todd & Barker, 1932,

p. 536) that the embryo had a mean length of 276 µm and a range from 204 µm to 340 µm. Their table (Todd & Barker, 1932, p. 539), however, lists details of the length of the embryo in five populations that they place in *Lepidocyclina peruviana*: the type material (265 - 295 µm), Bosworth's material of '*antillea*' (222 - 240 µm), material from the Cardo Grits (204 - 307 µm), specimens from the Organos Grits (207 - 307 µm) and material from the Yapato Grits (248 - 315 µm). We suspect a typographic error in the table and that 240 µm for Bosworth's '*antillea*' should read 340 µm (although we cannot confirm this). Todd and Barker (1932) argued that *L. antillea* Cushman (in Bosworth, 1922) and *Lepidocyclina rdouvillei* var. *armata* L. Rutten, 1928 had similar embryo lengths and were synonyms of *L. peruviana* Cushman (in Bosworth, 1922). *Lepidocyclina armata* L. Rutten, 1928 was redescribed by Eames *et al.* (1968) based on the type series. They demonstrated that the embryo ranged from 270 to 320 µm, and therefore matched the dimensions seen in *L. peruviana*. Coletti *et al.* (2019) clearly recognized that *L. rdouvillei* Lisson (*Lepidocyclina rdouvillei* Lisson) is a senior synonym of *L. peruviana*, recognizing that Todd and Barker (1932) relied on measurements given by Gorter and Vlerk (1931) rather than the description and figures of *L. rdouvillei* as given by Lisson (1921). We therefore place *L. peruviana* Cushman in Bosworth, 1922, *L. antillea* Cushman in Bosworth, 1922 and *L. rdouvillei* var. *armata* L. Rutten, 1928 in synonymy with *L. rdouvillei* Lisson, and place *L. rdouvillei* in the genus *Orbitoina*. We also consider *Lepidocyclina sherwoodensis* a synonym of *O. rdouvillei*. Vaughan (1928) recorded the length of the nucleus in three specimens as being 0.4 mm, 0.25 and 0.3 mm.

Coletti *et al.* (2019) recorded *O. rdouvillei* in southern Peru as occurring in zone CNE14 which is equivalent to parts of NP16 and CN14a. This occurrence of *O. rdouvillei*, with *Polylepidina* with two PACs (Coletti *et al.*, 2019), would suggest an assignment to ABZ11. *Or. rdouvillei* occurs in Jamaica in zone ABZ11.

Orbitoina trinitatis (Douvillé, 1924)

(Fig. 107)

Previous descriptions and illustrations. Vaughan & Cole, 1941 (described as *Isolepidina pustulosa* Douvillé), p. 65-66, Pls. 25-32; Caudri, 1996 (described as *Lepidocyclina pustulosa* Douvillé and *L. pustulosa trinitatis* Douvillé), p. 1218-1219, Pl. 15.3, 15.9.

Recognition. This species is recognised on the basis of its highly inflated axial section with well-developed pillars, and its equatorial section with broad, narrow, often double-arched PACs and equatorial chambers. Previous descriptions of the length of the nucleoconch are given as 300 to 480 µm by Douvillé (1917, 1924; Todd & Barker, 1932) and 400 to 650 µm (Eames *et al.*, 1962).

Remarks. Douvillé (1924) clearly distinguished *L. pustulosa* from *L. trinitatis* on the basis of the lateral chamberlets seen on the surface. *L. trinitatis* (both megalospheric and microspheric generations) is characterised by numerous polygonal pillars surrounded only by a small number of lateral chambers; in contrast *L. pustulosa* (stating only microspheric specimens being available) is characterised a large number of large pustules (300 µm) at the umbo, each surrounded by about fifteen small rounded chambers 70 to 120 µm in diameter. Douvillé (1924) gives measurements of the length of the embryo as ranging from 300 µm to 350 µm in *L. trinitatis*, and from 90 µm to 100 µm in *L. pustulosa* (despite stating that he only had microspheric forms). Vaughan and Cole (1941) made no mention of the lateral chamberlets in their discussion of the two species.

Eames *et al.* (1962) recognized that Vaughan and Cole (1941) had only figured specimens which would be attributable to *L. trinitatis* in their work under the name *L. pustulosa*, and this has been the source of much subsequent confusion. Eames *et al.* (1962, p. 302) gave the length of the nucleoconch for *L. pustulosa* as 0.25 - 0.35 mm with thick-walls and that for *L. trinitatis* as 0.40 - 0.65 mm (rarely over 0.55 mm) with thin walls. While we agree with these two groups, their *L. pustulosa* is equivalent to *L. peruviana* of Caudri (1975, 1996) which we have placed in *Or. rdouvillei*, and not with Douvillé's (1917, 1924) *L. pustulosa* which has a much smaller nucleoconch. *L. pustulosa* will remain enigmatic until the type material is studied (if it is still available), but should probably be attributed to *Orbitoina*.

In general form *Or. trinitatis* is similar to *Or. wrighti* sp. nov. However, *Or. trinitatis* has a larger embryo and the equatorial chamberlets are narrow and more strongly arched than those in *Or. wrighti* sp. nov.

Orbitoina wrighti

Mitchell, E. Robinson & Özcan sp. nov.

(Figs. 108 - 109)

1993 *Lepidocyclina pustulosa* Douvillé; Robinson & Wright (in part), p. 317, Figs. 23.1, 23.3 only.

Type Material. Holotype (UWIGM.WL3876.5). Paratypes (UWIGM.WL3876-06, WL3876-07, WL 3876A-3, WL3876A-4, WL3876A-10, WL3876A-11). All from the Swanswick Formation *sensu lato*, ABZ15, North-South Leg of Highway 2000, north of the Golden Vale Toll Plaza, parish of St Ann, Jamaica.

Diagnosis. A small species of *Orbitoina* with a thick diamond-shaped test in axial section; a relatively small embryo in equatorial section, with four simple spirals emanating from the two PACs and closing in symmetrical closing chambers. A few thick piles (pillars) producing pustules at the crown; and numerous rows of open lateral chamberlets.

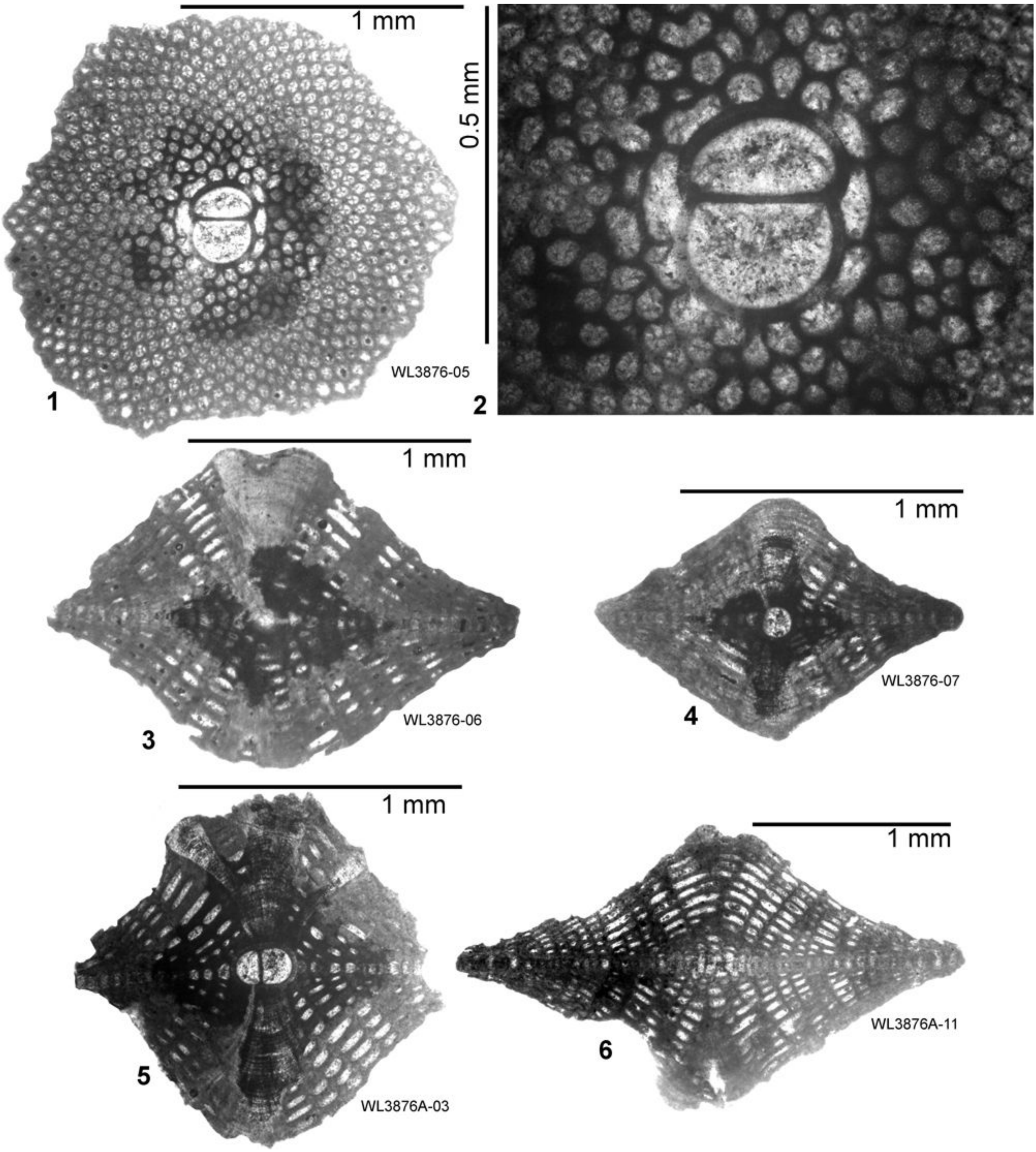


Figure 108: *Orbitoina wrighti* sp. nov. **1-2**, equatorial section, megalospheric specimen (holotype: UWIGM.WL 3876-05). **3**, slightly off-centre axial section, megalospheric specimen (Paratype: UWIGM.WL3876-06). **4**, axial section, megalospheric specimen (Paratype: UWIGM.WL3876-07). **5**, axial section, megalospheric specimen (Paratype UWIGM.WL3876A-03). **6**, axial section, microspheric specimen (Paratype: UWIGM.WL3876A-11). Swanswick Formation *sensu lato* (ABZ15), North-South Leg of Highway 2000, just north of the Goldon Vale Toll Plaza, parish of St Ann, Jamaica.

Origin of name. From the late Raymond WRIGHT, for his work on the foraminifers and stratigraphy of the White Limestone of Jamaica.

Description. A small species of *Orbitoina* with a strongly inflated test. Megalospheric specimens reach a diameter of 1.7 mm and a thickness of 1.2 mm. In equatorial sections it displays a typical *Orbitoina* arrangement of chambers. The nucleoconch is relatively small and comprises a protoconch that is slightly larger than the deuteroconch, with the protoconch and deuteroconch separated by an almost straight, or gently curved wall. The deuteroconch is marginally wider that the protoconch. The size of the embryo is rela-

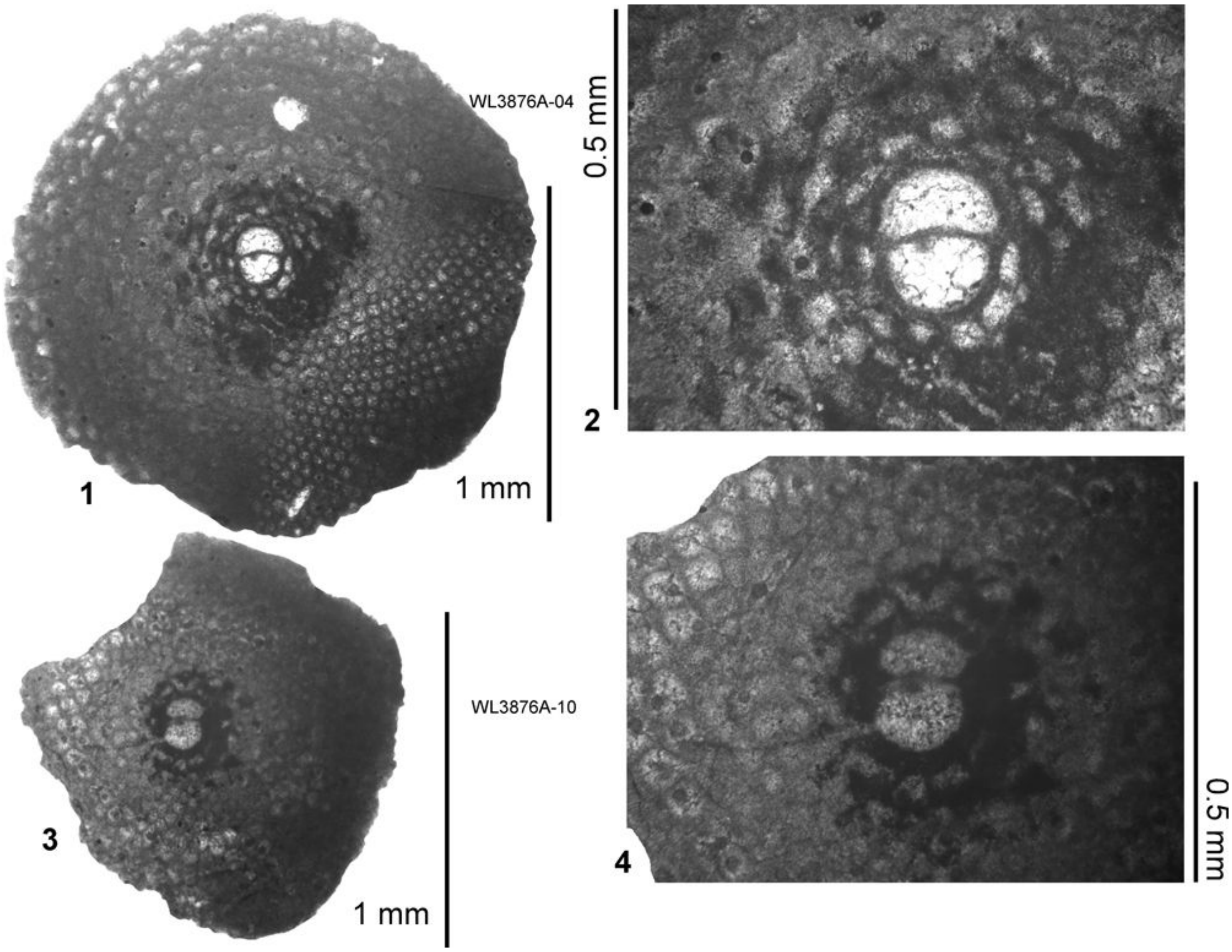


Figure 109: *Orbitoina wrighti* sp. nov. **1-2**, equatorial section, megalospheric specimen (holotype: UWIGM. WL 3876A-04). **3-4**, equatorial section, megalospheric specimen (Paratype: UWIGM. WL3876A-10). Swanswick Formation *sensu lato* (ABZ15), North-South Leg of Highway 2000, just north of the Goldon Vale Toll Plaza, parish of St Ann, Jamaica.

tively small (length 254 µm in the holotype). Two PACs are present which are slightly larger than the other peri-embryonic chambers and are regularly globular. There are four primary spires, two developed from each PAC, with the spires around the protoconch consisting each of three peri-embryonic chambers and a closing chamber, and those around the deuteroconch consisting of two peri-embryonic chambers and a closing chamber. There are no adauxilary chambers. The equatorial chamberlets are diamond shaped. In axial section, the test is very thick with the thickness nearly equaling or exceeding the diameter. One, two or rarely three pillars are seen in axial sections and extend from near the embryo towards the crown of the test where they form pustules with a diameter of up to 290 µm. The equatorial layer is relatively thin and shows only minor thickening towards the margin of the test. There are up to 13 rows of lateral chambers developed over the embryo, with the chambers arranged in tiers; the thickness of the chamber floors and chambers are about the same and the floors are straight and not curved.

Remarks. Specimens belonging to this species have typically been placed in *'Lepidocyclina' pustulosa* or *'L.' trinitatis* in previous studies (*e.g.*, Robinson & Wright, 1993, Fig. 23.1-3). In fact the species is clearly well-defined amongst *Orbitoina* in the late Eocene. *Or. cedarkeyensis* is less inflated that *Or. wrighti* sp. nov. This form is easily recognizable in random cuts in thin section due to its distinctive axial section and the presence of relatively few pillars projecting up towards the crowns.

Range. In Jamaica, the species occurs commonly in the Swanswick Formation *sensu lato* on N-S Highway 2000 (ABZ15), in the Swanswick Formation at Dallas Mountain (ABZ15), and in the type Swanswick Formation at Swanswick House (ABZ16). It also occurs in the middle part of the Ipswich Formation in St Elizabeth, Jamaica (ABZ14). The species serves as an index for ABZ15, although it ranges from ABZ14 to ABZ16.

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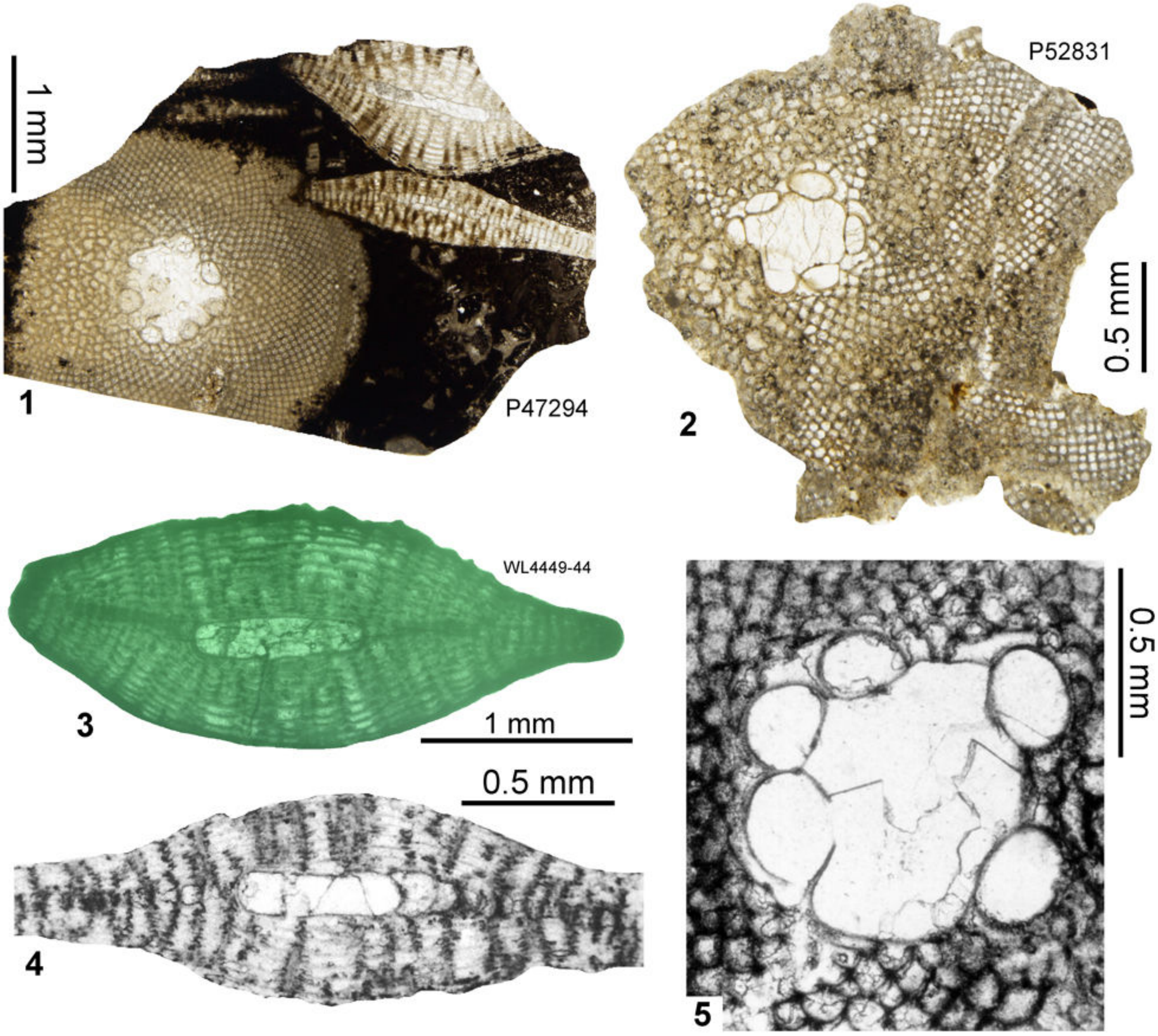

Figure 110: *Pliolepidina tobleri* DOUVILLÉ, 1917. **1**, random sections (equatorial and axial) in limestone (NHM.PM.P. 47294), Peñas Blancas Limestone, Rio Chacual, Venezuela. **2**, equatorial section (NHM.PM. P.52831), Nicaragua. **3**, axial section (sample UWIGM. WL4449-44), limestone above marlstones, Cold Spring, Westmoreland, Jamaica. **4**, axial section, and **5**, equatorial section, upper Ipswich Formation (ER2756), former Western Cement Company, Appleton, St Elizabeth, Jamaica. ABZ14 (reproduced from ROBINSON & MITCHELL, 1999).

Genus *Pliolepidina* DOUVILLÉ, 1915

Type species. *Lepidocyclina (Pliolepidina) tobleri* DOUVILLÉ, 1917 (by subsequent monotypy: DOUVILLÉ, 1917) from the middle or late Eocene of Trinidad (CAUDRI, 1975, 1996).

Synonyms. *Multicyclina* CUSHMAN, 1918 (type species: *Lepidocyclina (Multicyclina) duplicata* CUSHMAN, 1918 = *Lepidocyclina (Pliolepidina) tobleri* DOUVILLÉ, 1917) [junior synonym]; *Multilepidina* SILVESTRI, 1937 (*non* HANZAWA, 1932) (type species: *Pliolepidina tobleri* DOUVILLÉ, 1917) [objective junior synonym].

Pliolepidina tobleri DOUVILLÉ, 1917

(Figs. 110 - 111)

Previous descriptions and figures. DOUVILLÉ, 1917, p. 844, Fgs. 5-6 ; VAUGHAN & COLE, 1941, p. 66-67, Pl. 24; CAUDRI, 1975, p. 575, Pl. 27.4-7; CAUDRI, 1996, p. 1219, Pl. 15.7, 15.12.

Synonyms. *Lepidocyclina panamaensis* CUSHMAN, 1918; *Lepidocyclina (Multicyclina) duplicata* CUSHMAN, 1918.

Remarks. This is a very distinctive species with a short stratigraphic range and has been reported widely in the literature: Trinidad (DOUVILLÉ, 1915, 1917, 1924; VAUGHAN & COLE, 1941; CAUDRI, 1975, 1996), Panama (CUSHMAN, 1918; COLE, 1952), Venezuela (EAMES *et al.*, 1968) and Jamaica (ROBINSON & MITCHELL, 1999; ROBINSON *et al.*, 2018). Due to extensive reworking in sections in Trinidad, it is difficult to determine the succession of benthic larger foraminiferal assemblages, and it appears that *O. rdouvillei* (= *Lep. peruviana sensu* CAUDRI), *O. trinitatis* (= *Lep. pustulosa sensu* CAUDRI) and *Pl. tobleri*, which characterise different levels in the successions in Jamaica (herein) and Panama (COLE, 1952) occur as a mixed assemblage (indicating reworking) in Trinidad

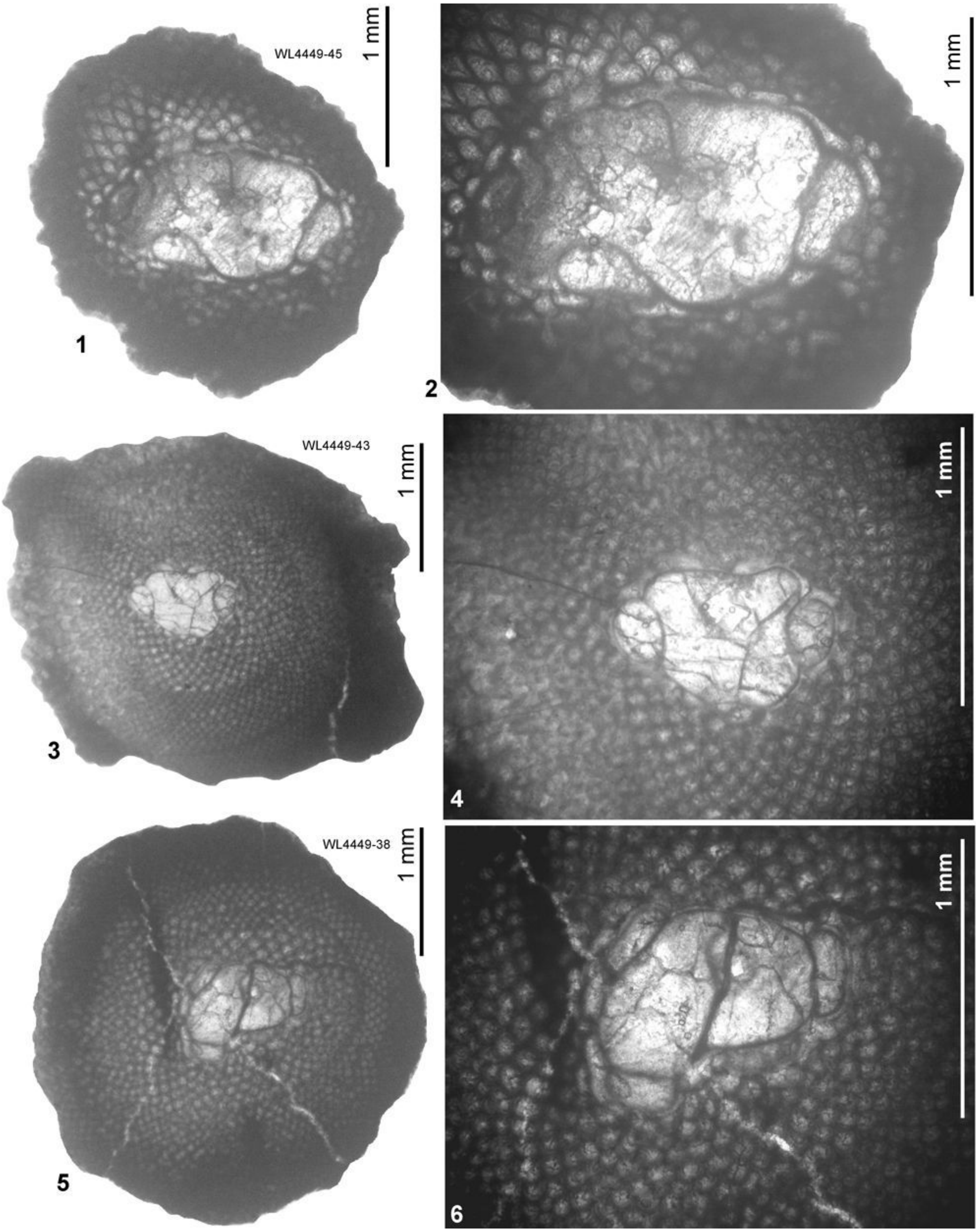

Figure 111: *Pliolepidina tobleri* Douvillé, 1917, equatorial sections from sample WL4449 (ABZ14), the deep-water limestones and the marlstones at Cold Spring, Westmoreland, Jamaica. **1-2** (UWIGM.WL4449-45), **3-4** (UWIGM.WL 4449-43), **5-6** (UWIGM.WL4449-38).

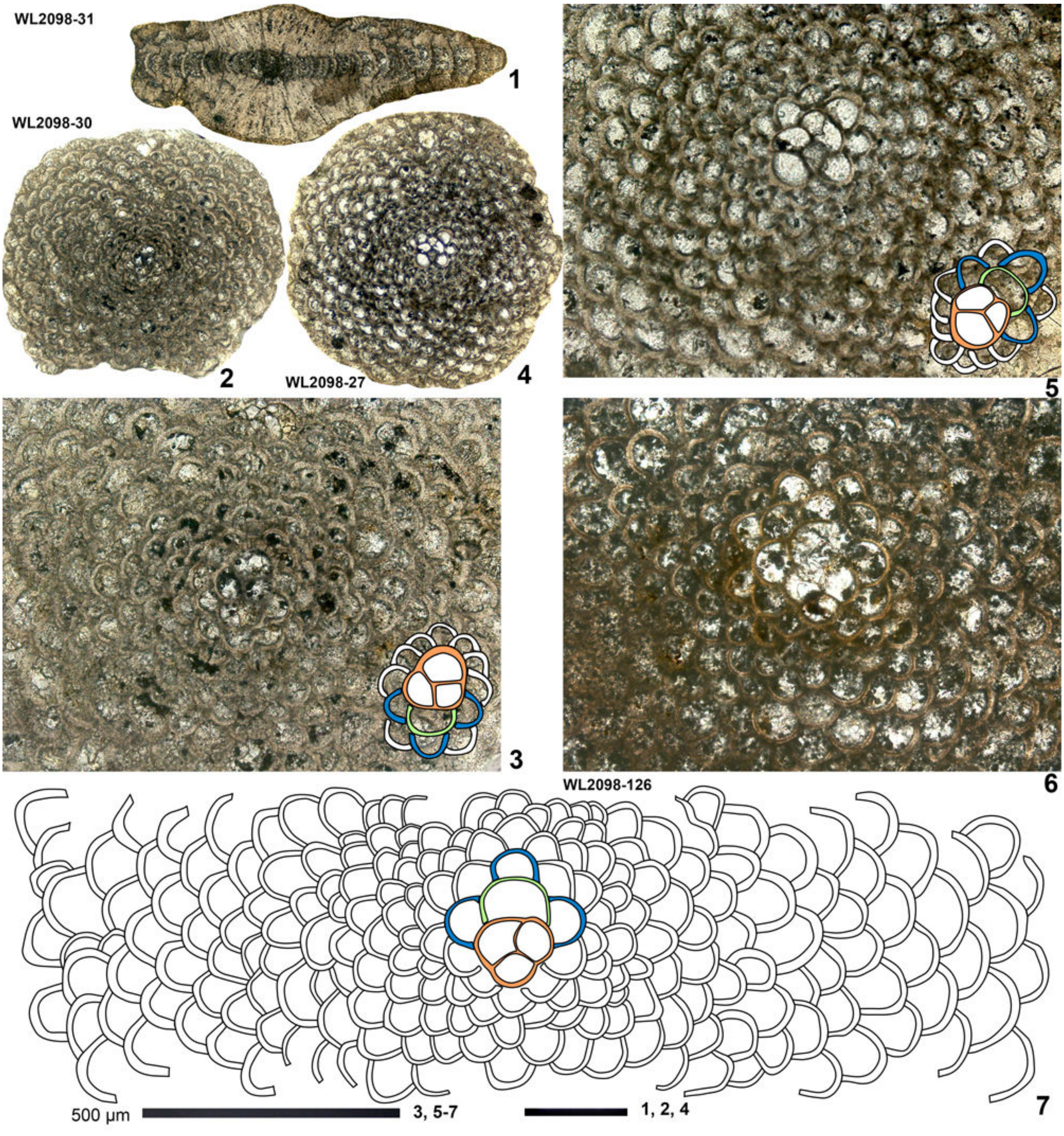

Figure 112: *Linderina floridensis* Cole, 1942. **1** (EO.WL2098-31), axial section. **2-3** (EO.WL2098-30), equatorial section. **4-5** (EO.WL2098-27), equatorial section. **6-7** (EO.WL2098-126), equatorial section. Sample WL2098, Preston Hill Formation (ABZ7), Farm Turn, St Mary, Jamaica. Notice that three chamberlets are formed consistently at the second growth stage following the embryonic apparatus (chamberlets with blue walls).

(Vaughan & Cole, 1941; Caudri, 1975, 1996). *Pl. tobleri* is the nominate species for ABZ14.

Superfamily ORBITOIDOIDEA SCHWAGER, 1876

Family LINDERINIDAE LOEBLICH & TAPPAN, 1984

Remarks. See Ferràndez-Cañadell & Serra-Kiel (1999) and Özcan *et al.* (2021b, 2022b) for a reclassification of the Linderinidae and a description of the embryo of *Linderina*.

Genus *Linderina* SCHLUMBERGER, 1893

Type species. *Linderina brugesi* Schlumberger, 1893 (by monotypy) from the Eocene of Bruges, Gironde, southwestern France.

Linderina floridensis COLE, 1942

(Figs. 112 - 113.1-5)

Previous descriptions and illustrations. Cole, 1942, p. 36-37, Pl. 11, fig. 8; Pl. 15, figs. 7-11.

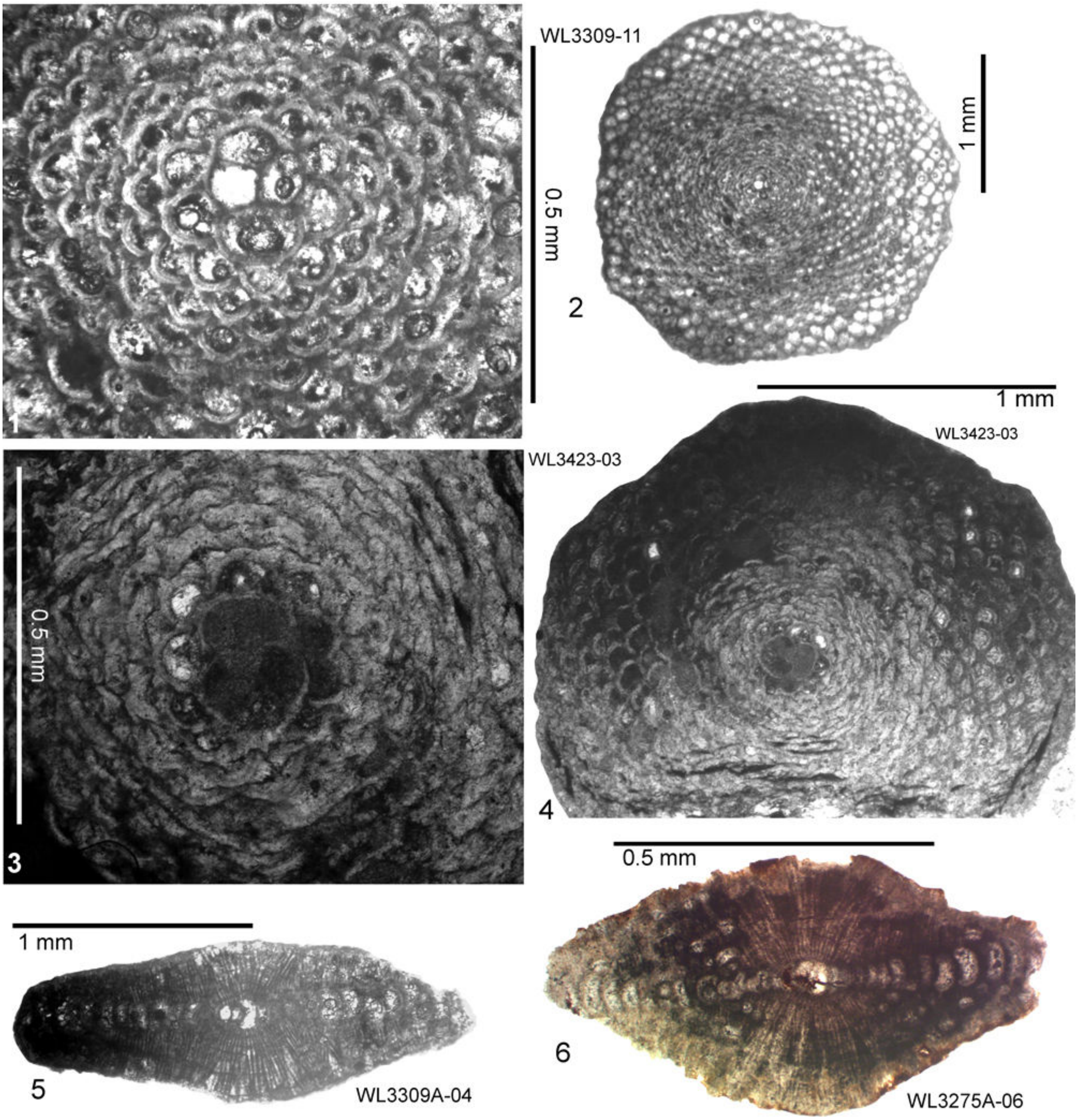

Figure 113: *Linderina* and *Caudriella*. **1-5**, *Linderina floridensis* Cole, 1942: **1-2**, equatorial section (WL3309-11); **3-4**, equatorial section (WL3423-03); **5**, axial section (WL3309A-04). **1-2, 5**: Preston Hill Marl, Farm Turn, St Mary, ABZ7. **3-4**: Preston Hill Marl, Kilancolly, St Mary, ABZ7. Note the embryonic apparatus in 1 and 3 (with drawings), which is typical for the genus *Linderina* (Ferràndez-Cañadell & Serra-Kiel, 1999). **6**, *Caudriella* sp., axial section (WL 3275A-06), Swanswick House, Trelawny, Jamaica, ABZ7.

Remarks. Cole (1942) nominated two specimens as cotypes, his Pl. 15, figs. 9 (axial section) and 10 (equatorial section) which therefore form the type series. We do not nominate a lectotype at present because a restudy of the type material is needed.

The embryo of *L. floridensis* (Figs. 112, 113.1) is comparable to the embryo of the type species of the genus, *Linderina brugesi* Schlumberger, as figured by Ferràndez-Cañadell and Serra-Kiel (1999) justifying assignment to *Linderina*. Hose and Versey (1956) defined a *Linderina* band in the limestone successions of Jamaica; however our studies indicate that *Linderina floridensis* is a rather long-ranging species occurring at at least three different stratigraphic levels (mid Ypresian, mid Lutetian, early Bartonian) and is not very useful in high-resolution biostratigraphy (it also occurs in the mid-Ypresian in Turkey: Özcan *et al.*, 2021b).

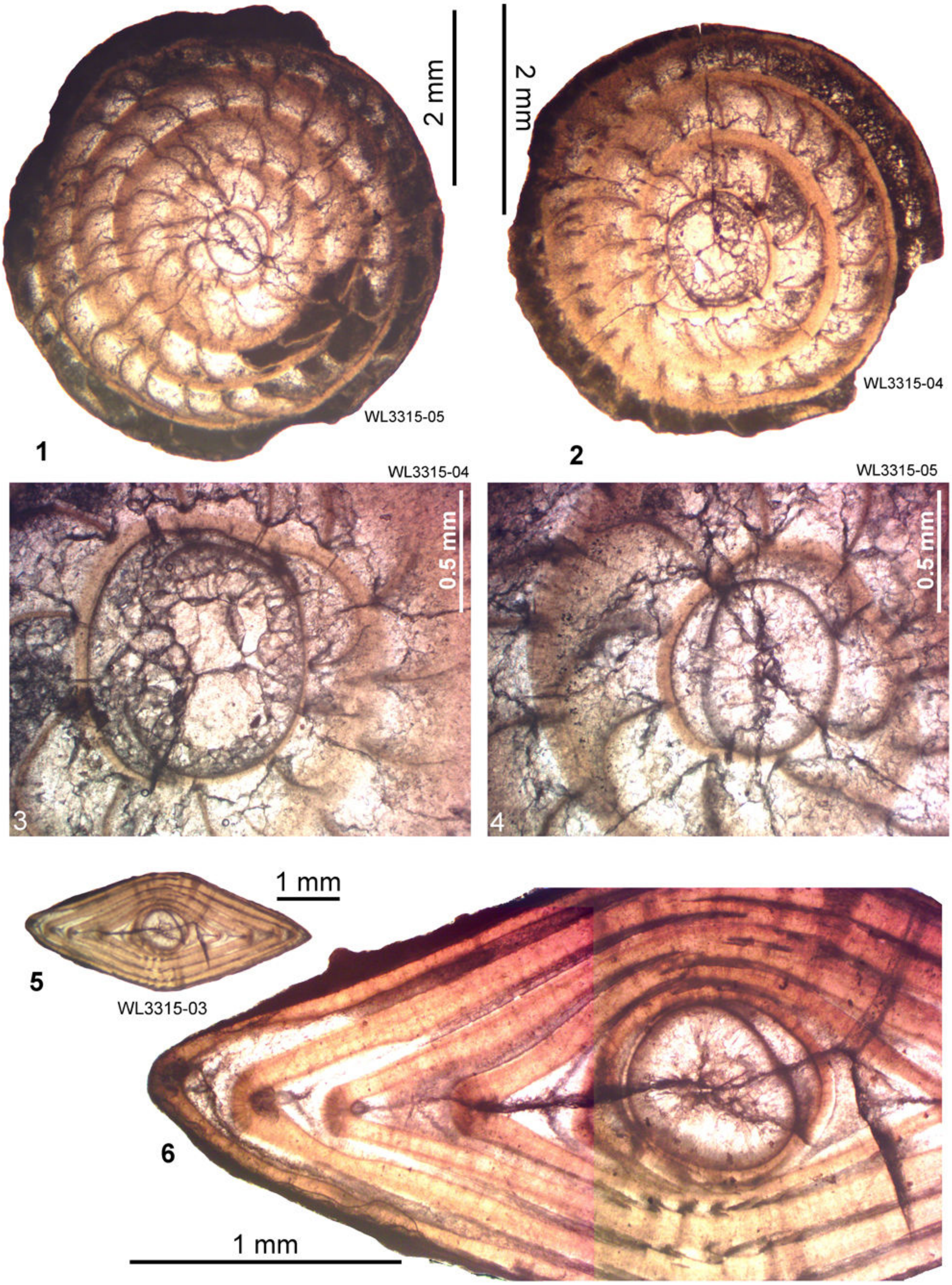

Figure 114: *Nephronummulites macgillavryi* (M.G. Rutten, 1935). **1-4**, megalospheric equatorial sections, **1, 4**, WL3315-05; **2-3**, WL3315-04. **5-6**, megalospheric axial section (WL3315-03). Palmetto Grove Formation (ABZ5), SW of Hampstead, St Ann, Jamaica.

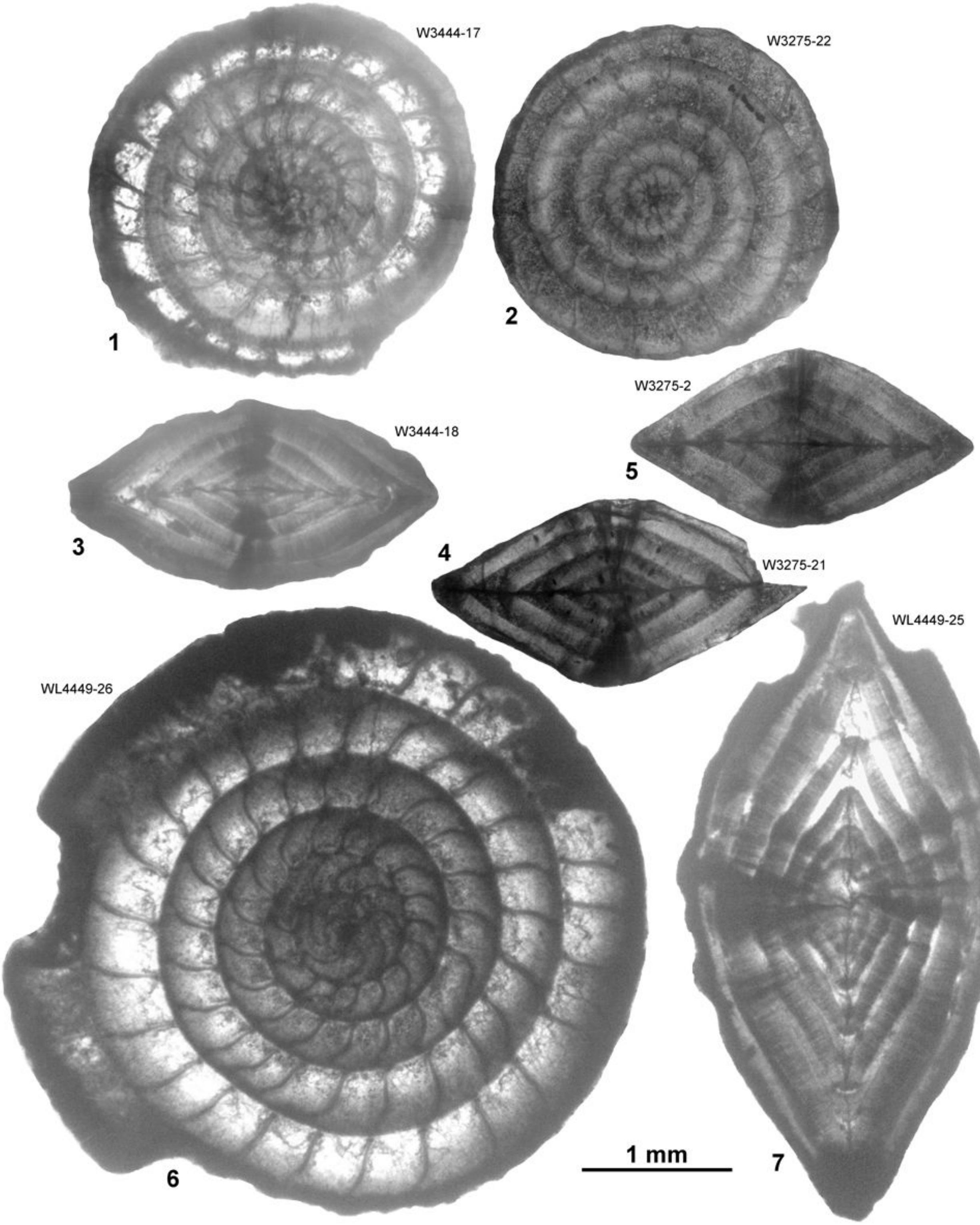

Figure 115: *Nummulites striatoreticularis* RUTTEN, 1928, from the mid Lutetian to Bartonian of Jamaica. **1** (UWIGM.WL3444-17), **2** (UWIGM.WL3275-22), **6** (UWIGM.WL4449-26): equatorial sections; **3** (UWIGM.WL3444-18), **4** (UWIGM.WL3275-21), **5** (UWIGM.WL3275-2), **7** (UWIGM.WL4449-25): axial sections. Sample WL3275: ABZ7, Swanswick type section, Trelawny, Jamaica; WL3444: ABZ9, Chapelton Formation, Albert Town, Trelawny, Jamaica; WL4449: ABZ14, limestones above marlstones, Cold Spring, Westmoreland, Jamaica.

Genus *Caudriella* Haman & Huddleston, 1984

Synonyms. *Margaritella* Caudri, 1974 (type species *Margaritella ospinae* Caudri, 1974) [preoccupied, non *Margaritella* Meek & Hayden, 1860 (a mollusc)].

Type species. *Margaritella ospinae* Caudri, 1974, from the early mid Bartonian of Margarita Island, Venezuela.

Caudriella sp.

(Fig. 113.6)

Previous descriptions and illustrations. Özcan *et al.*, 2022b, p. 26-27, Fig. 9J.

Remarks. Ferràndez-Cañadell & Serra-Kiel (1999) placed *Caudriella* in the Linderinidae based on the similarity of the embryos of *C. ospinae* and *L. brugesi*. *Caudriella* has lateral chamberlets whereas *Linderina* lacks lateral chamberlets. We have found *Caudriella* sp. in only one sample in Jamaica. Interestingly, samples from the type section of the Swanswick Formation at Swanswick House contain both *Linderina* and *Caudriella* (with a few lateral chamberlets: Fig. 113.6) demonstrating that there is unlikely to be a simple evolution from *Linderina* to *Caudriella*.

Superfamily NUMMULITOIDEA Blainville, 1827

Family NUMMULITIDAE Blainville, 1827

Genus *Nephronummulites* Mitchell, E. Robinson & Özcan gen. nov.

Type species. *Nummulites macgillavryi* M. G. Rutten, 1935 from the ?Ypresian of northern Santa Clara Province, Cuba.

Diagnosis. A genus of Nummulitidae with strongly dimorphic generations, and with the megalospheric forms having a large rounded proloculus and a thin crescent-shaped deuteroloculus.

Remarks. The genus differs from other American and Tethys *Nummulites* by the shape of the deuteroloculus. In *Nummulites* the deuteroloculus is only slightly smaller than the proloculus whereas in *Nephronummulites* the deuteroloculus is a narrow crescent-shaped chamber (Fig. 115).

Nephronummulites macgillavryi (M.G. Rutten, 1935)

(Fig. 114)

Previous descriptions. Rutten, 1935, p. 530, Pl. 59, figs. 6-10; Robinson & Wright, 1993, p. 331, Fig. 29.1-3.

Remarks. *Nephronummulites macgillavryi* is a very distinctive species characterised by its large megalospheric form with a large proloculus and its very large microspheric form (Rutten, 1935); it cannot be confused with any other described American nummulite. Orientated equatorial and axial sections of free megalospheric specimens are illustrated here for the first time and show that the deuteroloculus is small, crescent-shaped and embraces the protoconch. The species has a short stratigraphic range in the latest part of the Ypresian (ABZ5), is easily recognizable (even before sectioning) and is a valuable biostratigraphic marker.

Genus *Nummulites* Lamarck, 1801

Type species. *Camerina laevigata* Bruguière, 1792 (ICZN, 1945, Op. 192), from the middle Eocene (Lutetian) of Cayenne, France.

Nummulites striatoreticulatus L. Rutten, 1928

(Fig. 115)

Previous descriptions. Rutten, 1928, p. 1068; Robinson & Wright, 1993, p. 331, Figs. 29.5, 30.6.

Remarks. Small species of *Nummulites* are abundant from the mid Lutetian to the late Priabonian. They have been split into numerous taxa (*e.g.*, Barker, 1939) many of which have subsequently been synonymised (*e.g.*, Cole, 1958b). Some studies (*e.g.*, Wright & Swizer, 1971; Torres-Silva *et al.*, 2018) have attempted statistical studies on American *Nummulites*, but mostly using isolated populations. What is needed is a statistical treatment of populations collected sequentially from the mid Lutetian to the late Priabonian, but this is beyond the scope of this paper. The results of Torres-Silva *et al.* (2018) offer hope that some stratigraphic resolution can be achieved. We place all these small *Nummulites* from the Lutetian, Bartonian and Priabonian in the group of *N. striatoreticulatus* here.

Genus *Operculinoides* Hanzawa, 1935

Type species. *Nummulites (Nummulina) willcoxi* Heilprin, 1882 from the Priabonian of Florida.

Remarks. Although various studies have looked at *Operculinoides* (*e.g.*, Wright & Switzer, 1971; Torres-Silva *et al.*, 2018), there is too little biostratigraphic resolution at the present time (Torres-Silva *et al.*, 2018). The appearance of *Operculinoides* (with *Nummulites striatoreticularis*) at the base of ABZ7 is an important biostratigraphic datum in the mid Lutetian of the American region.

Operculinoides spp.

(Fig. 116)

Remarks. Details of various species of *Operculinoides* are present in Barker (1939) and Cole (1958b), with recent statistical treatments given in Torres-Silva *et al.* (2018). Individual species names are not assigned here. Small *Operculinoides* spp. appear in ABZ7 and range up to ABZ16.

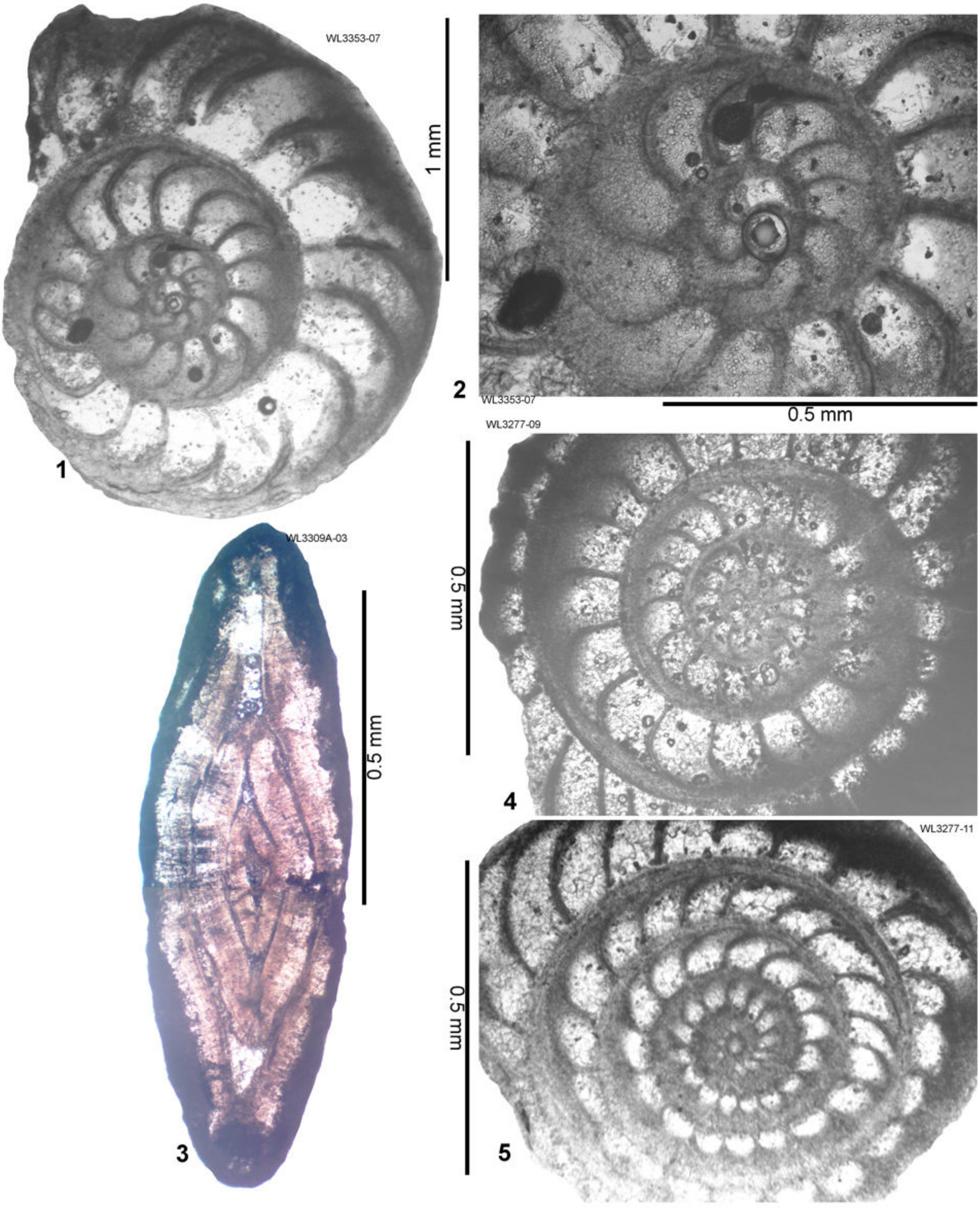

Figure 116: *Operculinoides* spp. **1-2** (UWIGM.WL3353-07), equatorial sections, ABZ9, Preston Hill Formation, Jeffrey Town, St Mary, Jamaica. **3** (UWIGM.WL3309A-03), axial section, ABZ7, Preston Hill Formation, Farm Turn, St Mary, Jamaica. **4** (UWIGM.WL3277-09), **5** (UWIGM.WL3277-11), equatorial sections, ABZ9, Preston Hill Formation, Clarkes Town, Trelawny, Jamaica.

Genus *Heterostegina* ORBIGNY, 1826

Type species. *Heterostegina depressa* ORBIGNY, 1826 (by subsequent designated by PARKER *et al.*, 1865, p. 36) from the Recent.

Remarks. The genus *Heterostegina* appears within the Eocene with two groups which are probably unrelated. *H. cubana* CIZANCOURT, 1948, is restricted to the upper Bartonian in Cuba (TORRES-SILVA *et al.*, 2017). *H. ocalana* is a widespread species in the upper part of the Priabonian (ROBINSON & WRIGHT, 1993; ROBINSON, 2004; TORRES-SILVA *et al.*, 2017).

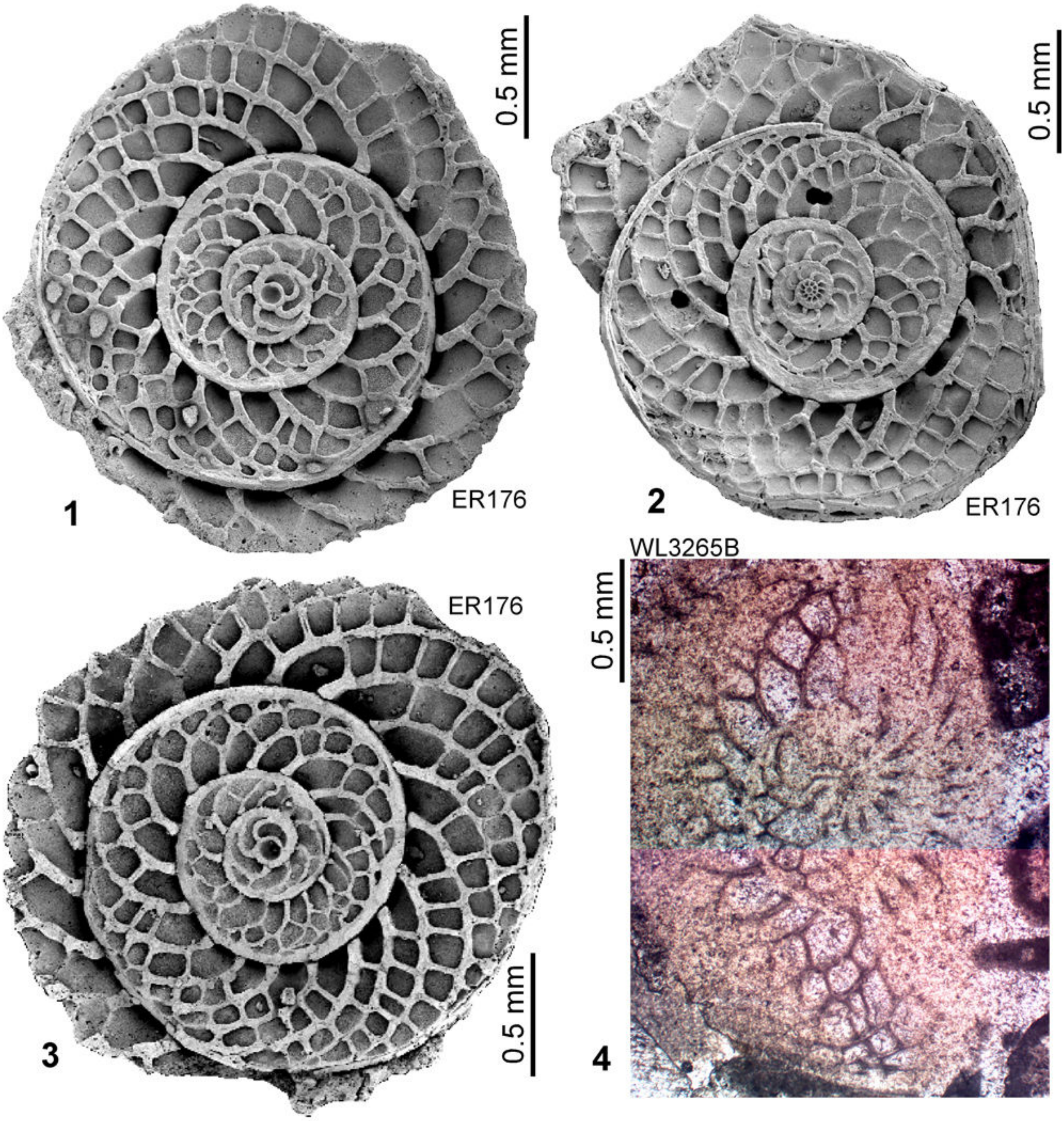

Figure 117: *Heterostegina ocalana* CUSHMAN, 1920. **1-3** (ER176), split specimens, equatorial sections: **1, 3**, megalospheric, **2**, microspheric; deep-water White Limestone (Chalk), ABZ16, Dressikie, St Ann, Jamaica. **4** (UWIGM. WL3265B), ABZ16, random section in rock, Swanswick House, Trelawny, Jamaica.

Heterostegina ocalana CUSHMAN, 1920

(Fig. 117)

Previous descriptions and figures. CUSHMAN, 1920, p. 130-131, Pl. XXI, figs. 15-18; ROBINSON, 2004, fig. 16A-B; TORRES-SILVA *et al.*, 2017, p. 586-587, Fig. 18A, B, D-H.

Remarks. The species is highly distinctive and easily identifiable even in random orientations in thin section (Fig. 117.4).

7. Conclusions

Our detailed work on selected LBF that have been calibrated against the nannofossil stratigraphy has allowed us to develop a high-resolution zonation for the Eocene of the Americas. This has also allowed us to revise the classification and phylogeny of the rapidly evolving clades that are useful in zoning these deposits.

The zonation reflects a series of migration events and the in situ evolution of different clades. Migration events are particularly associated with the nummulitids, with important migrations involving short-lived appearances of *Nephronummulites* and *Heterostegina* and a major influx of *Nummulites* and *Operculinoides*. In contrast, the Helicosteginidae and Lepidocyclinidae show a progressive evolution that is the main basis of the zonation scheme.

Future work will involve collecting larger populations to adequately characterise each species and more work on other groups (*e.g.*, orthophragmines and nummulitids) to improve the zonal resolution. We hope that our zonal scheme will be of value to the work of others and will help towards correlating the Eocene deposits across the Americas.

Contributions - Acknowledgements

SFM developed the project, logged and collected material from Jamaica, cut the LBFs, worked on the LBF taxonomy and developed the zonal scheme. ER worked on the taxonomy of the LBFs and provided extensive images of material. EÖ reviewed the taxonomy and provided extensive photomicrographs and measurements of specimens. MMJ provided nannofossil zonations on spot samples and samples collected from logged/collected sections. NR helped collect some of the samples, processed some of the material, cut the thin sections from Sherwood Content, and photographed material in the BMNH. The main text was prepared by SFM, but all authors contributed to the text and agree with the conclusions.

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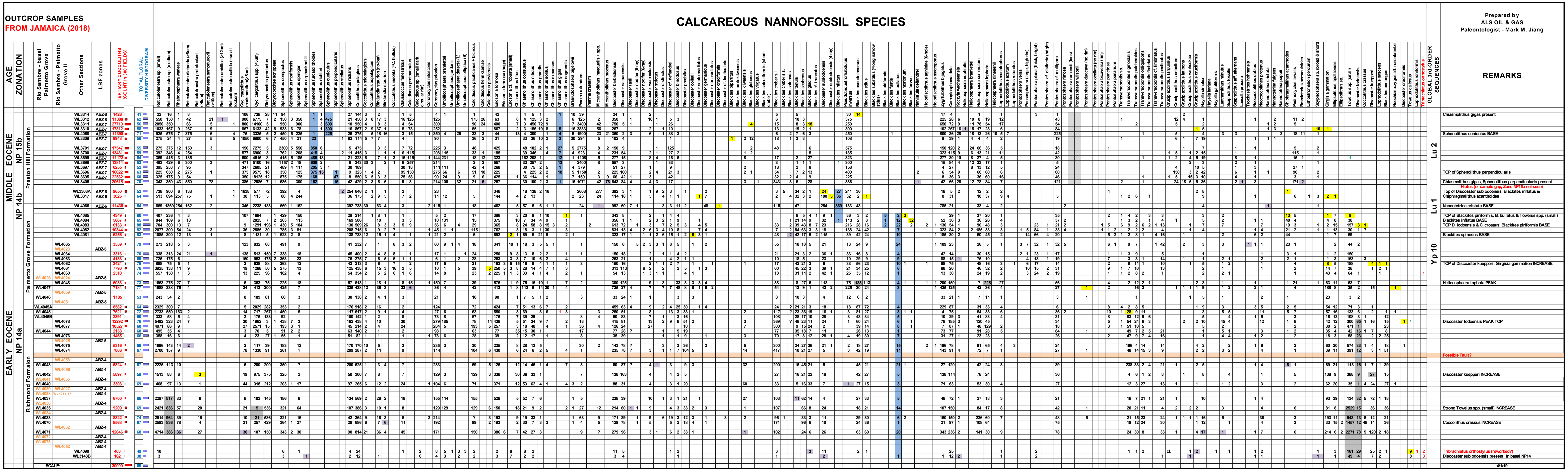
Appendix: Calcareous nannofossils

Two subsidiary files are available showing the distribution of calcareous nannofossils in selected samples analysed for this project. The first file (Appendix A1) shows analyses of samples from central and eastern Jamaica. The second file (Appendix A2) shows analyses of samples from western Jamaica.

Appendix 1

Nannofossils from samples from the lower part of the Eocene of Jamaica.



OUTCROP SAMPLES
FROM JAMAICA (2018)

CALCAREOUS NANNOFOSSIL SPECIES

Prepared by
ALS OIL & GAS
Paleontologist - Mark M. Jiang

AGE	ZONATION		Rio Sambre - basal Palmetto Grove	Rio Sambre - Palmetto Grove II	Other Sections	LBF zones	TERTIARY COCCOLITHS (COUNT in 300 FIELDS)	TOTAL FLORAL DIVERSITY HISTOGRAM	GLOBAL 3rd-ORDER SEQUENCES	REMARKS
MIDDLE EOCENE	NP 15b	Preston Hill Formation			WL3314	ABZ-8	1426	41	Lu 2	Chiasmolithus gigas present
					WL3312	ABZ-8	11888	62		
					WL3311	ABZ-7	27710	56		
					WL3310	ABZ-7	17312	58		
					WL4068	ABZ-7	11390	71		Sphenolithus cuniculus BASE
					WL3309	ABZ-7	9948	59		
					WL3701	ABZ-7	17547	55		
					WL3700	ABZ-7	13481	59		
					WL3699	ABZ-7	11173	64		
					WL3698	ABZ-7	13814	53		
					WL3697	ABZ-7	6255	52		
					WL3696	ABZ-7	16022	63		TOP of Sphenolithus perpendicularis
					WL3695	ABZ-7	22532	60		
					WL3405		20615	70		Chiasmolithus gigas, Sphenolithus perpendicularis present
										Hiatus (or sample gap; Zone NP15a not seen)
	NP 14b				WL3308A	ABZ-6	9650	52	Lu 1	Top of Discoaster sublodoensis, Blackites inflatus & Chiphragmalithus acanthoides
					WL3317	ABZ-6	3025	64		
		Palmetto Grove Formation			WL4066	ABZ-6	11435	54		Nannotetrina cristata BASE
					WL4085		4349	60		TOP of Blackites piriformis, B. bullatus & Toweius spp. (small)
					WL4084		5667	65		Blackites inflatus BASE
EARLY EOCENE	NP 14a				WL4083		6133	88	Yp 10	TOP D. lodoensis & C. croaaus; Blackites piriformis BASE
					WL4082		10344	82		
					WL4081		6256	83		Blackites spinosus BASE
				WL4065			3559	79		
				WL4023		ABZ-5				
				WL4064			3316	70		
				WL4063			4133	69		
				WL4062			3424	76		TOP of Discoaster kuepperi; Girgisia gammation INCREASE
				WL4061			7790	76		
				WL4060			2510	74		
			WL4026	WL4024		ABZ-5				
				WL4048			6083	73		Helicosphaera lophota PEAK
			WL4047				7184	77		
				WL4059		ABZ-5				
			WL4046				1185	53		
				WL4051		ABZ-5				
			WL4045A				8582	64		
		Richmond Formaion	WL4045				7621	72		
			WL4045B				2391	60		
				WL4078			12292	76		Discoaster lodoensis PEAK TOP
				WL4077			10527	60		
			WL4044				2138	60		
				WL4076			1465	66		
				WL4025		ABZ-5				
				WL4075			5316	68		
				WL4074			7806	67		
										Possible Fault?
				WL4058		ABZ-4				
			WL4043				5824	67		
				WL4056		ABZ-4				
			WL4042				5897	59		Discoaster kuepperi INCREASE
			WL4041	WL4055		ABZ-4				
			WL4040				3308	69		
			WL4039	WL4027		ABZ-4				
			WL4038	WL4054;57		ABZ-4				
			WL4037				6700	66		
			WL4036			ABZ-4				
			WL4035				9209	69		Strong Toweius spp. (small) INCREASE
			WL4034			ABZ-4				
			WL4033				8322	74		
			WL4070				8568	67		Coccolithus crassus INCREASE
				WL4032		ABZ-4				
			WL4071				12046	68		
			WL4072			ABZ-4				
			WL4073			ABZ-4				
				WL4052		ABZ-4				
					WL4090		403	49		Tribrachiatus orthostylus (reworked?)
					WL3148B		162	38		Discoaster sublodoensis present; in basal NP14
			SCALE:				30000	60		4/1/19

Appendix 2

Nannofossils from samples from the upper part of the Eocene of Jamaica.

OUTCROP SAMPLES
FROM JAMAICA (2019)

CALCAREOUS NANNOFOSSIL SPECIES

Prepared By
Paleontologist - Mark M. Jiang
Ellington Geological Services

AGE	ZONATION		Montpelier-New Market Belt	Spot Valley	Grant Pen	Salt Spring - Flower Hill	LBF Zone	TOTAL FLORAL DIVERSITY HISTOGRAM
	NP19	PRIABONIAN	WL4616				ABZ-16	24
			WL4617				ABZ-16	33
			WL4624A				ABZ-16	40
			WL4602				ABZ-16	28
	NP18		WL4622				ABZ-15	22
			WL4621				ABZ-15	34
			WL4620				ABZ-15	15
			WL4618				ABZ-15	34
	NP17		WL4445				ABZ-14	23
		BATONIAN		WL4243			ABZ-12	
				WL4241			ABZ-12	
	NP16				WL4628			35
					WL4629		ABZ-10	
					WL4630		ABZ-10	14
						WL4237	ABZ-9	
		?				WL4236	ABZ-9	17
						WL4234	ABZ-9	26
					SCALE:			50

	Reticulofenestra sp. (small)	Reticulofenestra sp. (medium)	Reticulofenestra dictyoda (>8um)	Reticulofrnestra onusta	Reticulofenestra umbilica (>12um)	Reticulofenestra hillae	Cyclicargolithus marismontium(>5um)	Cyclicargolithus spp. (<5um)	Cribrocentrum reticulatum (L)	Cribrocentrum reticulatum (>12um)	Cribrocentrum reticulatum (M)	Cribrocentrum reticulatum (S)	Cribrocentrum erbae	Dictyococcites bisectus	Dictyococcites scrippsae	Dictyococcites productus	Sphenolithus compactus	Sphenolithus moriformis	Sphenolithus pseudoradians	Sphenolithus radians	Sphenolithus predistentus	Sphenolithus intercalcaris	Sphenolithus spiniger	Sphenolithus furcatolithoides	Sphenolithus labradorensis	Sphenolithus cuniculus
WL4616	R	F	r		R		A	A	A	R	C						R				r					
WL4617	R	F	r		R		A	A	A	R	R				r		C	r	r	r	R	r				
WL4624A	F	r			r		A	A	C		A			r	R		F	r	r		R	r				
WL4602	C	R			C		r	A	r		r				r		C	R	r	r	r	r				
WL4622	C				r			A							A		C	r		r						
WL4621	C	r			r		R		r					1	A	C	F	r	r	r		r				
WL4620							R	A			R		r	r	C		F	r								
WL4618	A		1		R		A	A	A		A			r	F		C	r	R	r		R				
WL4445							r	A			r	F		r	F		F	r								
WL4243																										
WL4241															1											
WL4628			r		r	r	F	A	C		R				r		F	r	r							
WL4629							1																			
WL4630		r	r	cf.	r			C							r		R						1	10		
WL4237																										
WL4236			r		r		r	C							2		R						r	2		1
WL4234		r	F	2	r			C									F	r					r	R	3	

	Coccolithus pelagicus	Coccolithus eopelagicus	Hayella situliformis	Birklundia staurion (no-bar)	Calcidiscus protoannulus	Calcidiscus cf. kingii (large)	Cruciplacolithus cribellum	Calcidiscus bicircus	Ericsonia formosa	Chiasmolithus titus	Chiasmolithus consuetus	Chiasmolithus oamaruensis	Chiasmolithus nitidus	Chiasmolithus solitus	Chiasmolithus modestus	Braarudosphaera bigelowii	Braarudosphaera spp.	Pemma papillatum	Pemma basquensis	Pemma stradneri	Pemma angulatum	Micrantholithus aff. obtusus	Micrantholithus inaequalis + spp.	Micrantholithus procerus
WL4616	F				r				R								r							
WL4617	F		r			r			F	1							r							
WL4624A	C	R	r		C	r			R	1						r	r	r				1		
WL4602	C	r							F	r		3				r							r	
WL4622	F	r			R											r		r	R	R			r	
WL4621	R	r			r				r	2						R		R	R	R			r	
WL4620	R				R				r									r		r				
WL4618	F	R			R				R							r		r	r				r	
WL4445	R	r			R				R							r		R			r		r	r
WL4243																								
WL4241																								
WL4628	F				R	r			R		r					r		r					r	
WL4629																								
WL4630	r	1							r				1	2										
WL4237																								
WL4236	R								r		2		4	6										
WL4234	R			3	r	r	1	1	r		2		3	6	1									

	Discoaster barbadiensis	Discoaster saipanensis	Discoaster tanii	Discoaster nodifer	Discoaster distinctus	Discoaster deflandrei	Discoaster strictus	Discoaster binodosus	Blackites spinosus	Blackites tenuis	Zygrhablithus bijugatus	Campylosphaera dela	Koczyia wechesensis	Helicosphaera intermedia	Helicosphaera euphratis	Helicosphaera reticulata	Helicosphaera compacta	Helicosphaera papillata	Helicosphaera heezenii	Helicosphaera dinesenii	Helicosphaera lophota	Helicosphaera clarissima	Helicosphaera wilcoxonii	Pontosphaera oamaruensis	Pontosphaera multipora	Pontosphaera spp.
WL4616	R	F	r	r	r						r			r			r									r
WL4617	R	F	R	r							r			r	r		r							1	r	r
WL4624A	r	R	R	r	1						F			r	r	R	r		1			2		r		R
WL4602	r	r				r					R			r	r		R									
WL4622	r		r								r			r	r											1
WL4621	r	r	1			1		1			r			r	r		r		1							r
WL4620		r									r															
WL4618	r	R	R		1	r					F				r		r	1	1							r
WL4445	r					1					r						r		2							r
WL4243																										
WL4241																										
WL4628	r	r	r				r		r	r			r	r	R		r	1				r	1			F
WL4629																										
WL4630																										r
WL4237																										
WL4236												4														
WL4234	R											4							1	1	1					

	Transversopontis obliquipons	Lanthernithus minutus	Pedinocyclus larvalis	Scyphosphaera columella	GLOBAL 3rd-ORDER SEQUENCES	REMARKS
WL4616		r			Pr 2	Cc. reticulatum (L)ABUNDANT
WL4617		r				Cc. isabelae BASE
WL4624A	r	R				H. heezenii
WL4602						
WL4622		r			Pr 1	P. basquensis; P. stradneri
WL4621						
WL4620						Cc. erbae present
WL4618		r				
WL4445					Bart 1	M. procerus, M. angulatum (=crassum s.l.)
WL4243						Barren
WL4241						Barren
WL4628		r		r		S. columella, D. strictus; Cc. reticulatum BASE
WL4629					Lu 4	Barren
WL4630						S. furcatolithoides; C. solitus; C. nitidus, S. spiniger
WL4237						Barren
WL4236			1	1	Lu 3	S. cuniculus, C. solitus INCREASE
WL4234						R. onusta, H. lophota; R. umbilica (12um) present
SCALE:						15/8/19

Nomenclatural note:

Life Sciences Identifier (LSID)
http://zoobank.org/References/25df1e8e-d1f0-492f-b39e-2de1041dca79

Family Group

- Helicosteginidae MITCHELL, E. ROBINSON & ÖZCAN, 2022
http://zoobank.org/NomenclaturalActs/3C1F3886-2379-425C-986D-7EA19FA3440F
- Pseudolepidinidae MITCHELL, E. ROBINSON & ÖZCAN, 2022
http://zoobank.org/NomenclaturalActs/EB5DCCF1-9A5D-4E10-8B46-D4C5A739341E

Subfamily Group

- Orbitoininae MITCHELL, E. ROBINSON & ÖZCAN, 2022
http://zoobank.org/NomenclaturalActs/BDCD11E8-EFF4-45C9-921A-025FF95D3DE1

Genus Group

- *Butterliniana* MITCHELL, E. ROBINSON & ÖZCAN, 2022
http://zoobank.org/NomenclaturalActs/0499C40E-D407-44B7-91F2-39B9F1CD4171
- *Planorbitoinella* MITCHELL, E. ROBINSON & ÖZCAN, 2022
http://zoobank.org/NomenclaturalActs/55cd0576-1034-4875-9730-eec54bd52fd4
- *Polyorbitoinella* MITCHELL, E. ROBINSON & ÖZCAN, 2022
https://zoobank.org/NomenclaturalActs/22b603c6-1937-452d-ac16-f1a4310250dc
- *Nephronummulites* MITCHELL, E. ROBINSON & ÖZCAN, 2022
http://zoobank.org/NomenclaturalActs/B9A49C2D-D3AE-4C1C-B2C0-3AC605BB5903

Species Group

- *Helicostegina minor* MITCHELL, E. ROBINSON & ÖZCAN, 2022
http://zoobank.org/NomenclaturalActs/21470867-4E48-4DA9-9455-1CC11658B9E4
- *Helicostegina jamaicensis* MITCHELL, E. ROBINSON & ÖZCAN, 2022
http://zoobank.org/NomenclaturalActs/19877A83-E891-4E6C-8215-5250C30A2E10
- *Helicostegina jeannemairae* MITCHELL, E. ROBINSON & ÖZCAN, 2022
http://zoobank.org/NomenclaturalActs/82A7FE88-E81E-4138-B21D-69E998A4DC40
- *Polyorbitoinella lilyfieldensis* MITCHELL, E. ROBINSON & ÖZCAN, 2022
http://zoobank.org/NomenclaturalActs/56DF40C0-67C2-4329-ADAC-9BAE7783C101
- *Orbitoina wrighti* MITCHELL, E. ROBINSON & ÖZCAN, 2022
http://zoobank.org/NomenclaturalActs/8C3EF547-29F4-4FA4-A54C-0E3B676FBDDC