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A high-resolution biostratigraphy for the Upper Oligocene (Chattian) of Jamaica using miogypsinid foraminifers, and its stratigraphic and phylogenetic significance

Simon MITCHELL [1]

Abstract: Fourteen miogypsinid populations (ground-down free specimens, thin sections, and polished slabs) from Jamaica are analysed using univariate and bivariate statistics. The populations consist of one sample of free specimens from which orientated equatorial sections were prepared and thirteen populations with random equatorial sections on polished blocks. The populations are sorted into chronospecies based on mean X (X_m) values with four chronospecies (*Miogypsinoides complanatus*, *Miogypsina thalmanni*, *Mio. 'basraensis'*, and *Mio. tani*) identified. Three samples collected from a single traverse show a succession of three successive chornospecies (*Ms. complanatus*, *Mio. thalmanni*, and *Mio. 'basraensis'*). *Ms. complanatus* is calibrated to around the Rupelian/Chattian boundary (based on data from Antigua), whereas advanced forms of *Mio. tani* are calibrated with the latest Chattian (based on planktic foraminifers, calcareous nannofossils, and Sr isotopes). The zonation for the Chattian using Larger Benthic Foraminifers is revised and five zones based on miogypsininids are recognized. This zonation enables the unconformity between the Moneague Formation (Rupelian to mid Chattian) and Newport Formation (latest Chattian) in Jamaica to be quantified. Comparison between the Americas and the Neotethys/Indo-Pacific indicates that miogypsinid evolution in the Chattian was more rapid in the Americas and that by the base of the Miocene, American miogypsinids were two chronospecies more advanced compared with their allies in the Neotethys/Indo-Pacific. This demonstrates that high resolution scanning of polished slabs represents a valuable tool for biostratigraphy of Larger Benthic Foraminifers.

Keywords:

- *Miogypsina*;
- *Miogypsinoides*;
- White Limestone;
- biostratigraphy;
- phylogeny;
- paleogeography

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Résumé : *Une biostratigraphie à haute résolution de l'Oligocène supérieur (Chattien) de Jamaïque fondée sur les foraminifères miogypsinidés, et sa signification stratigraphique et phylogénétique.-* Quatorze associations de miogypsinidés (spécimens libres meulés, lames minces et plaques polies) provenant de Jamaïque sont analysées à l'aide de statistiques univariées et bivariées. Chaque association correspond à un prélèvement de spécimens libres à partir duquel des sections équatoriales orientées ont été préparées, ainsi que treize associations comportant des sections équatoriales aléatoires sur des blocs polis. Les associations sont classées en chronoespèces sur la base des valeurs moyennes de X (X_m), quatre chronoespèces étant identifiées : *Miogypsinoides complanatus*, *Miogypsina thalmanni*, *Mio. 'basraensis'* et *Mio. tani*. Trois échantillons prélevés le long d'une même coupe stratigraphique montrent une succession de trois chronoespèces successives (*Ms. complanatus*, *Mio. thalmanni* et *Mio. 'basraensis'*). *Ms. complanatus* est datée aux environs de la limite Rupélien/Chattien (sur la base de données provenant d'Antigua), tandis que les formes évoluées de *Mio. tani* sont attribuées au Chattien terminal (d'après les foraminifères planctoniques, les nannofossiles calcaires et les isotopes du Sr). La zonation du Chattien fondée sur les Grands Foraminifères Benthiques est révisée, et cinq zones basées sur les miogypsinidés sont reconnues. Cette zonation permet de

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quantifier la discordance entre la Formation de Moneague (Rupélien à Chattien moyen) et la Formation de Newport (Chattien terminal) en Jamaïque. Une comparaison entre les Amériques et la région Néotéthys/Indo-Pacifique indique que l'évolution des miogypsinidés durant le Chattien a été plus rapide dans les Amériques et que, à la base du Miocène, les miogypsinidés américains étaient avancés de deux chronoespèces par rapport à leurs homologues de la région Néotéthys/Indo-Pacifique. Cela montre que la numérisation haute résolution de plaques polies constitue un outil précieux pour la biostratigraphie des Grands Foraminifères Benthiques.

Mots-clefs :

- *Miogypsina* ;
- *Miogypsinoides* ;
- White Limestone ;
- biostratigraphie ;
- phylogénie ;
- paléogéographie

1. Introduction

The biostratigraphic subdivision of Oligocene and lower Miocene shallow-water, platform limestones in the Americas is difficult. While planktic foraminifers and calcareous nannoplankton represent the baseline for standardized Cenozoic biostratigraphy, they are difficult to study in indurated limestones and may be absent due to the character of the depositional environments. Larger benthic foraminifers (LBF) offer significant scope for biostratigraphy using objective criteria (MITCHELL *et al.*, 2022, 2024), but are difficult to extract and identify in indurated limestones lacking orientated thin sections. This paper uses a method (polished slabs) to investigate LBF (specifically miogypsinids) in indurated rocks, calibrates LBF biostratigraphy against chronostratigraphy using key samples, and uses this to explore geological problems in Jamaica and review the phylogenetic evolution of the miogypsinids across the Americas, Neotethys, and Indo-Pacific provinces.

2. Methodology

An understanding of the geology of the Oligocene and lower Miocene rocks in Jamaica has been achieved through geological mapping and the investigation of samples in the field and in the laboratory. Field mapping was undertaken along road and path transects with rock lithologies and bedding recorded in a notebook against GPS coordinates. A hand held GPS unit was used to record GPS positions. Samples of limestones and chalks were broken off with a 4 lb (1.8 kg) lump hammer, wetted with water, and examined in the field with a 10x hand lens. The lithology was recorded using an extended DUNHAM classifications (DUNHAM, 1962; EMBRY & KLOVAN, 1971; LOKIER & AL JUNAIBI, 2016) and bioclasts were identified. Larger benthic foraminifers (LBF) were identified to genus and species level (where possible) in the field. Samples (rock specimens and bulk samples of unlithified sediment) were collected for subsequent laboratory examination.

GPS data were used to construct geological maps in the drawing programme CanvasX19. Stratigraphic boundaries and faults were determined through geological mapping of lithologies and breaks in biostratigraphy. Some faults were visible in remote sensing imagery (aerial photographs and satellite imagery). Other faults (some of them with large offsets) had no representation on such imagery as they had not been active recently or fault planes had not been enhanced through geomorphological modification (limestone dissolution, etc.). Furthermore, some features on remote imagery do not represent faults and are related to other geomorphological features, such as, uplifted marine terraces (modified by karst processes) formed during the progressive uplift of Jamaica. Simplified geological maps of Jamaica and the area around Ulster Spring (parish of Trelawny) are presented here

Unlithified sediment samples were disaggregated by drying and soaking in water. If this was not successful, samples were put through several cycles of freezing and thawing in water to break them down. The broken down samples were sieved through 1 mm and 500 µm sieves, and LBF (and other bioclasts) were picked from the sieved residues. LBF were sorted into morphotypes and orientated equatorial and axial sections of individual LBF were prepared by careful grinding on a glass plate.

For lithified rock samples, standard 32 µm-thick thin sections were prepared as well as numerous polished rock slabs. Polished rock slabs were serially ground using progressively finer silicon carbide grits with a final polish using 1200 grade silicon carbide powder. Polished slabs were scanned at 6400 dpi and the scans searched for appropriate sections (equatorial and axial) of LBF. Because of the large surface area of the rock slabs, numerous approximately equatorial sections of miogypsinids (and other foraminifers) were located. Photomicrographs of LBF on the thin sections and slabs were then imaged using microscope cameras.

2.1. Measurements and statistics

Several characters have traditionally been measured on miogypsinids following DROOGER's (1952) statistical analysis of American populations (Fig. 1). These characters were analysed by statistical methods. Since the measurements made include categorical data (counts of numbers of chambers), with variable samples sizes, which may not be normally distributed, nonparametric univariate statistical tests are appropriate.

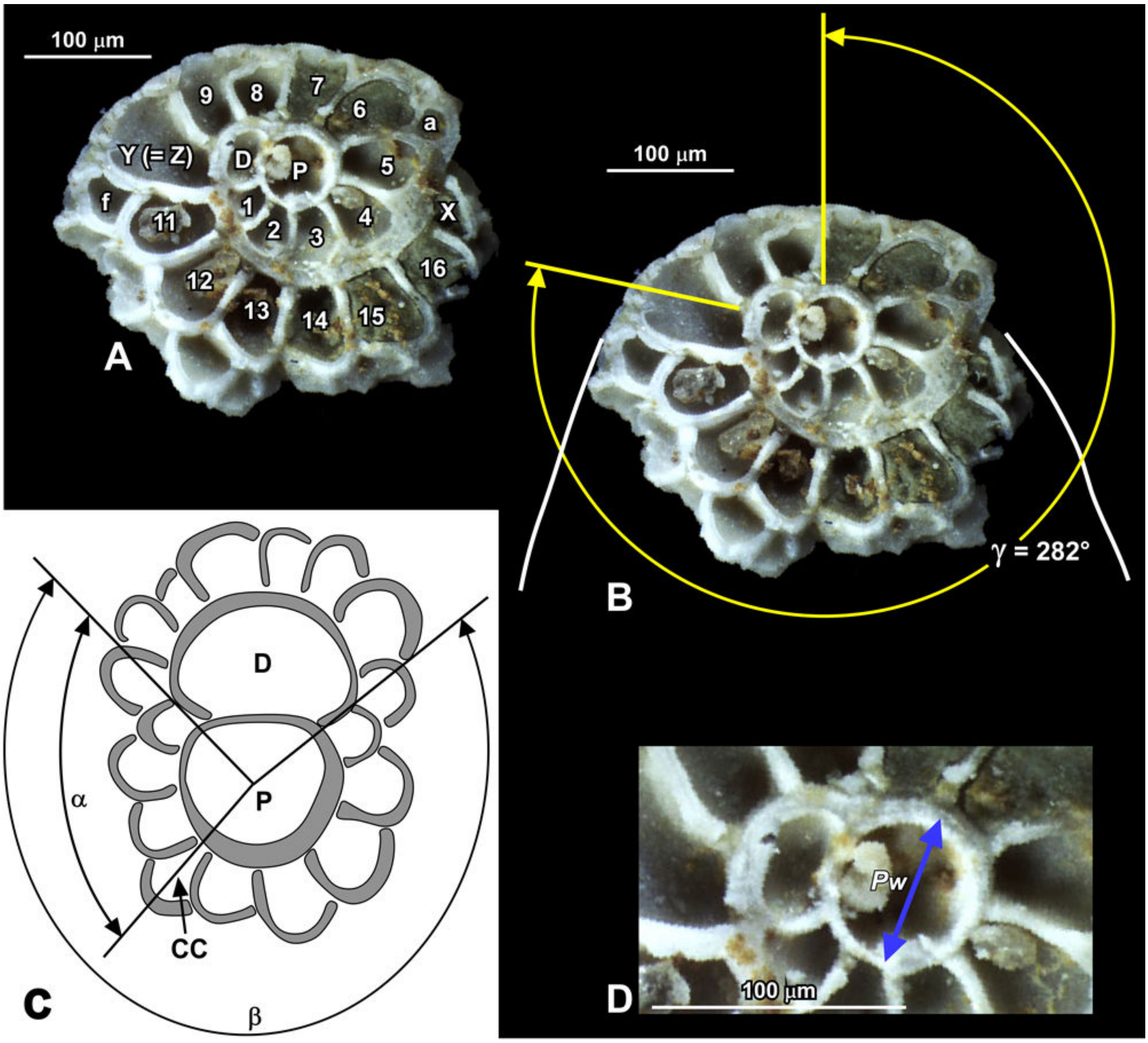

Figure 1: Characters measured on miogypsinids following Drooger (1952). The illustrated specimen in A, B, and C is *Miogypsinoides* cf. *formosensis* (image from https://foraminifera.eu used with permission), and shows a small additional equatorial chamber (a) that is not part of the fan of equatorial chambers (cf. chambers developed in *Neorotalia*). A. chambers numbered in the primary spire with number of chambers (excluding the protoconch [P] and the deuterioconch [D]), here X = 17. The largest chamber Z = 10 and the first chamber with two stolons that gives rise to the fan Y = 11 (these are more subjective than determining X). B. Measurement of the angle γ: the fan of equatorial chambers is broken off, but indicated by the white lines; angle γ is the amount in degrees that the P-D axis needs to be rotated to 'unwind the coil' such that D faces the apex (in this case γ = 282°). C. Measurement of angles *α* and *β* to determine V, where V = 200*α*/*β*. D. Measurement of the width of the protoconch Pw (including half the thickness of the wall).

Kruskal-Wallis rank sum tests for multiple independent samples were undertaken with post-hoc Dunn pairwise tests with *p*-values adjusted using the Benjamini-Hochberg FDR method (Benjamini & Hochberg, 1995). Univariate data are illustrated using dot plots and bar graphs. Bivariate analyses were investigated through graphical methods with fields for samples outlined by rounded polygons. The following sections describe the different characters that have been used for miogypsinids (Drooger, 1952).

Character X was introduced by Drooger (1952) and is the number of chambers (excluding the protoconch (P) and deuterioconch (D) - that is the embryo) in the neorotalid coil around the embryo of a miogypsinid (Fig. 1.A). Calculated mean values (X_m) are considered the most import characters in distinguishing populations of *Miogypsinoides* and early *Miogypsina*, although the genera themselves are distinguished by the lack (in the former) and presence (in the latter) of lateral chamberlets (*e.g.*, Drooger, 1952, 1963, 1993). However, the value of X_m for distinguishing chronospecies of *Miogypsina* is diminished once two spires of periembryonic chambers (from one or two Principal Auxillary Chambers - PACs) encircling the protoconch and meeting in a closing chamber are developed (Fig. 1.C). The first limi-

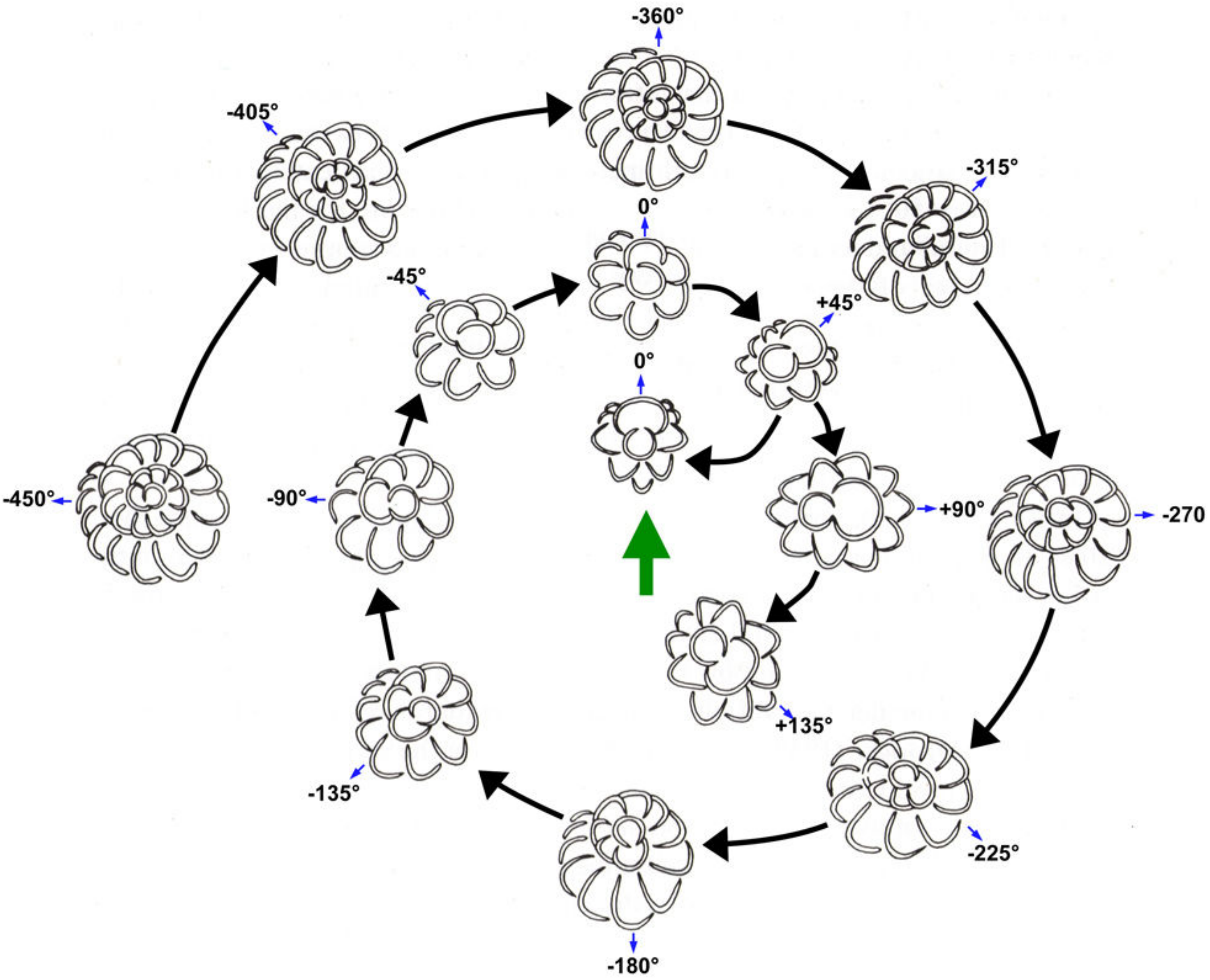

Figure 2: Range of variation of γ in different specimens of miogypsinid foraminfers (revised from Drooger, 1993, Fig. 47). Specimens are arranged with the apical region orientated towards the top (green arrow). The small blue arrow points along the embryonic axis towards the deuteroconch. The black arrows show the evolutionary trend towards less negative γ values and eventually positive γ values.

tation on character X is that it can only be measured if equatorial sections are available. When matrix-free specimens are available, suitable equatorial sections can be prepared (by grinding) so that this character can be measured. If only hard rock samples are available, then accidental sections in thin sections or on polished rock slabs (as used here) must be used. In the latter case, limitations are introduced, because an informed decision needs to be made for each random section on whether the section shows the complete neorotalid spire. Small errors here are not going to significantly affect the mean if a 'moderate'-sized population (8 or more specimens) is available. Counts on just one or two specimens are of limited biostratigraphic value, since they could belong to one of several successive chronospecies.

Some authors have used a typological approach for the study of miogypsinids. For instance, BouDagher-Fadel and Price (2010, p. 574) stated that for *Mio. gunteri*, X = 10 to 12, and for *Mio. tani*, X = 8. Yet, Drooger (1952, 1993) clearly stated that using mean values for X (that is X_m), *Mio. gunteri* was defined as having X_m between 10.5 and 9 (with a range of X-values from 14 to 8 - taken from Drooger's, 1952, Table 1), whereas *Mio. tani* was defined as having a X_m of less that 9 (and a range of X-values from 10 to 6 - taken from Drooger's, 1952, Table 1). Thus, individual specimens cannot be assigned to a particular chronospecies, only populations with a sufficient number of specimens. Drooger's (1952) figured specimens of *Mio. tani* showed X = 7 to 9 chambers (his plate 2, five drawings) and one photomicrograph (on his Plate 3) showing 7 chambers. It is, therefore, difficult to understand BouDagher-Fadel and Price's (2010) statement that for *Mio. tani* X = 8. Consequently, their typological identification of specimens assigned to either *Mio. gunteri* or *Mio. tani* (or for that matter, other miogyspsinid species) is suspect and their biostratigraphic conclusions are open to question. Equally, Baumgartner *et al.* (2008, p. 40) stated that "we can clearly identify the morphological characters of the two species *Mio. gunteri* and *Mio. tani*", and that "the X-value of *Miogypsina tani* ranges from 6 to 9 and that of *Mio-*

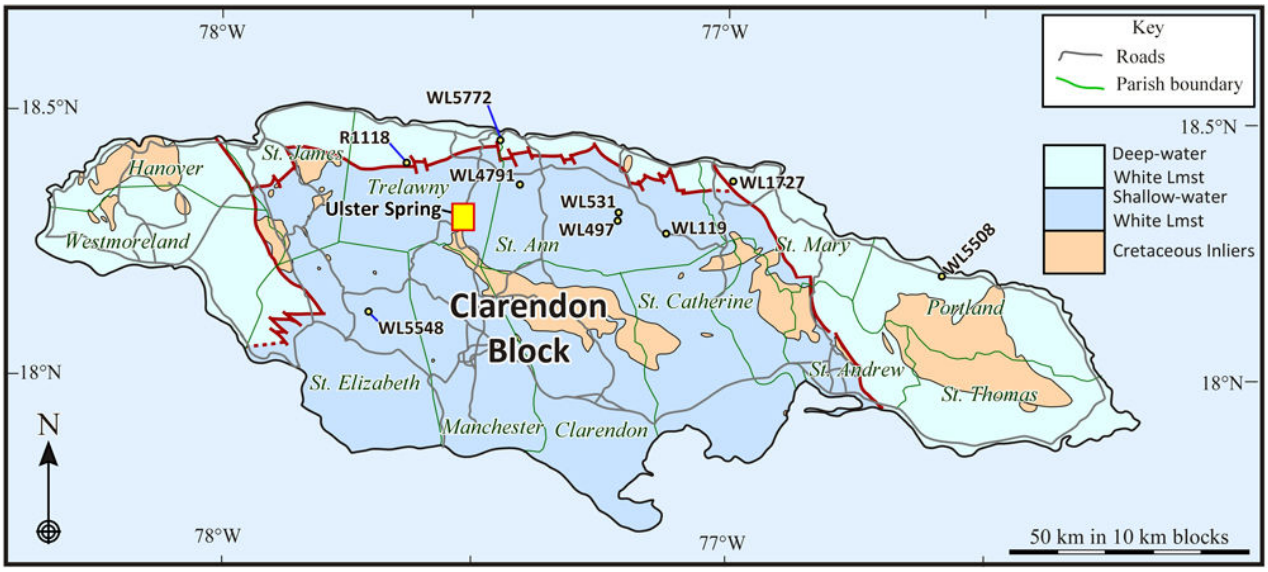

Figure 3: Simplified geological map showing deep-water basins (minor blocks in eastern and western Jamaica omitted) and the large, shallow-water Clarendon Block in Oligocene to early Miocene times. Cretaceous rocks (inliers), parish boundaries, and major roads are shown for reference. The location of the detailed map for samples around Ulster Spring is shown (yellow box at exaggerated size) together with other samples locations across Jamaica.

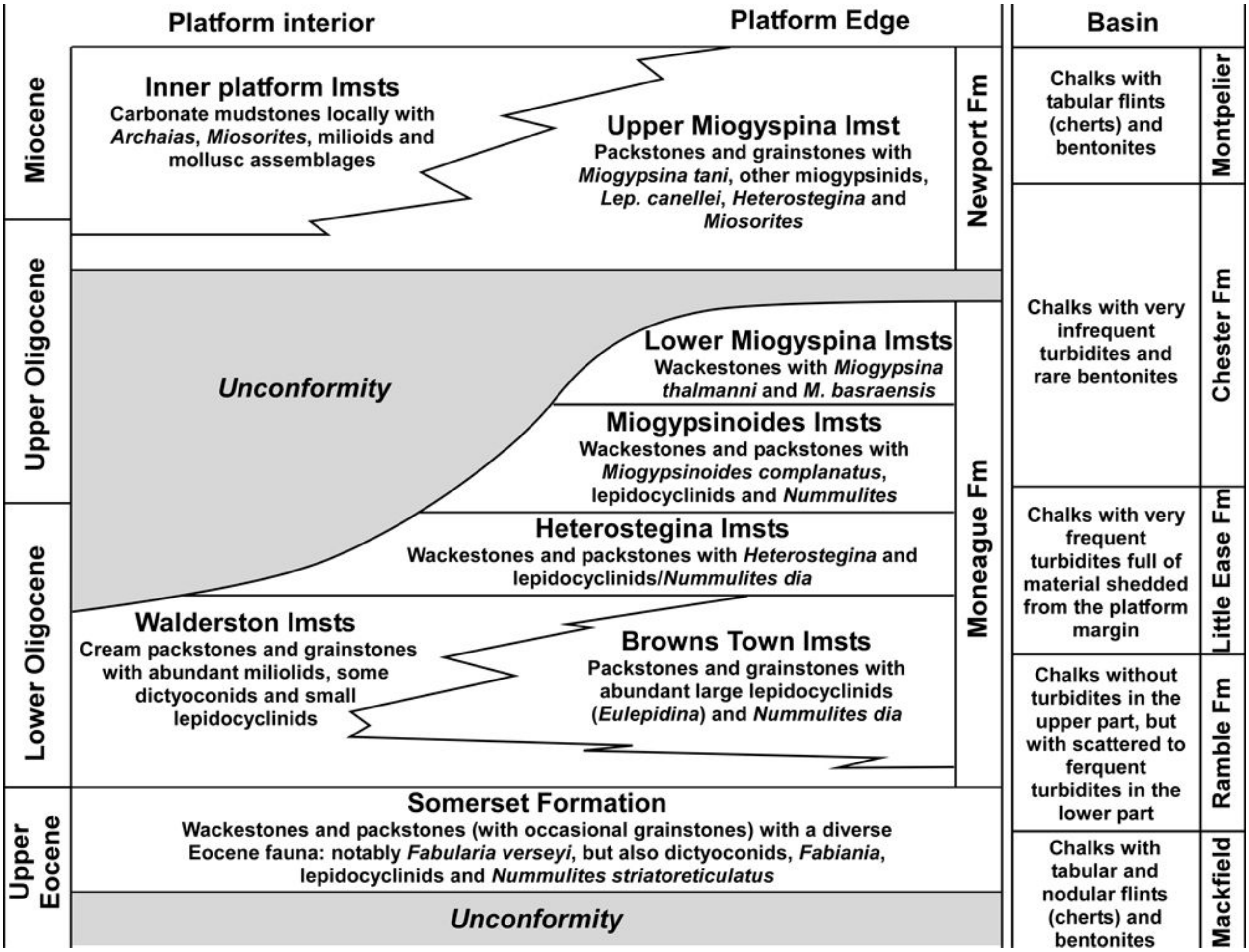

Figure 4: Subdivision of part (uppermost Eocene to mid Miocene) of the shallow'water White Limestone succession on the Clarendon Block (formations and beds based on lithology and foraminiferal assemblages) and the deep-water White Limestone (formations) in the basin. Formal descriptions will be published elsewhere.

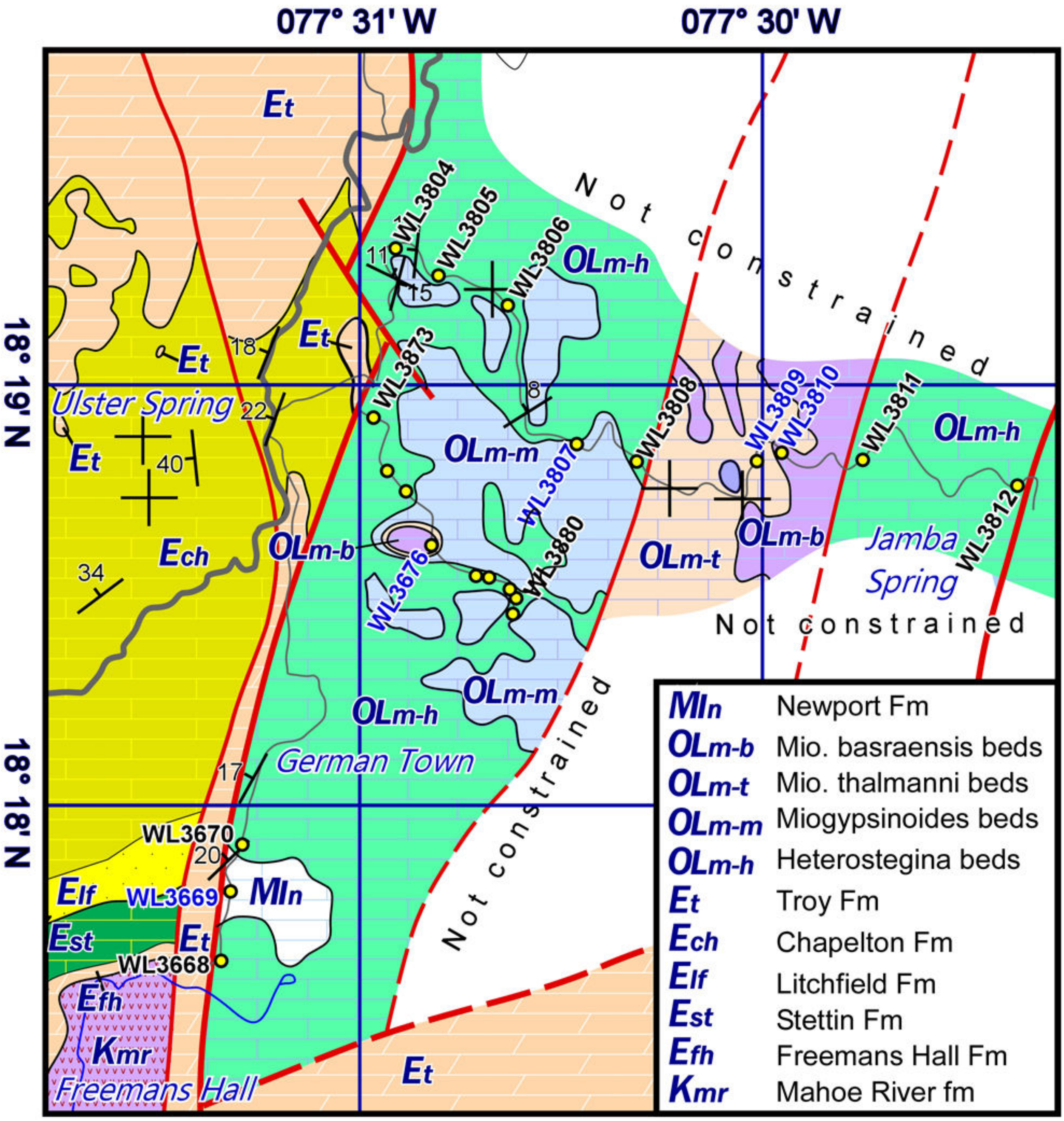

Figure 5: Detailed map of the area to the west of Ulster Spring (Trelawny) showing samples (those with miogypsinids in blue). The road transect (samples WL3804 - WL3810 shows foraminifers in their correct stratigraphic positions according to the theory of nepionic acceleration (TAN, 1936, 1937; DROOGER, 1952) suggesting a low dip of the strata to the east (the limestones are largely unbedded).

gypsina gunteri from 9 to 12.5". Yet these 'ranges' should be mean values of X (X_m) and, as such, individual specimens should not be assigned to chronospecies. So identifications of miogypsinid taxa in the Americas using X-values (rather than X_m values) post-DROOGER (1952) have been based on species names applied to individual specimens and, consequently, have limited biostratigraphic value.

Character Y (Fig. 1.A) represents the number of chambers in the neorotalid spire (excluding P and D) up to, but NOT including the first chamber that gives rise to the fan of equatorial chambers (DROOGER, 1952; RAJU, 1974). Character Y has generally not been used, since it shows a good positive correlation with the character X and it also represents a smaller number of chambers than character X (DROOGER, 1952, 1993; RAJU, 1974). Also, it is generally more difficult to determine character Y compared with character X since the first chamber with two stolons may be difficult to pick in poorly preserved specimens.

Character Z (Fig. 1.A) is the number of spiral chambers in the rotalid coil excluding the first two chambers (P and D), up to and including the largest chamber (DROOGER, 1952). The identification of the largest chamber may be difficult (subjective) in some forms and character Z has not generally been used in the discrimination of species.

Angle γ relates the orientation of the medial line through the embryo (centres of P and D) to the medial line through the fan of chambers forming the test (DROOGER, 1952; Fig. 1.B). Values of γ range from about -450 to +135 (Fig. 2) and there is a good correlation between X_m values and $γ_m$ values (RAJU, 1974; DROOGER, 1993). The measurement of γ has presented problems and DROOGER (1993, Fig. 47) introduced a useful diagram for visualizing different values of γ (redrawn with amendments in Fig. 2). Angle γ is negative for more tightly coiled specimens and positive for many biserial forms. Unfortunately, some authors (*e.g.*, BOUDAGHER-FADEL & PRICE, 2010, Fig. 3.B; NOVANDARU *et al.*, 2025, Fig. 4.b) have published figures that show an incorrect method for the measurement of γ and, unfortunately, their values for γ cannot be trusted.

Character V (Fig. 1.C) is a measure of the asymmetry of the two spires of chambers that emanate from the two PACs and meet in a closing chamber in more advanced ('biserial') species of *Miogypsina* (DROOGER, 1952). It is calculated as 200-times the ratio of the shorter arc of chambers (angle α) divided by the complete arc of chambers (β) and ranges from 0 (when there is just 1 PAC, *i.e.*, α = 0) to 100 when the embryo is symmetrical. For species discrimination it is the mean value of V (V_m) that is important. Character V has been widely used in defining chronospecies within biserial *Miogypsina* populations, yet V values are quite variable among specimens from a single population (DROOGER, 1952, Table 2).

Diameter Pw (D_I) is the width of the protoconch (Pw) measured perpendicular to the medial line of the embryo (DROOGER, 1952). This measurement, by definition, includes half the thickness of the embryonic wall (Fig. 1.D). Values of X and V show positive correlations with Pw (RAJU, 1974; DROOGER, 1993).

3. Geology of Upper Eocene to lower Miocene rocks of Jamaica and their biozonation

During the mid Cenozoic, Jamaica was represented by a series of carbonate platforms surrounded by deep-water troughs (EVA & MCFARLANE, 1985; ROBINSON & MITCHELL, 1999; Fig. 3) - a similar set of depositional environments to those found in the modern-day Bahamas (*e.g.*, FAUQUEMBERGUE *et al.*, 2024; LOPEZ-GAMUNDIM *et al.*, 2025). Defining lithostratigraphic schemes for the limestones on these blocks is problematic, because the limestones show relatively few lithological differences and many can only be distinguished by using biostratigraphy. Three (Somerset, Moneague, and Newport) formations are accepted here for the Upper Eocene to mid Miocene succession, with significant unconformities represented by the bases of the Somerset and Newport formations (HOSE & VERSEY, 1956; VERSEY in ZANS *et al.*, 1963; MITCHELL, 2004, 2013). The Moneague and Newport formations are divided into a series of 'beds' that are based on their LBF assemblages (Fig. 4). In contrast, the deep-water stratigraphic section can be easily divided into formations based on lithological criteria, such as, the presence or absence of flints/cherts and the relative abundance of turbidites (Fig. 4). Similar assemblages of LBF occur allochthonously in the turbidites within the deep-water succession providing an easy way to correlate between the deep-water and shallow-water successions. Full lithological and faunal descriptions will be published elsewhere and they are included here for reference purposes and should not yet be considered 'formal' or finalized.

Samples were taken from three areas on the Clarendon Block, with the zonation of the Oligocene to early Miocene based on LBF utilizing the American Benthic Zonation (ABZ) nomenclature of MITCHELL *et al.* (2022, 2024). The zonation for the late Oligocene is refined in Table 1 based on the evolution of miogypsinids demonstrated here. Sample locations are shown in Figures 3 and 5.

Table 1. Samples with miogypsinids (arranged by chronospecies) used in this study. All slabs and thins sections are in the Simon F. MITCHELL Collection currently stored in collections of the University of the West Indies Geology Museum (UWIGM).

Sample	GPS location	Details
WL5008	18°12.072'N 76°34.283'W	*Mio. tani*, Upper Chester Fm, near mouth of Swift River, Hope Bay, Portland.
WL1727	18°21.994'N 77°3.042'W	*Mio. tani*, Upper Chester Fm, North Coast Belt, St Mary.
WL5548	18°7.859'N 77°41.621'W	*Mio. tani*, Basal Newport Fm, SE of Maggotty, northern St Elizabeth.
WL3669	18°17.799'N 77°31.321'W	*Mio. tani*, Basal Newport Fm, Ulster Spring area, Trelawny.
WL119	18°15.974'N 77°7.225'W	*Mio. tani*, Basal Newport Fm, road cut on Highway 2000, St Ann.
WL3810	18°18.839'N 77°29.963'W	*Mio. 'basraensis'*, Lower Miogypsina beds, Moneague Fm, Ulster Spring area, Trelawny.
WL497	18°17.330'N 77°13.028'W	*Mio. 'basraensis'*. Faulted block, Lower Miogypsina beds, Prickly Pole, St Ann.
WL3676	18°18.620'N 77°30.824'W	*Mio. 'basraensis'*, Lower Miogypsina beds, Moneague Fm, Ulster Spring area, Trelawny.
WL3809	18°18.819'N 77°30.020'W	*Mio. thalmanni*, Lower Miogypsina beds, Moneague Fm, Ulster Spring area, Trelawny.
R1118	18°24.546'N 77°37.900'W	*Ms. complanatus*, lower Chester Fm, north of Sherwood Content, Trelawny.
WL531	18°18.087'N 77°12.796'W	*Ms. complanatus*, Miogypsinoides beds, Moenague Formation, Prickly Pole, St Ann.
WL3807	18°18.861'N 77°30.466'W	*Ms. complanatus*, Miogypsinoides beds, Moneague Fm, Ulster Spring area, Trelawny.
WL4791	18°21.238'N 77°24.695'W	*Ms. complanatus*, platform lmsts, Moneague Fm, SW of Browns Town, St Ann.
WL5772	18°27.297'N 77°27.385'W	*Ms. complanatus*, turbidite in chalks, Chester Fm, Rio Bueno, Trelawny.

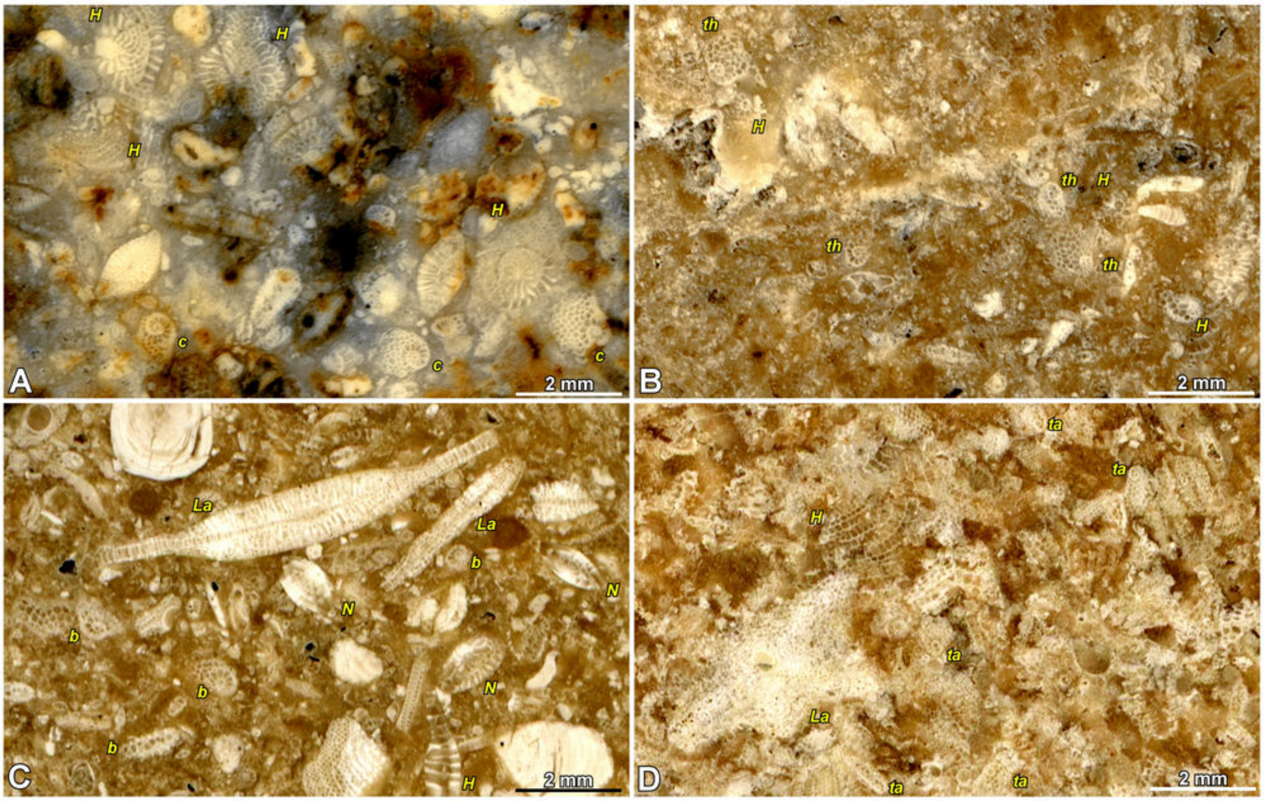

Figure 6: Representative carbonate facies (scans of polished slabs) from Jamaica containing miogypsinid populations. A (WL5772), turbidite in lower part of the Chester Formation, Rio Bueno River valley, Trelawny, with *Mio. complantus* (c) and *Heterostegina antillea* (*H*). B (WL3809), platform limestone from the Ulster Spring area with *Mio. thalmanni* (*th*) and *H. antillea*. C (WL3810), platform limestone from the Ulster Spring area with *Mio. 'basraensis'* (*b*), *H. antillea*, *Lepidocyclina asterodisca* (*La*), *H. antillea* (*H*), and *Nummulites dia* (*N*). D (WL5548), platform limestone from the basal Newport Formation SW of northern Maggotty, St Elizabeth, with *Mio. tani* (*ta*), *Lep. asterodisca* (*La*), and *H. antillea* (*H*).

Table 2. Revised Oligocene and lower Miocene American Benthic Zones

Zone	Details
ABZ22	Spiroclypeus bullbrooki TRZ. In the lower part of the zone, *S. bullbrooki* occurs with forms of *Mio. tani* transitional to *Mio.* '*globulina*' (sample WL5008). This level has yielded M1 planktic foraminifers, but it is before the appearance of NN1 nannofossils (MITCHELL *et al.*, 2024) indicating a position in the latest Oligocene. The Oligocene/Miocene boundary is therefore placed at the transition from *Mio. tani* to *Mio.* '*globulina*' in the Americas.
ABZ21D	Miogypsina tani PRZ. Upper Chattian.
ABZ21C	Miogypsina gunteri TRZ. Mid Chattian.
ABZ21B	Miogypsina 'basraensis' TRZ. Mid Chattian.
ABZ21A	Miogypsina thalmanni TRZ. Lower Chattian.
ABZ20	Miogypsinoides complanata TRZ. In Antigua, *Ms. complanata* occurs in rocks that have yielded a P22 planktic foraminifer and a NN24 to lower NN25 nannoflora assemblage indicating a level at the transition from the Rupelian to the Chattian (ROBINSON *et al.*, 2017; MITCHELL *et al.*, 2024).
ABZ19	Heterostegina antillea PRZ. From the FO of *H. antillea* to the FO of *Ms. complanata*. Assemblage includes *H. antillea*, *Lep. yurnagunensis*, *Lep. parvula*, *Num. dia*, and *Neorotalia mecatepecensis*; *Eu undosa*, and *Eu. favosa* in the lower part; *Lep. asterodisca* in the upper part. Upper Rupelian.
ABZ18	Eulepidina undosa PRZ. From the FO of *Eu. undosa* until the FO of *Heterostegina antillea*. Assemblage is characterised by *Eu. undosa*, *Eu. favosa*, *Lep. yurnagunensis*, *Lep. parvula*, *Num. dia*, and *Neo. mecatepecensis*. Mid Rupelian.
ABZ17	Eulepidina chaperi PRZ. From the LO of *H. ocalana* to the FO of *Eu. undosa*. A low diversity assemblage of LBF with *Eu. chaperi*, *Lep. yurnagunensis*, *Num. dia*, and *Neo. mecatepecensis.* Lower Rupelian.
ABZ16	Heterostegina ocalana TRZ. Last Eocene LBF assemblages. Upper Priabonian.

3.1. Deep-water sections

Miogypsinid assemblages were collected from four localities in the deep-water White Limestone (Fig. 3). Two samples with *Ms. complanatus* (WL5772, R1118, Figs. 6-9) were collected from the lower part of the Chester Formation in the parish of Trelawny (Table 1). These come from graded units with abundant LBF (Fig. 4) that are interpreted as turbidites. Two samples (WL1727, WL5008), containing *Mio. tani*, were also collected from the upper part of the Chester Formation, one each from the parishes of St Mary and Portland. Samples from the mid-Chester Formation generally lack turbidites, so there are no LBF assemblages. The sample from Portland was collected from the road section extending along the east bank southwards of the mouth of the Swift River at Hope Bay. This section (Fig. 9) is across the Chattian/Aquitanian boundary (ROBINSON, 2004; MITCHELL *et al.*, 2024). It has yielded Lower Miocene (NN1 and NN2) nannofossil assemblages and an Oligocene-Lower Miocene (M1) planktonic

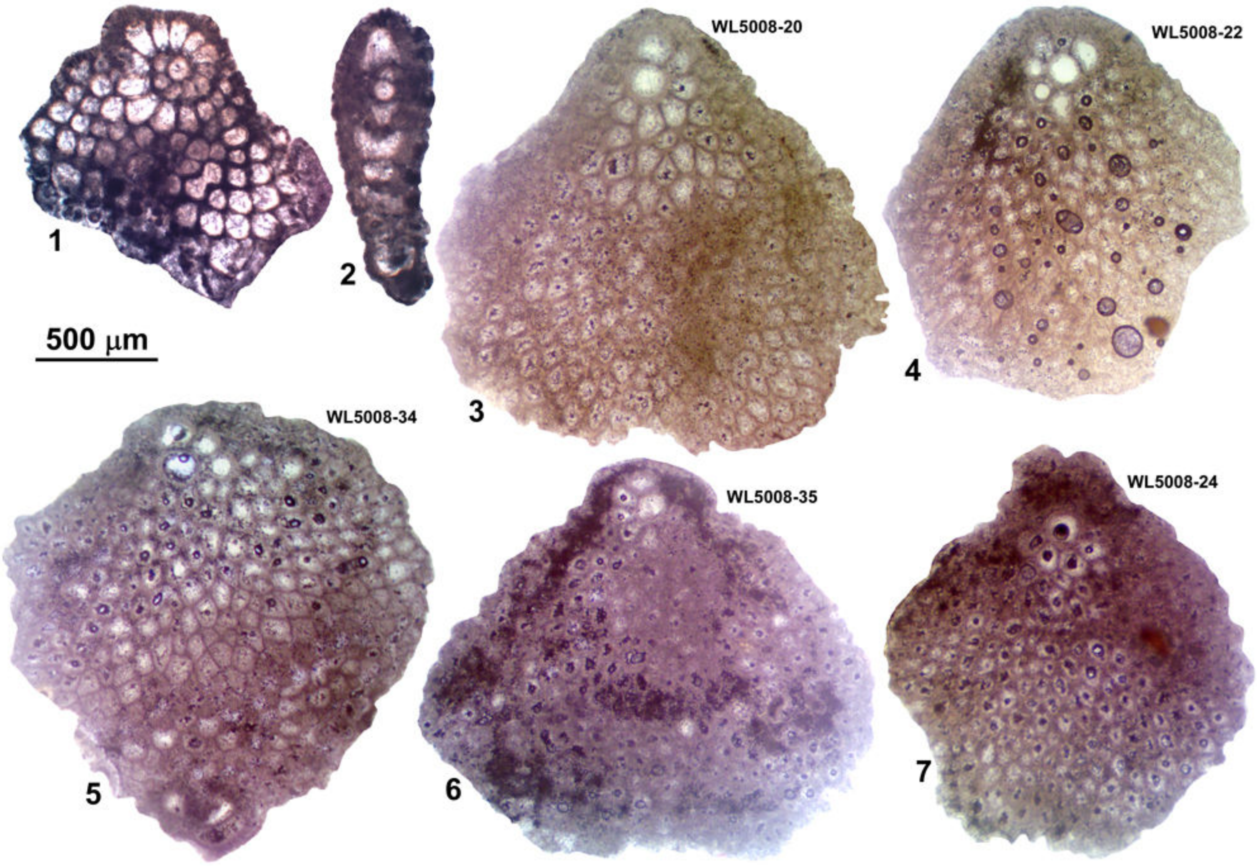

Figure 7: Thin sections of selected miogypsinids from Jamaica. 1 (equatorial), 2 (axial) sections of *Miogypsinoides complanatus*, Chester Formation, Sherwood Content). 3-7, equatorial sections of *Miogypsina tani*, Chester Formation, Hope Bay. Scale bar = 500 µm.

foraminifer assemblage (BLOW in ROBINSON, 1969; ROBINSON, 2004; MITCHELL *et al.*, 2024). The foraminifer sample contains *Mio. tani* and *Spiroclypeus bullbrooki* that indicates ABZ22 (MITCHELL *et al.*, 2024; Table 2).

3.2. Manchester Plateau and northern St Elizabeth

These areas expose extensive swaths of Oligocene and lower Miocene rocks (HOSE & VERSEY, 1956; VERSEY in ZANS *et al.*, 1963; ROBINSON, 2004; MITCHELL, 2004, 2013). On the Manchester plateau, the Moneague Formation is represented by the Walderston beds with at least one intercalation of Browns Town beds. The foraminiferal assemblages of the Walderston beds represent an inner platform facies dominated by miliolids, archaiasids, and *Praerhapidionina delicata* with sporadic examples of *Neorotalia* (ROBINSON & WRIGHT, 1993; ROBINSON, 2004) with the latter suggesting the Rupelian. The interval with the Browns Town beds contains a LBF assemblage with *Eu. undosa* and *Num. dia* without *H. antillea* (without *Heterostegina*), indicating ABZ18 (mid Rupelian; Table 2). The Moneague Formation is succeeded unconformably by the Newport Formation, with VERSEY (in ZANS *et al.*, 1963) reported a sparse fauna in the lower part of his Newport Limestones containg *Heterostegina*, peneroplids, and rare *Miogypsina*. STEMANN (2004) reported a rich coral fauna (32 genera and 64 species) from a section near Albion (Manchester Plateau) at the base of the Newport Limestones. This locality contains *Heterostegina antillea* and *Archaias* cf. *kirkukensis* (ROBINSON, 2004, Fig. 10.B) and has given a $^{87}Sr/^{86}Sr$ ration on a *Kuphus* tube of 0.70823 suggesting, if unaltered, an age of 23.4 to 23.77 Ma [recalibrated from ROBINSON *et al.*, 2018, based on Geological Timescale 2020 (RAFFI *et al.*, 2020)] and attributed to the highest part of the Oligocene (ROBINSON, 2004; ROBINSON *et al.*, 2018). According to ROBINSON *et al.* (2018), nearby localities have yielded *Heterostegina antillea*, *Miogypsina* sp., and small *Lepidocyclina* sp. Because of its rarity, no suitable samples with populations of *Miogypsina* have so far been collected from the Manchester Plateau for statistical analyses.

Maggotty in northern St Elizabeth (Fig. 3) straddles an east-west fault that throws Eocene rocks (Yellow Limestone and White limestone) to the north against Oligocene and Miocene rocks to the south. The succession around Maggotty has yielded good foraminiferal assemblages in the Moneague and Newport formations. As on the Manchester Plateau, the Moneague Formation consists of Walderston beds and Browns Town beds, but here the Browns Town beds are thicker and occur in close proximity, and sometimes immediately below, the Newport Formation. The Browns Town beds contain an abundant fauna of *Eu. undosa*, *Num. dia*, and *Neo. mecatepecensis*,

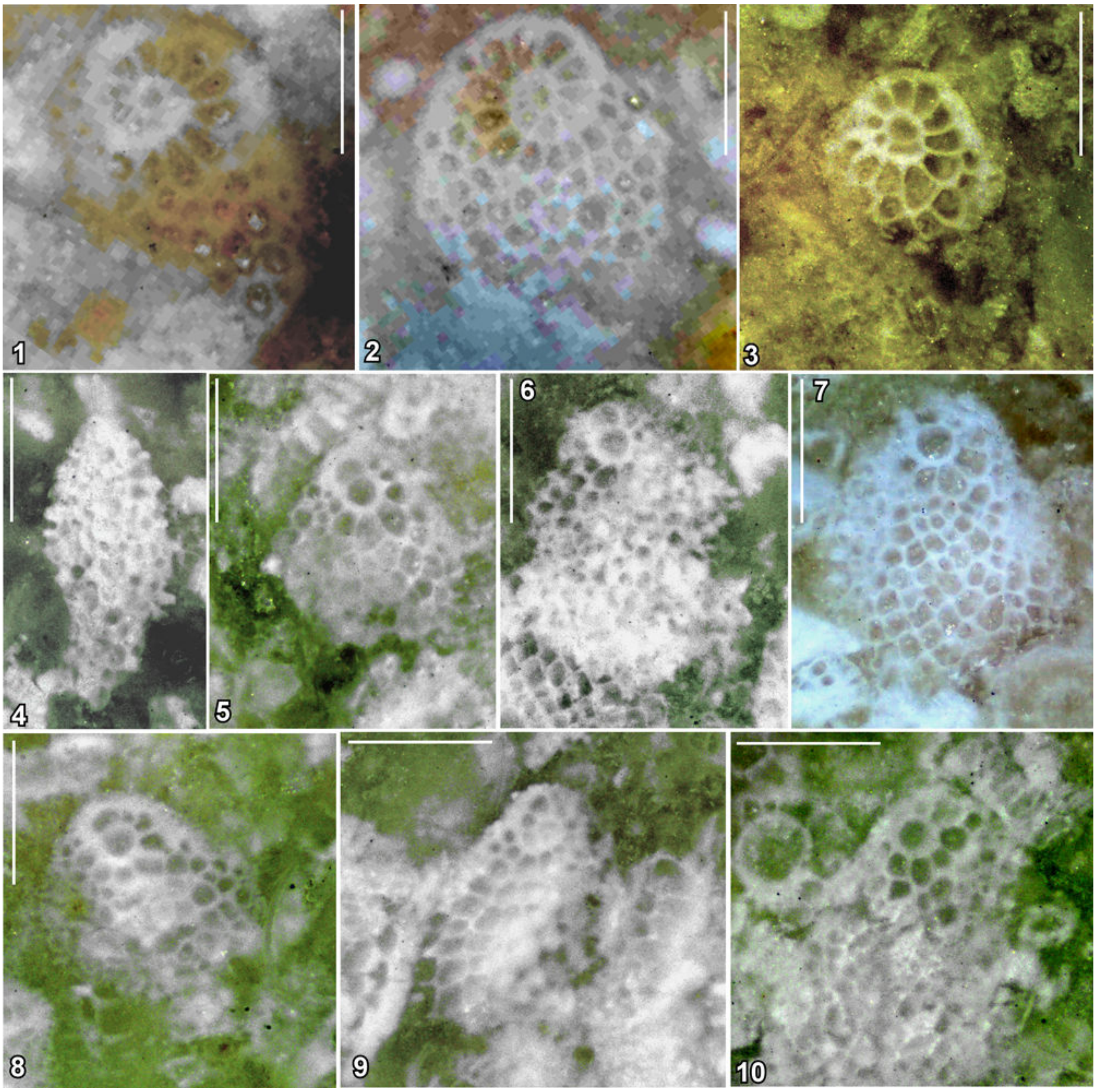

Figure 8: Photographs of representative specimens of miogypsinids on polished slabs from Jamaica. 1-2, equatorial sections of *Miogypsinoides companatus*, sample WL5772, Chester Formation, Rio Bueno. 3, equatorial section of *Miogypsina basraensis*, sample WL3810, Moneague Formation, Ulster Spring. 4-10, axial (4), and equatorial (5-10) sections of *Miogypsina tani* from sample WL5546, Newport Formation, St Elizabeth. Scale bar = 500 µm.

without *Heterostegina antillea*, and can be assigned to ABZ18 (Table 2). The basal part of the overlying Newport Formation contains a very abundant LBF assemblage with *H. antillea*, *Mio. tani*, *Lepidocyclina asterodisca*, and *Heterostegina antillea* (Fig. 6.D), and can be assigned to ABZ21D (Table 2). This is in good agreement with the Sr-isotopic age from Albion (Manchester) from the base of the Newport Formation and the sample with advanced *Mio. tani* from Hope Bay, Portland. The foraminiferal assemblages from the Maggotty area demonstrate that on this part of the Clarendon Block rocks containing foraminifers belonging to ABZ19 through ABZ20C have been cut out by the unconformity at the base of the Newport Formation (Fig. 4).

3.3. Northern St Ann

In St Ann, on the northern part of the Clarendon Block, it was generally believed that the Miocene succession (Newport Formation) had been removed by erosion caused during the uplift of Jamaica (Hose & Versey, 1956; Versey in Zans *et al.*, 1963; McFarlane, 1977). Robinson *et al.* (2018) speculated that there might be an outlier of Newport Formation in the Tobolski area based on ^{87}Sr/^{86}Sr dates provided by Land (1991), but mapping in the Tobolski area has not identified anything younger that ABZ19 (Heterostegina beds) or ABZ20 (*Miogypsinoides* beds) at the

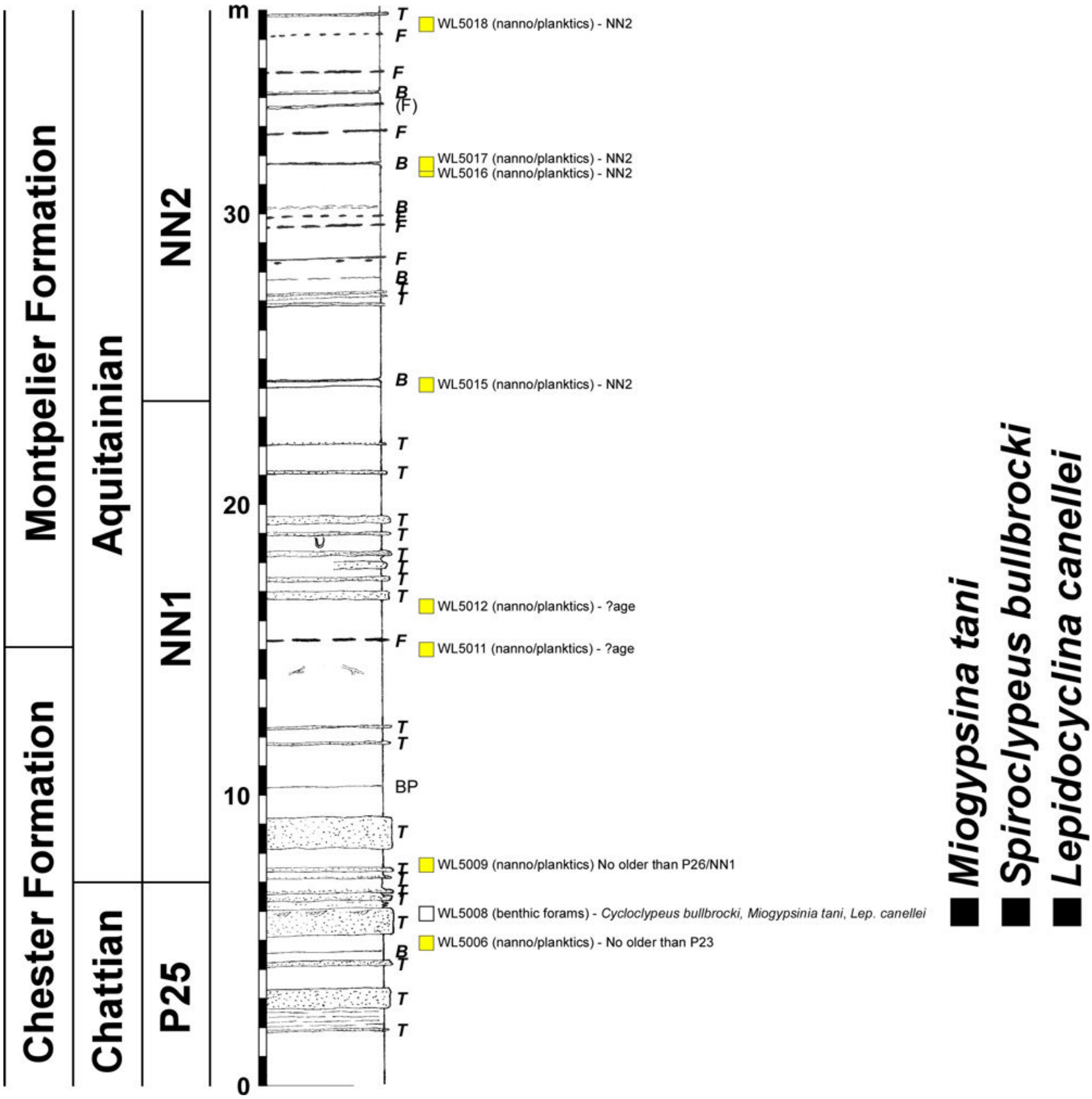

Figure 9: Section across the Chattian/Aquitanian boundary exposed in the road cutting along the east bank of the Swift River, south of its mouth, Hope Bay, Portland, with nannofossil occurrences and foraminifer samples (yellow boxes). The sample with *Mio. tani* comes from the upper part of the Chester Formation in the highest part of the Chattian. T, turbidite; B, bentonite; BP, bedding plane; F, flint. Partial details have been given by ROBINSON (2004) and MITCHELL *et al.* (2024).

present time. Levels high in the Oligocene (ABZ19 through ABZ21B) are, however preserved locally, and levels within the Newport Formation are exposed above the basal-Newport unconformity (with *Mio. tani*) and in a down-faulted outlier in the Griefield area to the west of Moneague (containing *Miogypsina irregularis* and *Miogypsinita mexicana*). The Oligocene miogypsinid assemblages (with *Ms. complanata*, *Mio. 'basraensis'*, *and Mio. tani*: Table 2) are considered in this paper, but the Miocene assemblage (with *Mio. irregularis* and *Miog. mexicana*) will be discussed elsewhere.

3.4. Area to the east and north of Ulster Spring, parish of Trelawny

In this area (Fig. 3), the top of the Moneague Formation and the basal part of the Newport Formation are preserved in road cuts and yield good assemblages of LBF (Table 1). An excellent road section shows a gently dipping succession of limestones in the upper part of the Moneague Formation which yields assemblages showing: ABZ19 (Heterostegina beds, with *Neo. mecatepecensis*); ABZ20 (Miogypsinoides beds, with *Ms. complanata*); ABZ21A (Miogypsina beds, with *Mio. thal-*

manni - Fig. 6.B); and ABZ21B (Miogypsina beds, with *Mio. 'basraensis'* - Fig. 6.C). Nearby exposures yield *Mio. 'basraensis'* (WL3676 - from the lower Miogypsina beds of the Moneagure Formation) and *Mio. tani* (WL3669 - from the upper Miogypsina beds of the Newport Formation). Across the exposures in St Ann and Trelawny, ABZ17 through ABZ21B are present in the Moneague Formation, overlain unconformably by the Newport Formation (ABZ21D). Here, the unconformity below the Newport Formation only cuts out ABZ20C (the *Mio. gunteri* TRZ).

4. Miogypsinid palaeontology

The study of LBF in the early part of the 20th century in the Americas (as elsewhere) resulted in a proliferation of named miogypsinid species using a typological approach based on small numbers of specimens (Cushman, 1918, 1919; Hodson, 1926; Koch, 1926; Vaughan, 1928a; Gravell, 1933; Nuttall, 1933; Tan, 1936; Cole, 1938; Hanzawa, 1940; Drooger, 1951). While some individual specimens could be related to published 'species', others showed transitional characteristics and were more difficult to place within named 'species'. Using a typological approach, Tan (1936, 1937) introduced the concept of nepionic acceleration in the miogypsinids. His work set out a theoretical evolutionary pathway for the group that showed a progressive reduction in the length of the neorotalid spire over time followed by the development of two PACs.

Drooger (1952) introduced a biometrical approach based on the study of miogypsinid populations from different parts of the Americas. Unfortunately, Drooger (1952) could not independently date his samples and arranged his populations into the hypothetical order based on Tan's (1936, 1937) concept of nepionic acceleration. Subsequently, population studies of miogypsinids were extended into the Neotethys and India (*e.g.*, Drooger, 1954a, 1954b, 1963, 1993; Drooger & Freudenthal, 1964; Drooger & Raju, 1973, 1978; Drooger & Laagland, 1986; amongst others) and have become the standard for the late Oligocene to early Miocene shallow-water benthic zonation using larger foraminifers (Cahuzac & Poignant, 1997). Akers and Drooger (1957) even suggested that the appearance of *Miogypsina* could be used as a marker for the base of the Miocene for correlation between Europe and the Americas.

In the Americas, palaeontologists rejected the statistical study of populations stating that this was 'very time-consuming and unsatisfactory' (Barker, 1965) or that 'the division is artificial rather than natural' (Cole, 1957, p. 318). Yet Cole would subsequently go on to reduce the number of miogypsinid species in the Americas to five (Cole, 1964) and eventually three (Cole, 1967), recognizing only uniserial forms lacking lateral chambers (*Miogypsinoides complanatus*), uniserial forms with lateral chambers (*Miogypsina gunteri*), and biserial forms with lateral chambers (*H. antillea*). Yet this lumping approach, significantly limited the biostratigraphic value of successive populations (Drooger, 1952, 1963; Akers & Drooger, 1957). Subsequent studies in the Americas have either used excessive lumping, following Cole's 'species' (*e.g.*, Frost & Langenheim, 1974; Robinson, 2004), or typological approaches (*e.g.*, Baumgartner-Mora *et al.*, 2008; BouDagher-Fadel & Price, 2010).

There has also been a progressive splitting of the miogypsinids into genera in different geographical regions based on minor morphological features that have little value when populations are studied. It is worth discussing the development of the classification of the miogypsinids, prior to setting out the simplified formal scheme that is used here.

Barker and Grimsdale (1937) reported the presence of a canal system in the genus *Miogypsinoides* and postulated that *Miogypsinoides* had evolved from *Rotalia mexicana* var. *mecatepecensis* Nuttall that had a similarly developed canal system. Subsequently, *Rotalia mexicana* Nuttall was selected by Bermúdez (1952) as the type species for his genus *Neorotalia*. Some authors (*e.g.*, Cahuzac & Poignant, 1991, 1997, amongst others) have considered that *Neorotalia* was a junior synonym of *Pararotalia* Le Calvez and placed *Rotalia mexicana* and related species in the genus *Pararotalia*. However, Hottinger *et al.* (1991) established that, unlike *Pararotalia*, *R. mexicana*, possessed an enveloping canal-system (as recorded by Barker & Grimsdale, 1937) and must be attributed generic status. Other authors (*e.g.*, Salmerón, 1972; Cahuzac & Poignant, 1991, 1997) have recognized that at some levels in Mexico and France specimens of *Neorotalia* possess one or two 'supplementary equatorial chambers' possibly pre-empting the development of a fan of equatorial chambers that is characteristic of the genus *Miogypsinoides*. The name *Paleomiogypsina boninensis* Matsumaru was subsequently introduced by Matsumaru (1996) for similar forms found in Japan, where they were associated with: *Neorotalia* (cited as *Pararotalia*) *mecatepecensis* in his assemblage IV and *N. mecatepecensis* and *Miogypsinella boninensis* Matsumaru in his Assemblage V. The generic name *Paleomiogypsina* is not retained here and is synonymised with *Neorotalia* since the holotype of *P. boniensis* came from Assemblage IV without *Miogypsinella* (Matsumaru, 1996).

The genera *Miogypsinoides* Hanzawa, 1940, and *Miogypsinella* Hanzawa, 1940, were established with *Miogypsina dehaartii* Vlerk, 1924, and *Miogypsinella borodinensis* Hanzawa, 1940, as type species, respectively. Both lack lateral chambers and only differ in the fact that their early coiled stage shows either planispiral coiling (*Miogypsinoides*), or low trochospiral coiling (*Miogyp-*

sinella). Low trochospiral coiling is seen in early forms of *Miogypsinoides* as well as in the earliest forms of *Miogypsina* (*e.g.*, specimens of *Mio. thalmanni* - Drooger, 1952) and there is a progressive change from specimens within successive populations from low trochospiral coiling to planispiral coiling. This is a case of gradational change of characters within populations and it is therefore not logical to split specimens into multiple genera based on such minor gradual changes. As such, the genus *Miogypsinella* is regarded as a junior synonym of *Miogypsinoides* (following Loeblich & Tappan, 1988, p. 680).

The phylogenetic development of lateral chamberlets was discussed by Bock (1976). He suggested two methods of formation: 1) as slits originating late in ontogeny between successive laminae added to the sides of the test; and 2) small cavities formed through an association with pillars. The former seems most likely and since it happens in later ontogeny, it would be absent in younger specimens. Subsequently, the genus *Postmiogypsinella* Sirel & Gedik, 2011 (type species *Postmiogypsinella intermedia* Sirel & Gedik, 2011), was introduced for specimens with weakly developed lateral chambers. As with *Miogypsinella*, *Postmiogypsinella* is considered a transitional form and is therefore regarded as a junior synonym of *Miogypsina* here.

BouDagher-Fadel and Price (2010, 2013) suggested differences in the wall structure between American (and South African) and Neotethys (Mediterranean)/Indo-Pacific miogypsinids. They stated that "the Mediterranean forms lack one of the typical features of American miogypsinids, namely, strong fissures around the periphery of the test, indicating that they are a distinct, yet parallel, lineage". Yet Bock (1976, p. 6, Fig. 3, Pls. 5 & 8) clearly illustrated that a "marginal fringe" is present in *Miogypsinoides bantamensis* from France. It is therefore doubtful if this feature can be used to separate miogypsinids from different provinces.

Several different branches extend away from the main *Miogypsina* lineage, all of which show a relative movement of the neorotalid coil/embryo from a peripheral position towards a more centripetal position within the fan of equatorial chambers. These branches occur at different times within the different provinces and have generally been regarded as subgenera within *Miogypsina*. The earliest side branch (*Heterosteginoides*) occurred in the American Province with the development of intercalary chambers within the outer parts of the planispiral neorotalid stage, mimicking genera like *Helicostegina*. The intercalary chambers begin initially as a single row but increase in numbers to form multiple rows. A second side branch (*Miogypsinita*) developed in the early Miocene of the American Province, with the development of two spirals developing from each PAC and the fan of equatorial chambers extending around the counter spirals, but the separation of these forms from *Miogypsina s.s.* is debatable (Drooger, 1993). *Miolepidocyclina* and *Lepidosemicyclina* developed as side branches to the main *Miogypsina* lineage in the Neotethys and Indo-Pacific, respectively, with their own distinct characteristics. The side branches are only dealt with in the evolutionary conclusions in this paper.

4.1. Outline classification of the miogypsinids and *Neorotalia*

A revised classification of *Neorotalia* and the Miogyspinidae is presented here based on the morphological discussion provided above. At present, it seems likely that *Miogypsinoides* developed at the same time in all provinces (Americas, Neotethys, and Indo-Pacific). However, the case is probably not the same for *Miogypsina*, which clearly developed earlier in the Americas than in the Neotethys and Indo-Pacific. At the present time, the name *Miogypsina* is retained for both lineages, but a separate name (*Miogypsinopsis* Hanzawa, 1940, being available, but considered a junior synonym of *Miogypsina* by Loeblich & Tappan, 1988) might be needed for forms in the American Province. Furthermore, *Miogypsina* species names in all provinces are retained in a purely morphological sense in this paper (*i.e.*, they are 'form chronospecies'). In this paper the 'form chronospecies' names are retained and used in a formal sense (*e.g.*, *Miogypsina gunteri*) when occurring in the province in which they were named, but in open nomenclature (*e.g.*, *Miogypsina 'gunteri'*) in other provinces. In the future, as more information becomes available, it may be that separate species names will be required for distinct lineages within each province (but his will also require a thorough investigation of all the names that are available in the literature).

Family Calcarinidae Orbigny, 1826

Subfamily Pararotaliinae Reiss, 1963

Genus *Neorotalia* Bermúdez, 1952

Type species. *Rotalia mexicana* Nuttall, 1928, from the Eocene of Mexico.

Remarks. If the canal system is taken as a defining characteristic of the Miogypsinidae, then *Neorotalia* should be transferred to that family and then it can be considered as the route of all subsequent forms. I prefer this course of action.

Family Miogypsinidae Vaughan, 1928b

Genus *Miogypsinoides* Hanzawa, 1940

Type species. *Miogypsina dehaartii* Vlerk, 1924, from the Lower Miocene of Larat Island (part of the Tanimbar Islands archipelago) in the province of Maluku, Aru Sea, Indonesia.

Synonyms. *Miogypsinella* Hanzawa, 1940 (type species *Miogypsinella borodinensis* Hanzawa, 1940, from the Chattian of Japan); subjective junior synonym.

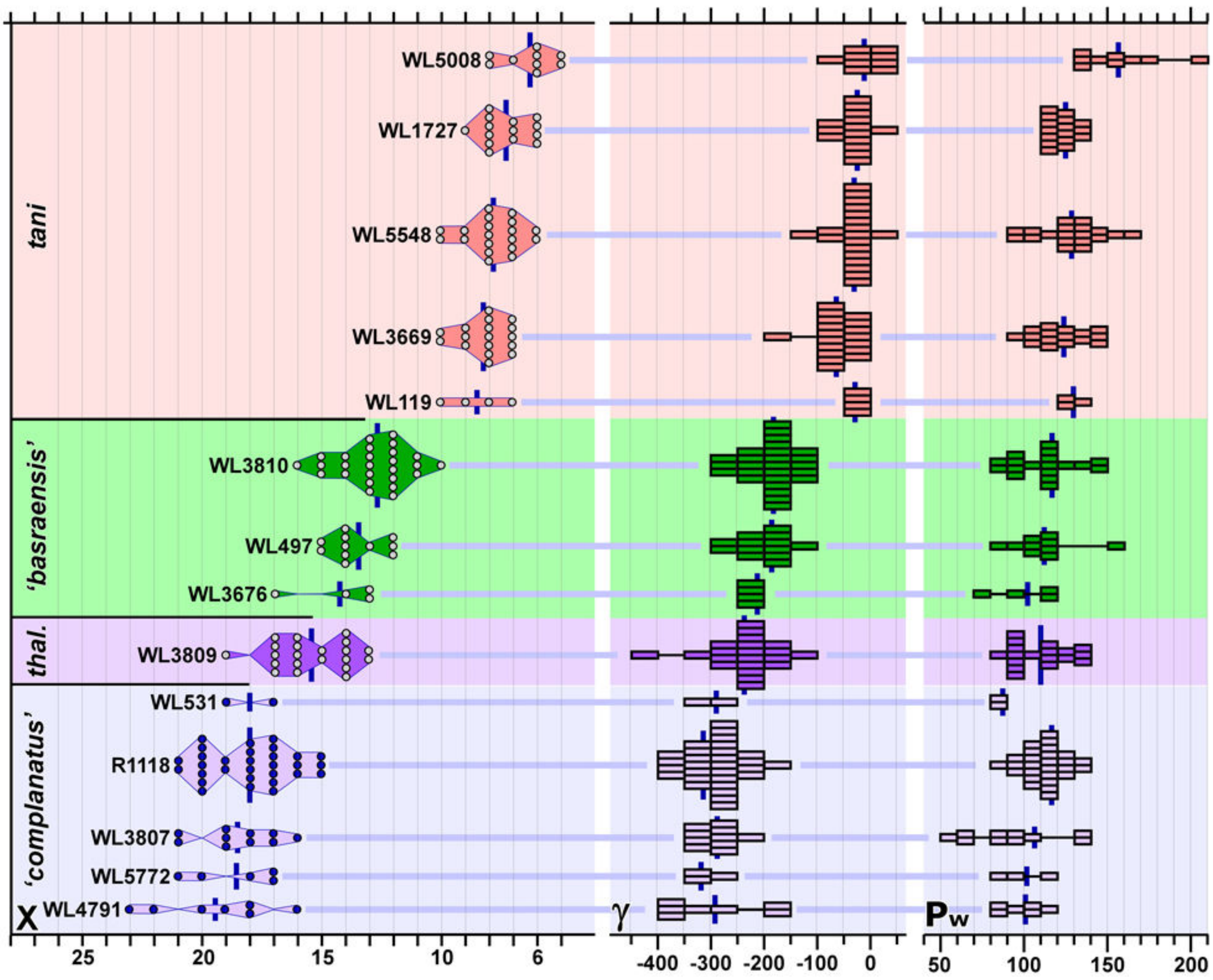

Figure 10: Dot plots (categorical data) for X and bar graphs (for grouped continuous data) for γ and P_w for populations from Jamaica, with means (X_m, $γ_m$, and Pw_m). X and γ show progressive changes through populations, whereas Pw shows little systematic change (although a weak overall trend, with reversals, to higher values is present).

Remarks. The name *Miogypsinoides* is used for miogypsinids that have a low trochospiral or planispiral neorotalid stage, have a fan of equatorial chambers and lack lateral chambers. Two species are present in the Americas:

- *Miogypsinoides 'complanatus'* SCHLUMBERGER, 1900 (Figs. 7.1-2, 8.1-2). The name is used here (in inverted commas) for American specimens of *Miogypsinoides* with X_m between 24, and 17.
- *Miogypsinoides butterlinus* SALMERÓN, 1972. The name is used here for what appears to be a separate branch of *Miogypsinoides* in the Americas with smaller X_m values (DROOGER, 1993). The species has not been reported from Jamaica and is not considered in detail herein.

Genus *Miogypsina* SACCO, 1893

Type species. *Nummulina globulina* MICHELOTTI, 1841, by original designation, from the Miocene of Italy.

Synonyms. *Flabelliporus* DERVIEUX, 1894 (type species *Flabelliporus dilatatus* DERVIEUX, 1894, from the Miocene of Italy). *Miogypsinopsis* HANZAWA, 1940 (type species *Miogypsina (Miogypsina) gunteri* COLE, 1938, from the Oligocene of Florida); subjective junior synonym. *Miogypsinitella* HANZAWA, 1968 (type species *Miogypsina (Miogypsina) indonesiensis* TAN, 1936, from the Miocene of Java). *Tania* MATSUMARU, 1990 (type species *Tania inokosiensis* MATSUMARU, 1990, from the Miocene of Japan). *Postmiogypsinella* SIREL & GEDIK, 2011 (type species *Postmiogypsinella intermedia* SIREL & GEDIK, 2011, from the Chattian of Turkey).

Remarks. The name *Miogypsina* is used for miogypsinids with lateral chamberlets. As further work is undertaken, it may be advisable to retain the Neotethys/Indo-Pacific forms within *Miogypsina* and place the American forms in a separate genus (*Miogypsinopsis* HANZAWA, 1940). The four branch lines that derived from *Miogypsina* are given generic status herein. The species of *Miogypsina* considered here from the Americas are: *Mio. thalmanni* DROOGER, 1952; *Mio. 'basraensis'* BRÖNNIMANN, 1940; *Mio. gunteri* COLE, 1938; *Mio. tani* DROOGER, 1952; and *Mio. 'irregularis'* MICHELOTTI, 1841.

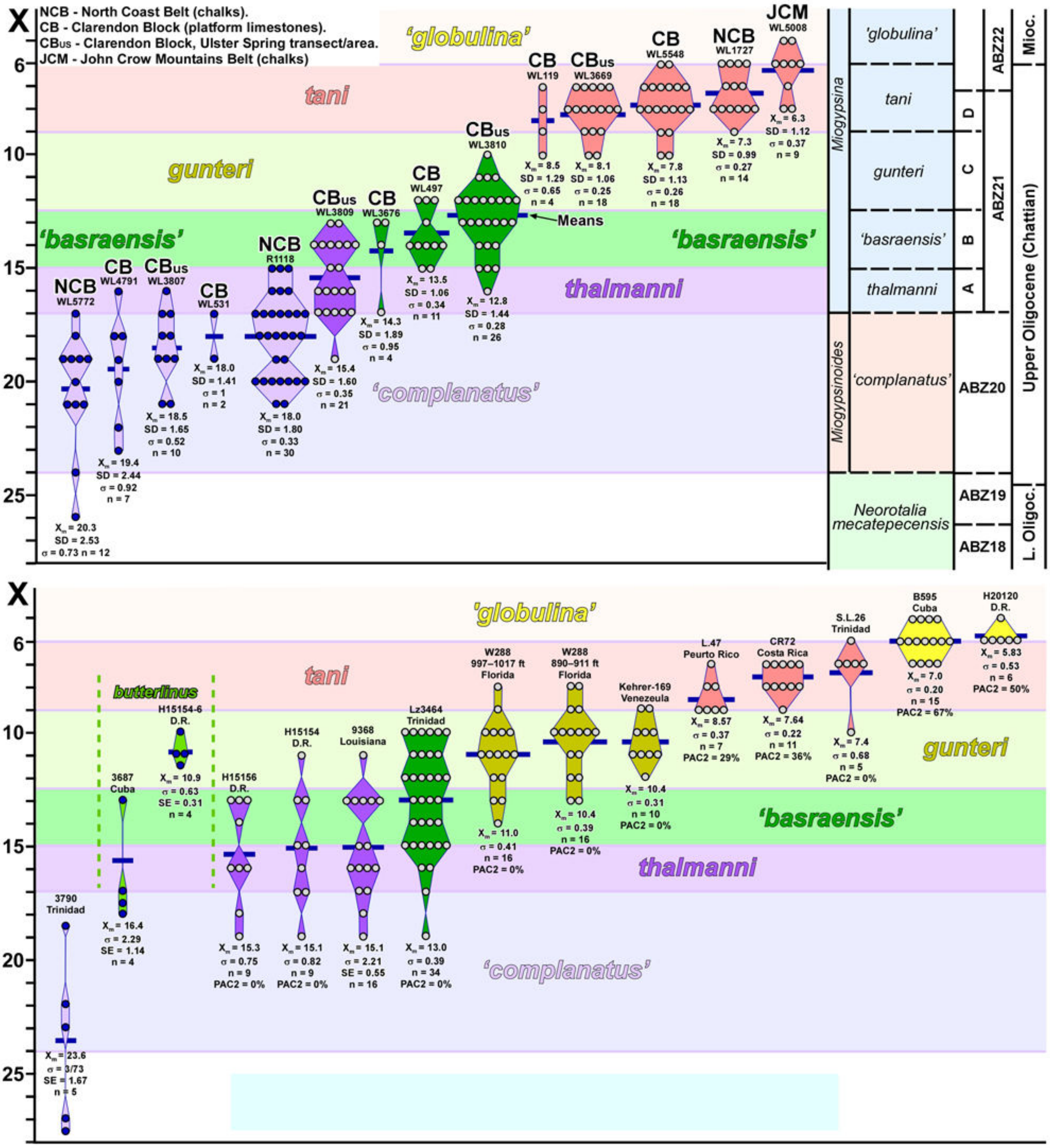

Figure 11: Dot plots (categorical data) for X for populations from Jamaica (upper) and Drooger (Drooger, 1952, 1963; Akers & Drooger, 1957) (lower) arranged by X_m with Jamaican dataset tied to ABZ for the mid to late Oligocene.

Genus *Heterosteginoides* Cushman, 1918

Type species. *Heterosteginoides panamensis* Cushman, 1918, from Oligocene of Panama.

Synonyms. *Americogypsina* BouDagher-Fadel & Price, 2010 (type species *Americogypsina braziliana* BouDagher-Fadel & Price, 2010, from the Oligocene of Brazil).

Remarks. This is the earliest branch that develops from *Miogypsina* in the Americas. Loeblich and Tappan (1988, p. 88, p. 680) considered *Heterosteginoides* Cushman as a junior synonym of *Miolepidocyclina* Silvestri. However, *Heterosteginoides* is a Chattian genus that developed from *Miogypsina thalmani* in the Americas, whereas *Miolepidocyclina* is a Burgundian genus that developed from *Mio. globuilina* in the Neotethys. In my opinion, both genera are valid and developed independently from different miogypsinid ancestors in different palaeogeographic provinces and at different times. The genus is not considered in detail here.

Genus *Miogypsinita* Drooger, 1952

Type species. *Miogypsina mexicana* Nuttall, 1933, from the Miocene of Mexico.

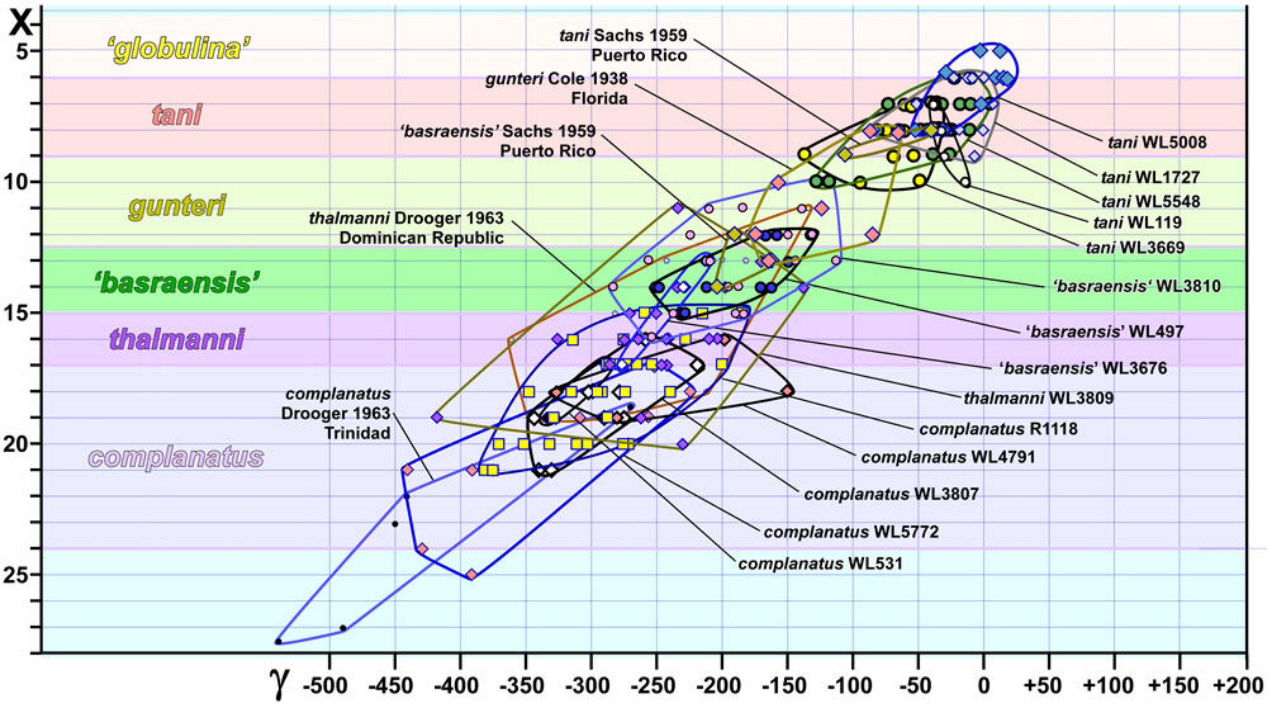

Figure 12: Scatter plot for X against γ for populations of uniserial miogypsinids from the Americas. Note the strong correlation (linear trend). Jamaican samples named on the right, other samples on the left.

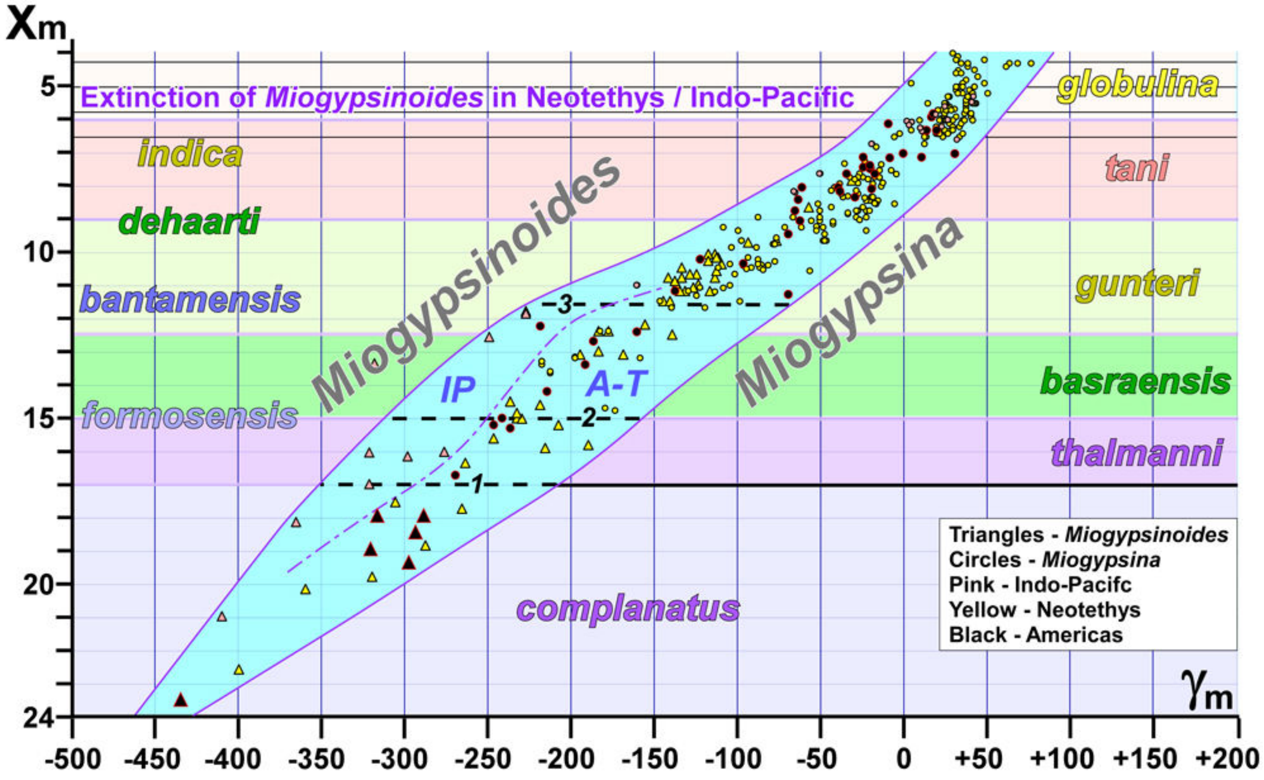

Figure 13: Scatter plot for X_m against γ_m for populations of uniserial miogypsinids from the Americas, Neotethys, and Indo-Pacific. Note the strong correlation (linear trend) showing that all provinces show a similar type of development with regard to X_m versus γ_m (but not necessarily at the same time). Note however that Indo-Pacific values plot to the left (lower γ_m values) compared to Tethys and American X_m values between around 20 and 11. Data from: DROOGER, 1954a, 1954b, 1963; DROOGER *et al.*, 1955; DROOGER & FREUDENTHAL, 1964; FERRERO, 1965, 1987; SOEDIONO, 1969; CERUTTI, 1973; MULDER, 1975; BOCK, 1976, 1977; SCHÜTTENHELM, 1976; SCHIAVINOTTO, 1979, 1985; DELICAT & SCHIAVINOTTO, 1985; WILDENBORG, 1991; FERRERO *et al.*, 1994; ÖZCAN *et al.*, 2010.

Remarks. This is the Miocene branch that develops from *Miogypsina* in the Americas, but may be difficult to distinguish from *Miogypsina* (DROOGER, 1993). The genus is not considered in detail here.

Genus *Lepidosemicyclina* Rutten, 1911

Type species. *Orbitoides* (*Lepidosemicyclina*) *thecideaeformis* Rutten, 1911, from the Miocene of Borneo.

Remarks. This is the Miocene branch that develops from *Miogypsina* in the Indo-Pacific. The genus is not considered in detail here.

Genus *Miolepidocyclina* Silvestri, 1907

Type species. *Orbitoides* (*Lepidocyclina*) *burdigalensis* Gümbel, 1870, from the Miocene of Italy.

Remarks. This is the Miocene branch that develops from *Miogypsina* in the Neotethys. The genus is not considered in detail here.

4.2. Biometry and statistics

A biometric study of the miogypsinids from the American Province is undertaken here. Both univariate and bivariate statistics are used and comparisons are made, where possible, with other populations from the Americas and populations from the Neotethys and Indo-Pacific. Unfortunately, primary data has not been published for many studies and this makes comparisons difficult. In some cases specimens have been illustrated and can be measured, but this may not include the full range of X, γ, and Pw (etc.) values. I urge that in future studies, all measurements of specimens should be published in full (either is appendices, as supplementary files or in repositories).

4.3. Univariate analyses

Univariant statistical analysis is carried out on three characters here: X, γ, and Pw. Character V is not significant for Oligocene miogypsinids, whereas character Dw (from visual observations) is also unlikely to be of value and was not tested. Therefore, results are provided below for analyses on X, γ, and Pw.

4.3.1. Analyses of character X

Drooger (1952, 1993) used mean values of X (X_m) to divide the 'main' *Miogypsinoides-Miogypsina* lineage into chronospecies and set limits for each species. The available populations from Jamaica include sporadic samples from both deep-water and shallow-water sections and a succession of three samples from the Ulster Spring Transect. The samples from the Ulster Spring Transect show a progressive decrease in mean X values (X_m), with populations being assigned to *Ms. complanatus*, *Mio. thalmanni*, and *Mio. 'basraensis'*, suggesting an evolutionary series (as hypothetically suggested by Drooger, 1952). These and the other populations, from Jamaica are therefore arranged in order based on their X_m values and assigned to species using Drooger's (1952, 1993) species limits (Fig. 10). Bar graphs (for continuous data) and means for γ and Pw are also plotted on Figure 10 for comparison with dot plots (categorical data) for X. For γ there is a progressive change towards smaller negative numbers, whereas for Pw any pattern is less obvious. A dot plot for Drooger's (1952, 1963) dataset in shown in Figure 11, for comparison.

A Kruskal-Wallis rank sum test for multiple independent samples for X on the combined Jamaica-Drooger dataset gave a Kruskal-Wallis chi-squared statistic of 308.4 (26 degrees of freedom), with $p = 4.42e^{-50}$, showing that some populations were significantly different. Extracted values of *p* (for the Jamaican, Drooger, and Jamaica-Drooger [Drooger, 1952, 1963; Akers & Drooger, 1957] subsets) from a pairwise Dunn post-hoc test (adjusted by the Benjamini-Hochberg FDR method) for the combined Jamaican-Drooger (Drooger, 1952, 1963; Akers & Drooger, 1957) dataset are shown in Tables 3-5. These results show high *p*-values for populations with similar X_m values justifying the use of X_m as a measure for the populations (even if the populations are not normally distributed) and notable statistical differences between Drooger's (1952) chronospecies. Small samples (*e.g.*, WL531) show relative high *p*-values for both *Ms. complanata* and *Mio. thalmanni* (Tables 3, 5), thus demonstrating the problems of trying to identify samples with low numbers of specimens to chronospecies. The results demonstrate that X_m values are very suitable for defining chronospecies in American Oligocene miogypsinids.

Two notable breaks in the tabulated *p*-values for populations from Jamaica (Table 3) are apparent: the first between *Ms. complanata* and *Mio. thalmanni* (excluding WL531 with only 2 specimens) and the second between *Mio. 'basraensis'* and *Mio. tani*. This indicates, assuming that the change in populations was due to gradational and not punctuated evolution, that representatives of all populations were not sampled. The 'gap' between *Ms. complanata* and *Mio. thalmanni* corresponds to an influx of platform interior species in which miogypsinids are not present; this suggests that this 'gap' is due to a facies change. The 'gap' between *Mio. 'basraensis'* and *Mio. tani* is interpreted to represent an unconformity between the underlying Moneague Formation and the overlying Newport Formation, with the chronospecies *Mio. gunteri* missing. As discussed in the geological succession, this unconformity is clearly demonstrated in the area around Maggotty in northern St. Elizabeth, where limestones containing ABZ18 foraminiferal assemblages are overlain by limestones containing ABZ21D foraminiferal assemblages (*i.e.*, ABZ19 to ABZ21C are cut out), but only cuts out ABZ21C in the northern part of the Clarendon Block (Fig. 11).

4.3.2. Analyses of character γ

A Kruskal-Wallis rank sum test for multiple independent samples for γ on the Jamaica dataset gave a Kruskal-Wallis chi-squared statistic of 146.6 (13 degrees of freedom), with $p = 1.0e^{-24}$, showing that some populations are significantly different. Extracted values of *p* from a pairwise Dunn post-hoc test (adjusted by the Benjamini-

Table 3. Extracted *p*-values (arranged by X_m values) for the Jamaican X subset from a pairwise DUNN post-hoc test (adjusted by the BENJAMINI-HOCHBERG FDR method) for the combined Jamaican-DROOGER (DROOGER, 1952, 1963; AKERS & DROOGER, 1957) dataset. High probabilities are colour-coded. Samples with low numbers of specimens highlighted. Note the moderately sharp break between *Ms. complanata* (sample R1118) and *Mio. thalmanni* (sample WL3809) and the sharper break between *Mio. 'basraensis'* (sample WL3810) and *Mio. tani* (sample WL119) suggesting that a continuous suite of populations is not represented.

DUNN p-values adjusted by the BENJAMINI-HOCHBERG FDR method					***complanata***					***thalm.***	***basraensis***			***tani***				
					WL5772	**WL4791**	**WL3807**	**WL531**	**R1118**	**WL3809**	**WL3676**	**WL497**	**WL3810**	**WL119**	**WL3669**	**WL5548**	**WL1727**	**WL5008**
				Xm	**20.3**	**19.4**	**18.5**	**18.0**	**18.0**	**15.4**	**14.3**	**13.5**	**12.8**	**8.5**	**8.1**	**7.8**	**7.3**	**6.3**
Location	**Sample**	**Xm**	**Xm ID**	**N**	**12**	**7**	**10**	**2**	**30**	**21**	**4**	**11**	**26**	**4**	**18**	**18**	**14**	**9**
Chalk	WL5772	18.6	*complanata*	12		0.87413	0.76357	0.82514	0.54049	0.07532	0.13784	0.01343	0.00043	0.00019	0.00000	0.00000	0.00000	0.00000
Platform	WL4791	19.4	*complanata*	7	0.87413		0.90383	0.90240	0.77551	0.21251	0.22015	0.05569	0.00830	0.00097	0.00000	0.00000	0.00000	0.00000
Platform	WL3807	18.5	*complanata*	10	0.76357	0.90383		0.95760	0.86779	0.21466	0.23898	0.05024	0.00477	0.00074	0.00000	0.00000	0.00000	0.00000
Platform	WL531	18.0	*complanata*	2	0.82514	0.90240	0.95760		0.97933	0.59780	0.48052	0.31279	0.19614	0.02910	0.00777	0.00500	0.00345	0.00174
Chalk	R1118	18.0	*complanata*	30	0.54049	0.77551	0.86779	0.97933		0.15357	0.23898	0.02479	0.00024	0.00032	0.00000	0.00000	0.00000	0.00000
Platform	WL3809	15.4	*thalmanni*	21	0.07532	0.21251	0.21466	0.59780	0.15357		0.73099	0.35292	0.07106	0.00713	0.00000	0.00000	0.00000	0.00000
Platform	WL3676	14.3	*basraensis*	4	0.13784	0.22015	0.23898	0.48052	0.23898	0.73099		0.84626	0.61781	0.09441	0.02063	0.01137	0.00733	0.00383
Platform	WL497	13.5	*basraensis*	11	0.01343	0.05569	0.05024	0.31279	0.02479	0.35292	0.84626		0.68826	0.07040	0.00237	0.00074	0.00053	0.00033
Platform	WL3810	12.8	*basraensis*	26	0.00043	0.00830	0.00477	0.19614	0.00024	0.07106	0.61781	0.68826		0.10009	0.00122	0.00027	0.00024	0.00020
Platform	WL119	8.5	*tani*	4	0.00019	0.00097	0.00074	0.02910	0.00032	0.00713	0.09441	0.07040	0.10009		0.92753	0.80426	0.67270	0.45316
Platform	WL3669	8.1	*tani*	18	0.00000	0.00000	0.00000	0.00777	0.00000	0.00000	0.02063	0.00237	0.00122	0.92753		0.79415	0.58844	0.31074
Platform	WL5548	7.8	*tani*	18	0.00000	0.00000	0.00000	0.00500	0.00000	0.00000	0.01137	0.00074	0.00027	0.80426	0.79415		0.78725	0.45858
Chalk	WL1727	7.3	*tani*	14	0.00000	0.00000	0.00000	0.00345	0.00000	0.00000	0.00733	0.00053	0.00024	0.67270	0.58844	0.78725		0.67270
Chalk	WL5008	6.3	tani	9	0.00000	0.00000	0.00000	0.00174	0.00000	0.00000	0.00383	0.00033	0.00020	0.45316	0.31074	0.45858	0.67270	

Probabilities	<0.01	>0.01	>0.05	>0.50	>0.75	>0.90

Table 4. Extracted *p*-values (arranged by X_m values) for the DROOGER X subset from a pairwise DUNN post-hoc test (adjusted by the BENJAMINI-HOCHBERG FDR method) for the combined Jamaican-DROOGER (DROOGER, 1952, 1963; AKERS & DROOGER, 1957) dataset. High probabilities are colour-coded. Note that larger gaps in X_m values (*e.g.*, between *Ms. complanata* and *Mio. 'basraensis'*, *Mio. 'basraensis'* and *Mio. gunteri* and *Mio. gunteri* and *Mio. tani*) suggesting that a complete suite of populations has not been sampled.

DUNN p-values adjusted by the BENJAMINI-HOCHBERG FDR method				***compl.***	***thalmanni***			***basrae.***	***gunteri***			***tani***			***irregularis***	
				comp-TT	**thal-DR6**	**thal-DR4**	**thal-LA**	**bas-TT**	**gunt-F9**	**gunt-F8**	**gunt-V**	**tani-PR**	**tani-CR**	**tani-TT**	**glob-Cu**	**glob-DR**
			Xm	**23.6**	**15.3**	**15.1**	**15.1**	**13.0**	**11.0**	**10.4**	**10.4**	**8.6**	**7.6**	**7.4**	**7.0**	**5.8**
Sample	**Xm**	**Xm ID**	**N**	**5**	**9**	**9**	**16**	**34**	**16**	**16**	**10**	**7**	**11**	**5**	**15**	**6**
comp-TT	23.6	*complanata*	5		0.15639	0.13642	0.09780	0.00662	0.00071	0.00027	0.00067	0.00000	0.00009	0.00002	0.00000	0.00000
thal-DR6	15.3	*thalmanni*	9	0.15639		0.93900	0.92274	0.23898	0.03812	0.01564	0.03063	0.00025	0.00453	0.00090	0.00000	0.00007
thal-DR4	15.1	*thalmanni*	9	0.13642	0.93900		0.98774	0.28521	0.05015	0.02092	0.03933	0.00035	0.00589	0.00123	0.00000	0.00010
thal-LA	15.1	*thalmanni*	16	0.09780	0.92274	0.98774		0.19478	0.02006	0.00635	0.01871	0.00005	0.00214	0.00039	0.00000	0.00002
bas-TT	13.0	*basraensis*	34	0.00662	0.23898	0.28521	0.19478		0.19478	0.08013	0.15311	0.00069	0.02141	0.00445	0.00000	0.00026
gunt-F9	11.0	*gunteri*	16	0.00071	0.03812	0.05015	0.02006	0.19478		0.76357	0.79943	0.06399	0.24739	0.08917	0.00139	0.01395
gunt-F8	10.4	*gunteri*	16	0.00027	0.01564	0.02092	0.00635	0.08013	0.76357		0.98774	0.13653	0.40199	0.15795	0.00531	0.03036
gunt-V	10.4	*gunteri*	10	0.00067	0.03063	0.03933	0.01871	0.15311	0.79943	0.98774		0.17898	0.44080	0.18916	0.01415	0.04511
tani-PR	8.6	*tani*	7	0.00000	0.00025	0.00035	0.00005	0.00069	0.06399	0.13653	0.17898		0.74707	0.87413	0.36401	0.43731
tani-CR	7.6	*tani*	11	0.00009	0.00453	0.00589	0.00214	0.02141	0.24739	0.40199	0.44080	0.74707		0.65725	0.22508	0.27819
tani-TT	7.4	*tani*	5	0.00002	0.00090	0.00123	0.00039	0.00445	0.08917	0.15795	0.18916	0.87413	0.65725		0.60496	0.61217
irreg-Cu	7.0	*globulina*	15	0.00000	0.00000	0.00000	0.00000	0.00000	0.00139	0.00531	0.01415	0.36401	0.22508	0.60496		0.93224
irreg-DR	5.8	*globulina*	6	0.00000	0.00007	0.00010	0.00002	0.00026	0.01395	0.03036	0.04511	0.43731	0.27819	0.61217	0.93224	
			Probabilities	<0.01	>0.01	>0.05	>0.50	>0.75	>0.90							

Table 5. Extracted *p*-values (arranged by X_m values) comparing the Jamaica and Drooger X subsets from a pairwise Dunn post-hoc test (adjusted by the Benjamini-Hochberg FDR method) for the combined Jamaican-Drooger (Drooger, 1952, 1963; Akers & Drooger, 1957) dataset. High probabilities are colour-coded. Samples with low numbers of specimens for the Jamaican dataset highlighted. Note that sample WL5008 has higher *p*-values when compared against populations of *Mio. irregularis* than with *Mio. tani*, suggesting that it may be younger than other populations of *Mio. tani*.

Dunn p-values adjusted by the Benjamini-Hochberg FDR method					***compl.***	***thalmanni***			***basrae.***	***gunteri***			***tani***			***irregularis***	
					comp-TT	**thal-DR6**	**thal-DR4**	**thal-LA**	**bas-TT**	**gunt-F9**	**gunt-F8**	**gunt-V**	**tani-PR**	**tani-CR**	**tani-TT**	**glob-Cu**	**glob-DR**
				Xm	**23.6**	**15.3**	**15.1**	**15.1**	**13.0**	**11.0**	**10.4**	**10.4**	**8.6**	**7.6**	**7.4**	**7.0**	**5.8**
Location	**Sample**	**Xm**	**Xm ID**	**N**	**5**	**9**	**9**	**16**	**34**	**16**	**16**	**10**	**7**	**11**	**5**	**15**	**6**
Chalk	WL5772	20.3	*complanata*	12	0.84611	0.12898	0.10314	0.05441	0.00042	0.00003	0.00000	0.00005	0.00000	0.00000	0.00000	0.00000	0.00000
Platform	WL4791	19.4	*complanata*	7	0.76357	0.24546	0.21665	0.16368	0.00935	0.00083	0.00027	0.00085	0.00000	0.00010	0.00002	0.00000	0.00000
Platform	WL3807	18.5	*complanata*	10	0.65725	0.26292	0.22888	0.16368	0.00512	0.00035	0.00009	0.00045	0.00000	0.00005	0.00001	0.00000	0.00000
Platform	WL531	18.0	*complanata*	2	0.74707	0.58844	0.55133	0.52566	0.21251	0.07707	0.05015	0.05983	0.00585	0.01762	0.00653	0.00074	0.00153
Chalk	R1118	18.0	*complanata*	30	0.50574	0.24546	0.20616	0.11006	0.00017	0.00001	0.00000	0.00005	0.00000	0.00000	0.00000	0.00000	0.00000
Platform	WL3809	15.4	*thalmanni*	21	0.12898	0.93784	0.86779	0.83322	0.07929	0.00564	0.00133	0.00644	0.00000	0.00066	0.00011	0.00000	0.00000
Platform	WL3676	14.3	*basraensis*	4	0.14528	0.79248	0.83450	0.83450	0.67270	0.24546	0.16394	0.19478	0.01491	0.05524	0.01896	0.00105	0.00370
Platform	WL497	13.5	*basraensis*	11	0.03316	0.51432	0.57387	0.52530	0.76357	0.18894	0.09544	0.14428	0.00224	0.02517	0.00612	0.00002	0.00055
Platform	WL3810	12.8	*basraensis*	26	0.00600	0.21251	0.24946	0.17042	0.89318	0.26546	0.13000	0.20554	0.00167	0.03316	0.00713	0.00000	0.00050
Platform	WL119	8.5	*tani*	4	0.00066	0.01871	0.02264	0.01444	0.07907	0.36401	0.51894	0.53451	0.78242	0.99569	0.70425	0.32854	0.35794
Platform	WL3669	8.1	*tani*	18	0.00000	0.00023	0.00033	0.00002	0.00038	0.08815	0.19177	0.24546	0.77092	0.91472	0.67454	0.15311	0.24546
Platform	WL5548	7.8	*tani*	18	0.00000	0.00007	0.00010	0.00000	0.00007	0.03885	0.09979	0.15311	0.94104	0.76357	0.82514	0.24546	0.35230
Chalk	WL1727	7.3	*tani*	14	0.00000	0.00005	0.00007	0.00000	0.00007	0.02457	0.06366	0.10051	0.86574	0.59780	0.98724	0.46785	0.52566
Chalk	WL5008	6.3	*tani*	9	0.00000	0.00003	0.00005	0.00000	0.00007	0.01223	0.03036	0.05015	0.55706	0.35759	0.76059	0.86779	0.83450

Probabilities	<0.01	>0.01	>0.05	>0.50	>0.75	>0.90

Table 6. Extracted *p*-values (arranged by X_m values) for the Jamaica γ dataset from a pairwise DUNN post-hoc test (adjusted by the BENJAMINI-HOCHBERG FDR method). High probabilities are colour-coded. Samples with low numbers of specimens for the Jamaican dataset highlighted.

DUNN p-values adjusted by the BENJAMINI-HOCHBERG FDR method					***complanata***					***thal.***	***basraensis***			***tani***				
					WL4791	**WL5772**	**WL3807**	**WL531**	**R1118**	**WL3809**	**WL3676**	**WL497**	**WL3810**	**WL119**	**WL3669**	**WL5548**	**WL1727**	**WL5008**
				Xm	**18.6**	**19.4**	**18.5**	**18.0**	**18.0**	**15.4**	**14.3**	**13.5**	**12.8**	**8.5**	**8.1**	**7.8**	**7.3**	**6.3**
Location	**Sample**	**Xm**	**Xm ID**	**N**	**7**	**5**	**10**	**2**	**30**	**21**	**4**	**11**	**26**	**4**	**18**	**18**	**14**	**9**
Platform	WL4791	18.6	*complanata*	7		0.81609	0.88594	0.84212	0.97876	0.31394	0.31929	0.08808	0.03830	0.00280	0.00031	0.00001	0.00001	0.00001
Chalk	WL5772	19.4	*complanata*	5	0.81609		0.85719	0.99377	0.80834	0.26009	0.25017	0.09712	0.06601	0.00427	0.00273	0.00035	0.00029	0.00028
Platform	WL3807	18.5	*complanata*	10	0.88594	0.85719		0.88594	0.88594	0.16280	0.22504	0.03331	0.00806	0.00105	0.00001	0.00000	0.00000	0.00000
Platform	WL531	18.0	*complanata*	2	0.84212	0.99377	0.88594		0.84212	0.36171	0.31929	0.17546	0.13765	0.01248	0.01316	0.00284	0.00242	0.00195
Chalk	R1118	18.0	*complanata*	30	0.97876	0.80834	0.88594	0.84212		0.09383	0.22476	0.01367	0.00061	0.00058	0.00000	0.00000	0.00000	0.00000
Platform	WL3809	15.4	*thalmanni*	21	0.31394	0.26009	0.16280	0.36171	0.09383		0.82514	0.34195	0.17546	0.01124	0.00041	0.00000	0.00000	0.00001
Platform	WL3676	14.3	*basraensis*	4	0.31929	0.25017	0.22504	0.31929	0.22476	0.82514		0.84212	0.79875	0.08028	0.09996	0.01999	0.01492	0.01252
Platform	WL497	13.5	*basraensis*	11	0.08808	0.09712	0.03331	0.17546	0.01367	0.34195	0.84212		0.92204	0.07479	0.05543	0.00320	0.00280	0.00290
Platform	WL3810	12.8	*basraensis*	26	0.03830	0.06601	0.00806	0.13765	0.00061	0.17546	0.79875	0.92204		0.06601	0.02077	0.00041	0.00045	0.00085
Platform	WL119	8.5	*tani*	4	0.00280	0.00427	0.00105	0.01248	0.00058	0.01124	0.08028	0.07479	0.06601		0.54765	0.90533	0.99883	0.88594
Platform	WL3669	8.1	*tani*	18	0.00031	0.00273	0.00001	0.01316	0.00000	0.00041	0.09996	0.05543	0.02077	0.54765		0.31929	0.24300	0.18421
Platform	WL5548	7.8	*tani*	18	0.00001	0.00035	0.00000	0.00284	0.00000	0.00000	0.01999	0.00320	0.00041	0.90533	0.31929		0.85719	0.68688
Chalk	WL1727	7.3	*tani*	14	0.00001	0.00029	0.00000	0.00242	0.00000	0.00000	0.01492	0.00280	0.00045	0.99883	0.24300	0.85719		0.84212
Chalk	WL5008	6.3	*tani*	9	0.00001	0.00028	0.00000	0.00195	0.00000	0.00001	0.01252	0.00290	0.00085	0.88594	0.18421	0.68688	0.84212	

Probabilities <0.01 >0.01 >0.05 >0.50 >0.75 >0.90

Table 7. Extracted *p*-values (arranged by X_m values) for the Jamaica Pw dataset from a pairwise DUNN post-hoc test (adjusted by the BENJAMINI-HOCHBERG FDR method). High probabilities are colour-coded. Samples with low numbers of specimens for the Jamaican dataset highlighted. Probabilities are considerably lower than for corresponding tests for X and γ suggesting that Pw is not a good discriminator at the species level and that other factors may be influencing Pw.

DUNN p-values adjusted by the BENJAMINI-HOCHBERG FDR method					***complanata***					***thal.***	***basraensis***			***tani***				
					WL4791	**WL5772**	**WL3807**	**WL531**	**R1118**	**WL3809**	**WL3676**	**WL497**	**WL3810**	**WL119**	**WL3669**	**WL5548**	**WL1727**	**WL5008**
				Xm	**18.6**	**19.4**	**18.5**	**18.0**	**18.0**	**15.4**	**14.3**	**13.5**	**12.8**	**8.5**	**8.1**	**7.8**	**7.3**	**6.3**
Locality	**Sample**	**Xm**	**Xm ID**	**N**	**7**	**5**	**10**	**2**	**30**	**21**	**4**	**11**	**26**	**4**	**18**	**18**	**14**	**9**
Platform	WL4791	18.6	*complanata*	7		0.86325	0.86404	0.57515	0.15175	0.24326	0.65818	0.32255	0.06294	0.05274	0.02471	0.00361	0.01313	0.00009
Chalk	WL5772	19.4	*complanata*	5	0.86325		0.94362	0.53412	0.40513	0.50464	0.80387	0.55471	0.23516	0.10575	0.12816	0.05324	0.08385	0.00360
Platform	WL3807	18.5	*complanata*	10	0.86404	0.94362		0.49611	0.12950	0.23725	0.71216	0.33563	0.04484	0.05274	0.01317	0.00099	0.00474	0.00001
Platform	WL531	18.0	*complanata*	2	0.57515	0.53412	0.49611		0.12950	0.16002	0.38889	0.19376	0.07450	0.04044	0.04044	0.01628	0.02471	0.00099
Chalk	R1118	18.0	*complanata*	30	0.15175	0.40513	0.12950	0.12950		0.76902	0.53984	0.74524	0.49020	0.18147	0.15175	0.02310	0.07648	0.00022
Platform	WL3809	15.4	*thalmanni*	21	0.24326	0.50464	0.23725	0.16002	0.76902		0.66201	0.92924	0.36239	0.15175	0.12816	0.02233	0.06294	0.00022
Platform	WL3676	14.3	*basraensis*	4	0.65818	0.80387	0.71216	0.38889	0.53984	0.66201		0.71216	0.42072	0.12950	0.15175	0.06294	0.10575	0.00360
Platform	WL497	13.5	*basraensis*	11	0.32255	0.55471	0.33563	0.19376	0.74524	0.92924	0.71216		0.39537	0.15175	0.15175	0.04044	0.08813	0.00089
Platform	WL3810	12.8	*basraensis*	26	0.06294	0.23516	0.04484	0.07450	0.49020	0.36239	0.32072	0.39537		0.32072	0.49611	0.12816	0.27498	0.00245
Platform	WL119	8.5	*tani*	4	0.05274	0.10575	0.05274	0.04044	0.18147	0.15175	0.12950	0.15175	0.32072		0.50464	0.71216	0.63373	0.60114
Platform	WL3669	8.1	*tani*	18	0.02471	0.12816	0.01317	0.04044	0.15175	0.12816	0.15175	0.15175	0.49611	0.50464		0.49611	0.71216	0.02471
Platform	WL5548	7.8	*tani*	18	0.00361	0.05324	0.00099	0.01628	0.02310	0.02233	0.06294	0.04044	0.12816	0.71216	0.49611		0.76284	0.08591
Chalk	WL1727	7.3	*tani*	14	0.01313	0.08385	0.00474	0.02471	0.07648	0.06294	0.10575	0.08813	0.27498	0.63373	0.71216	0.76284		0.06294
Chalk	WL5008	6.3	*tani*	9	0.00009	0.00360	0.00001	0.00099	0.00022	0.00022	0.00360	0.00089	0.00245	0.60114	0.02471	0.08591	0.06294	

Probabilities	<0.01	>0.01	>0.05	>0.50	>0.75	>0.90

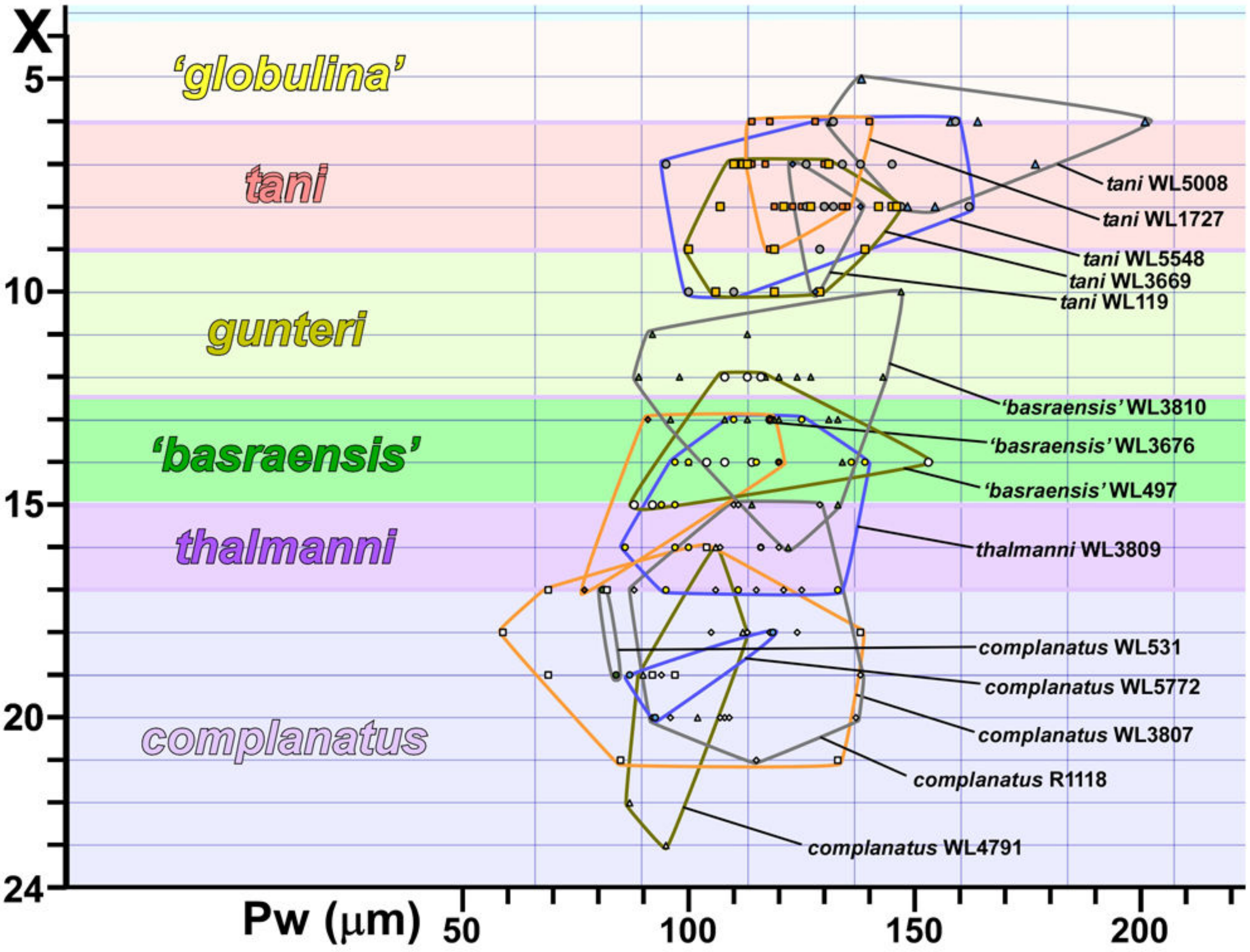

Figure 14: Scatterplot of X versus Pw (in µm) for Jamaican populations of uniserial miogypsinids. Pw shows only a very gradual increase and cannot be used to separate chronospecies. Note that the youngest sample (WL5008), however, has notably higher values.

HOCHBERG FDR method) for the Jamaican dataset are shown in Table 6. The tabulated results show a similar pattern to those for X_m (Table 6) with notable breaks in high *p*-values between *Ms. compalanta* and *Mio. thalmanni*, on the one hand, and *Mio. 'basraensis'* and *Mio. tani*, on the other. Clearly, both X_m and γ populations have similar value for discrimination between chronospecies and both should be used. In practice, however, X values are easier to measure than γ values (as is seen in the literature), yet measuring both might provide extra biostratigraphic value.

4.3.3. Analyses of character Pw

A KRUSKAL-WALLIS rank sum test for multiple independent samples for Pw on the Jamaica dataset gave a KRUSKAL-WALLIS chi-squared statistic of 63.0 (13 degrees of freedom) with $p = 1.51e^{-08}$ (but note the orders of magnitude difference the chi-squared statistic between X, γ, and Pw), showing that some populations are significantly different. Extracted values of *p* from a pairwise DUNN post-hoc test (adjusted by the BENJAMINI-HOCHBERG FDR method) for the Jamaican dataset are shown in Table 7. The tabulated results show much lower *p*-values for comparisons between pairs of populations, with some populations (*e.g.*, WL3810) showing low *p*-values for all populations. This suggests that Pw values have low value in discriminating species in *Miogypsinoides* and early *Miogypsina* populations in the Americas. It has been established (*e.g.*, NIGAM & RAO, 1987; BRYAN, 1995; YU *et al.*, 2016) that Pw is dependent on various environmental conditions (*e.g.*, water depth) and it clearly is less suitable to separate chronospecies in Oligocene miogypsinids.

4.4. Bivariate analyses

In this section the relationship between X versus γ and X versus Pw will be explored. This will include analyses of the Jamaican dataset (where complete suites of character values are available) and the global (Americas, Neotethys, and Indo-Pacific) dataset where only mean values are available.

4.4.1. Bivariate analysis of X versus γ

Some scatter plots for X versus γ have previously been published (*e.g.*, RAJU, 1974; DROOGER, 1993), but have largely presented mean values (X_m and $γ_m$) rather than plots for populations. Understanding the fields in which values of X and γ for each population plot is clearly desirable before plotting mean values for multiple populations.

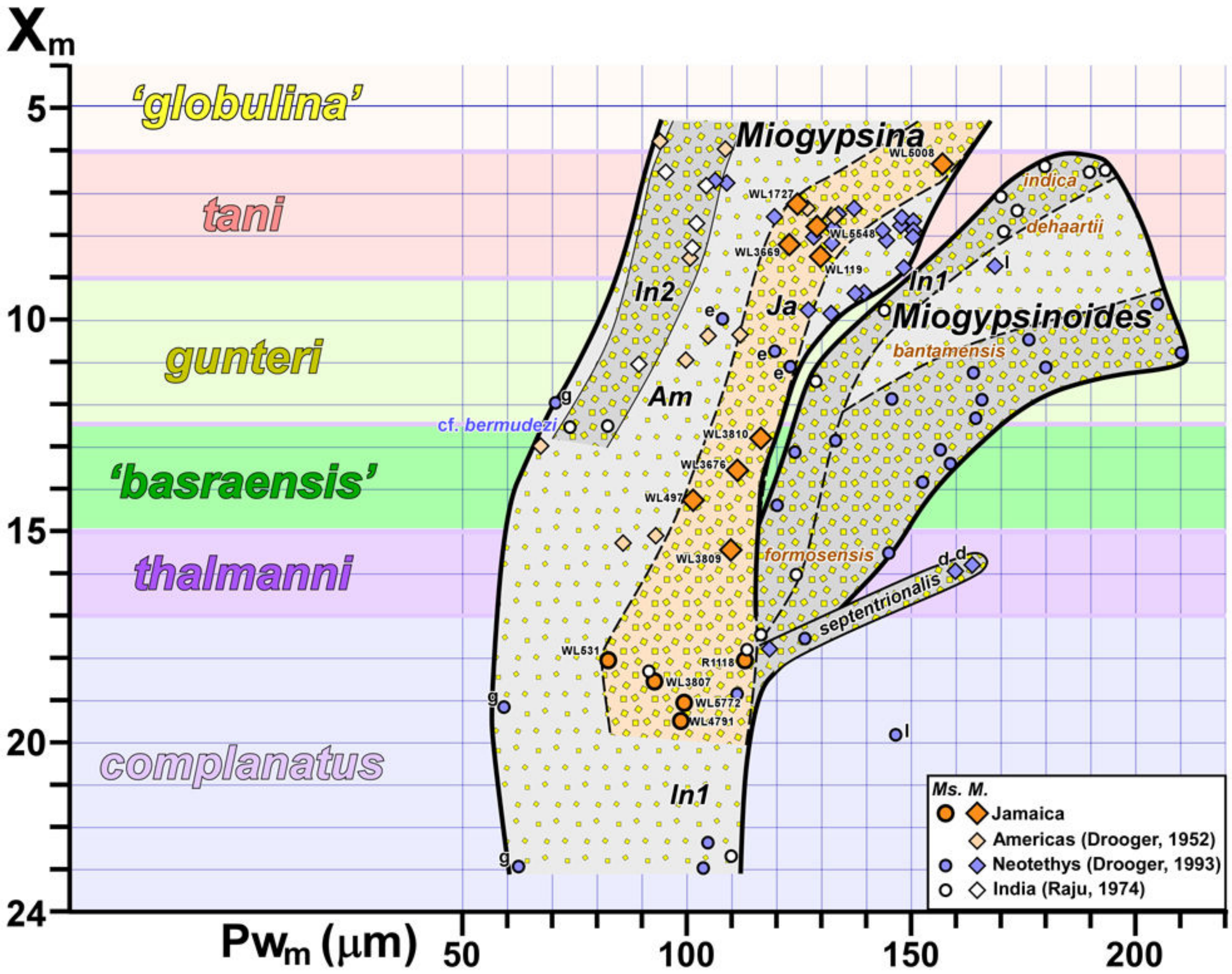

Figure 15: Scatterplot of X_m versus Pw_m for Jamaican dataset and selected other populations (Drooger, 1952, 1993; Raju, 1974). This scatterplot considers only morphology and not age of populations. Note the broad *Miogypsina* field, with populations from the Americas occupying the whole width of the field, yet those from Jamaica (a single carbonate platform) only occupy the right-hand side of the field). Similar restrictions to parts of the fields for *Miogypsina* and *Miogypsinoides* are shown for populations from different geographical areas (*e.g.*, India and Neotethys).

Herein, I will start by plotting fields and then look at the distribution patterns of means and ranges for each population. Finally I will compare with published populations (largely mean values).

A scatter plot for X versus γ for populations of Oligocene miogypsinids from the Americas (Fig. 12) shows a strong correlation between X and γ. The fields overlap significantly (as expected) and show a progressive evolution from high values of X and strongly negative values of γ to lower values of X and less negative/neutral values of γ. This reflects the trends in the univariate analyses for both X and γ. A scatterplot of X_m and γ_m values for the American, Neotethys and Indo-Pacific populations shows similar relations (Fig. 13), indicating the relationship between these variables is similar in all three provinces (although there is a departure of γ toward more negative values for X_m = 11 to 18 for the Indo-Pacific Province). Since the number of chambers in the spire should be related to the orientation of the embryonic axis this is not a surprising result.

4.4.2. Bivariate analysis of X versus Pw

Figure 14 shows a scatterplot for X versus Pw for the Jamaican dataset. Although there is a gradual increase in Pw values for increasing X values, the trend cannot be used to separate chronospecies.

Scatter plots for selected global populations of X_m versus Pw_m show broad fields for *Miogypsina* and *Miogypsinoides* with populations from some geographical areas only occupying parts of each field (Fig. 15). The field for *Miogypsina* for the Americas is wide and occupies most of the field for all *Miogypsina* populations (Fig. 15), yet the populations from Jamaica only occupy part of the overall field. Similarly, European populations (Eu) occupy the right-hand side of the *Miogypsina* field, whereas Indian populations (In) occupy the left-hand side of the field. The populations in the *Miogypsinoides* field generally have larger Pw_m values and European (Eu) and Indian (In) populations occupy different parts of the field. Other *Miogypsinoides* populations (g - Guinea; e - Egypt)

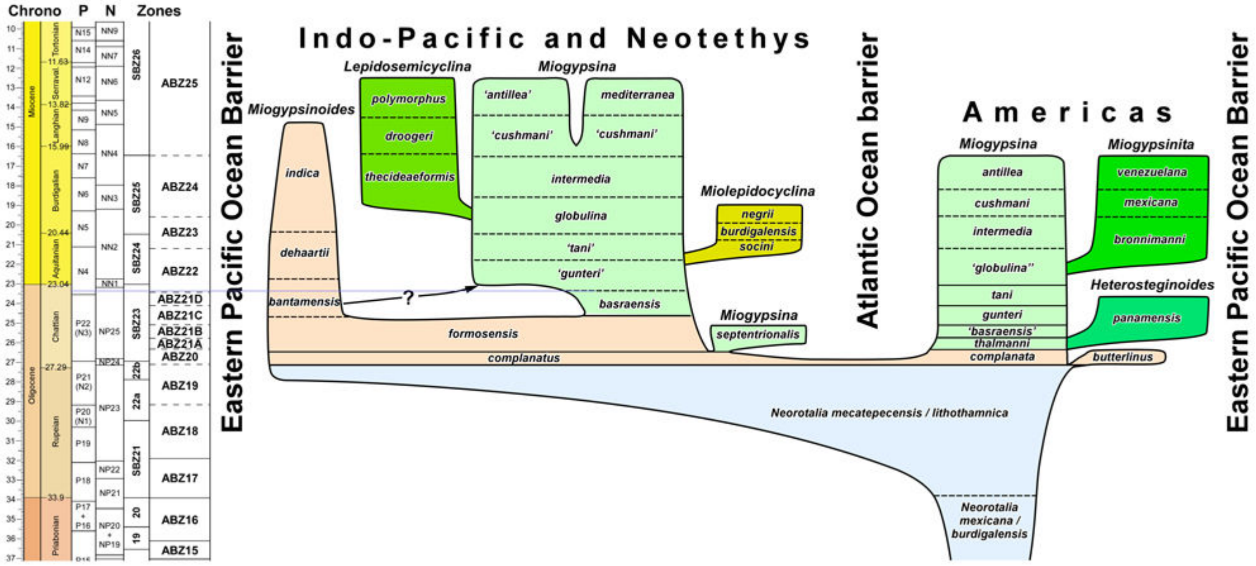

Figure 16: Provisional evolution of the Miogyspinids. The evolution of *Miogypsina* in the Indo-Pacific and Neotethys is split by the emergence of a land barrier in the mid Miocene. Minor offshoots and South African miogypsinids not included.

occupy parts of the *Miogypsina* field, whereas *Miogypsina septentrinalis* (d - from Germany) forms a small field with larger Pw_m values and there are other populations that represent outliers. This suggests that populations with local Pw_m values developed on a particular carbonate platform (*e.g.*, the *Miogypsinoides*-*Miogypsina* lineage on the Clarendon Block for Jamaica) or within a restricted geographical area. Consequently, the use of Pw_m to define chronospecies would seem to be unwise.

5. Evolution of the miogypsinids

Specimens of *Neorotalia* in the Rupelian of the Americas (SALMERÓN, 1972), northern Europe (CAHUZAC & POIGNANT, 1991, 1997), and Japan (MATSUMARU, 1990) occasionally develop one or two equatorial chambers indicating that a few chambers in the neorotalid spire sometimes developed two stolons. The development of a complete fan of equatorial chambers (the transition from *Neorotalia* to *Miogypsinoides*) can be placed at about the boundary between calcareous nannoplankton zones NP22 and NP23 in all areas (*e.g.*, CAHUZAC & POIGNANT, 1997; ROBINSON *et al.*, 2017; LUNT & LUAN, 2022; MITCHELL *et al.*, 2024). The apparently synchronous development of *Miogypsinoides* from *Neorotalia* in all provinces (Americas, Neotethys, Indo-Pacific) suggests gene flow at this time between all miogypsinid populations. The transition between *Miogypsinoides* and *Miogypsina* (the acquisition of lateral chamberlets) occurred sometime during zone NP25, however, the long duration of this zone makes it impossible to judge if this was synchronous across all the provinces. The fact that *Miogypsina* rapidly evolved in the Americas, but saw slower evolution in the Neotethys and Indo-Pacific, almost certainly suggest that *Miogypsina* developed earlier in the Americas than in the other provinces (Figs. 16-17). If this is the case, it would suggest that gene flow had become restricted between the Americas and the Neotethys with the growing width of the Atlantic becoming a physical barrier to migration. Perhaps the development of *Mio. septentrionalis* in northern Europe was related to the final gene flow across the Atlantic, but that the main evolutionary development of *Miogypsina* in the Neotethys and Indo-Pacific provinces was delayed. Certainly by the mid Chattian, the evolutionary development of *Miogypsina* was well advanced in the American province, but had only just begun in the Neotethys and Indo-Pacific provinces (Figs. 16-17).

The base of the Miocene (using the base of NN1 as a proxy) is the next obvious time to compare the evolutionary development of miogyspinids. In the Americas, the base of the Miocene corresponds to the transition from *Mio. tani* to *Mio. 'globulina'* (Figs. 16-17). In contrast, in the Neotethys and Indo-Pacific provinces the base of the Miocene corresponds to the transition from *Ms. formosensis* or *Mio. basraensis* to *Mio. 'gunteri'* (Figs. 16-17). Thus, the evolution of the *Miogypsina* lineage in the Neotethys and Indo-Pacific was 'delayed' by two chronospecies (some 2.5 million years) in comparison to the Americas by the start of the Miocene (Fig. 17). Thus, *Miogypsina* may potentially be polyphyletic, but more studies of the transition between *Miogypsinoides* and *Miogypsina* are needed to establish this. In the Americas *Miogypsinoides* disappears, whereas in the Indo-Pacific and Neotethys a *Miogypsinoides* lineage persists into the mid Miocene (LUNT & LUAN, 1922; Fig. 16). Short-lived offshoots occurred throughout the evolution of the miogypsinids (Fig. 16); I include in these: *Miogypsinoides butterlinus*, *Miogypsina septentrionalis*, and four genera (*Lepidosemicyclina*, *Miolepidocyclina*, *Heterosteginoides*, and *Miogypsinita*).

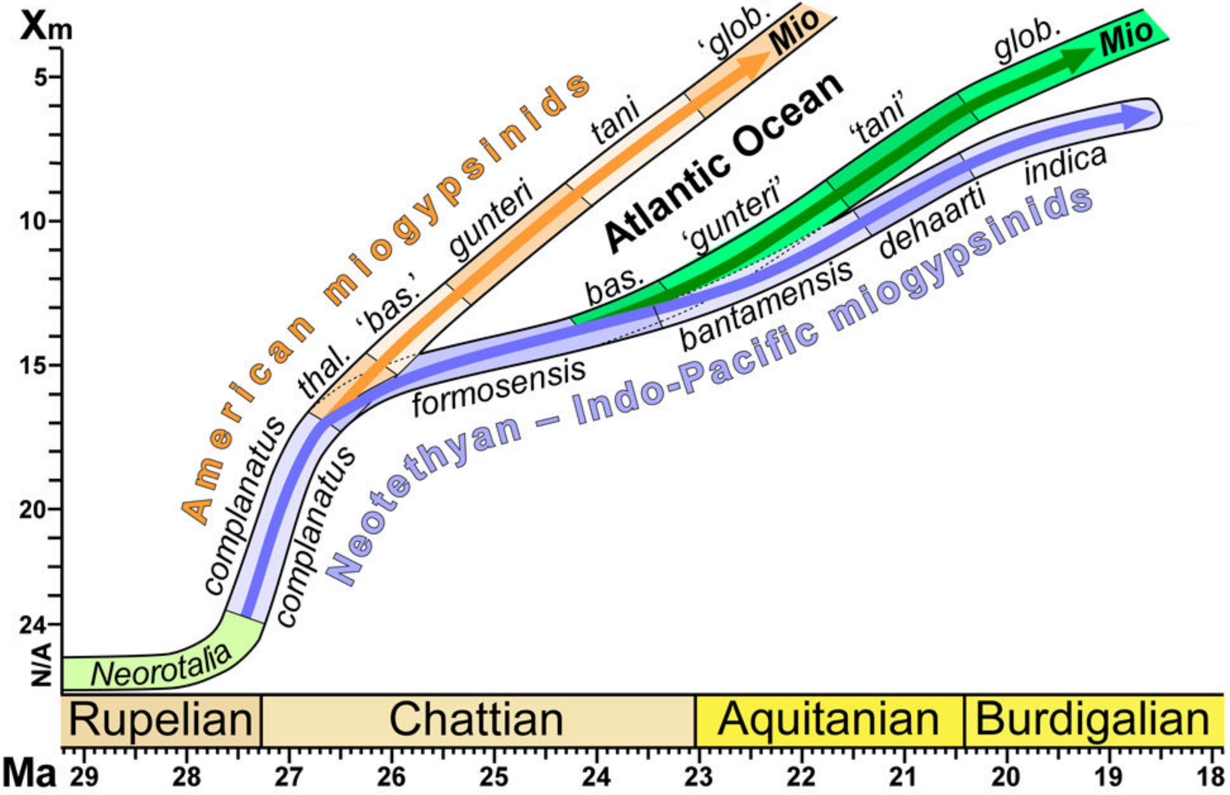

Figure 17: Comparison of the evolutionary changes for uniserial miogypsinids between the Americas and the Neotethys/Indo-Pacific provinces plotted in X_m vs. time (Ma) space. Note the distinct time offset (2 to 2.5 Ma) for the 'same' chronospecies (*e.g.*, *gunteri* and *tani*) between provinces.

6. Conclusions

A detailed study of the miogypsinids from the Oligocene of Jamaica demonstrates that DROOGER's (1952) population approach is valid and that typological-based approaches are of limited use and should not be used. The evolution of *Miogypsinoides* from *Neorotalia* seems to be synchronous across all provinces, yet the subsequent development of *Miogypsina* is probably diachronous, with the American forms showing a more-advanced development than coeval forms from the Neotethys and Indo-Pacific. For the present, the chronospecies names are retained, but with further work separate chronospecies names may well be needed for the Americas and the Neotethys/Indo-Pacific. The base of the Miocene corresponds to the appearance of *Mio. 'globulina'* in the Americas, but to the appearance of *Mio. 'gunteri'* in the Neotethys/Indo-Pacific. This indicates that by this time, the miogypsinids of the America were two chronospecies more advanced that their compatriots in the Neotethys/Indo-Pacific. The miogypsinids can be used for detailed biostratigraphy within each province, but cannot be used for correlation between the Americans and the Neotethys/Indo-Pacific. This research demonstrates that LBF lineages can become separated over time and can show different rates of evolution in different, isolated populations.

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Appendix

Data on Jamaica miogypsinids used in this work.

Sample	Slab	No	Formation	Location	Species	X	γ	Pw
R1118	...	T/S	Chester Fm	Sherwood Content	*complanatus*	20	-269	108
R1118	...	T/S	Chester Fm	Sherwood Content	*complanatus*	18	-297	118
R1118	Slab 1	3	Chester Fm	Sherwood Content	*complanatus*	15	-213	110
R1118	Slab 1	4	Chester Fm	Sherwood Content	*complanatus*	21	-380	115
R1118	Slab 1	5	Chester Fm	Sherwood Content	*complanatus*	18	-240	113
R1118	Slab 1	6	Chester Fm	Sherwood Content	*complanatus*	20	-370	96
R1118	Slab 1	7	Chester Fm	Sherwood Content	*complanatus*	17	-252	115
R1118	Slab 1	8	Chester Fm	Sherwood Content	*complanatus*	20	-310	92
R1118	Slab 1	9	Chester Fm	Sherwood Content	*complanatus*	17	-201	106
R1118	Slab 1	10	Chester Fm	Sherwood Content	*complanatus*	17	-285	125
R1118	Slab 1	11	Chester Fm	Sherwood Content	*complanatus*	16	-275	116
R1118	Slab 1	12	Chester Fm	Sherwood Content	*complanatus*	17	-273	
R1118	Slab 1	13	Chester Fm	Sherwood Content	*complanatus*	19		138
R1118	Slab 2a	14	Chester Fm	Sherwood Content	*complanatus*	20	-304	137
R1118	Slab 2a	15	Chester Fm	Sherwood Content	*complanatus*	18	-274	105
R1118	Slab 2b	16	Chester Fm	Sherwood Content	*complanatus*	16	-231	107
R1118	Slab 2b	17	Chester Fm	Sherwood Content	*complanatus*	21	-375	115
R1118	Slab 3a	18	Chester Fm	Sherwood Content	*complanatus*	17	-281	88
R1118	Slab 3a	19	Chester Fm	Sherwood Content	*complanatus*	17	-285	121
R1118	Slab 3a	20	Chester Fm	Sherwood Content	*complanatus*	16	-320	120
R1118	N/A	21	Chester Fm	Sherwood Content	*complanatus*	17	-261	
R1118	N/A	22	Chester Fm	Sherwood Content	*complanatus*	15	-185	129
R1118	N/A	23	Chester Fm	Sherwood Content	*complanatus*	20	-336	107
R1118	N/A	24	Chester Fm	Sherwood Content	*complanatus*	20	-353	109
R1118	N/A	25	Chester Fm	Sherwood Content	*complanatus*	18	-294	124
R1118	N/A	26	Chester Fm	Sherwood Content	*complanatus*	18	-348	118
R1118	N/A	27	Chester Fm	Sherwood Content	*complanatus*	18	-317	113
R1118	N/A	28	Chester Fm	Sherwood Content	*complanatus*	15	-260	111
R1118	N/A	29	Chester Fm	Sherwood Content	*complanatus*	20	-272	
R1118	N/A	30	Chester Fm	Sherwood Content	*complanatus*	19	-327	94
WL119	N/A	1	Basal Newport Fm	Highway 2000	*tani*	9	-31	
WL119	N/A	2	Basal Newport Fm	Highway 2000	*tani*	8	-32	138
WL119	N/A	3	Basal Newport Fm	Highway 2000	*tani*	10	-18	128
WL119	N/A	4	Basal Newport Fm	Highway 2000	*tani*	7	-39	123
WL1727	N/A	3	Chester Fm	St Mary	*complanatus*	6	-8	114
WL1727	N/A	4	Chester Fm	St Mary	*complanatus*	6	-12	128
WL1727	N/A	5	Chester Fm	St Mary	*complanatus*	6	-21	140
WL1727	N/A	6	Chester Fm	St Mary	*complanatus*	8	-85	123
WL1727	N/A	9	Chester Fm	St Mary	*complanatus*	8	-28	135
WL1727	N/A	10	Chester Fm	St Mary	*complanatus*	8	0	130
WL1727	N/A	12	Chester Fm	St Mary	*complanatus*	7	-53	114
WL1727	N/A	13	Chester Fm	St Mary	*complanatus*	9	-9	118
WL1727	N/A	14	Chester Fm	St Mary	*complanatus*	7	-40	117
WL1727	N/A	16	Chester Fm	St Mary	*complanatus*	8	-53	134
WL1727	N/A	17	Chester Fm	St Mary	*complanatus*	7	7	130
WL1727	N/A	18	Chester Fm	St Mary	*complanatus*	6	0	118
WL1727	N/A	19	Chester Fm	St Mary	*complanatus*	8	-31	125
WL1727	N/A	21	Chester Fm	St Mary	*complanatus*	8	-21	119
WL3669	Slab3	1	Basal Newport Fm	Ulster Spring	*tani*	8	-61	145
WL3669	Slab3	2	Basal Newport Fm	Ulster Spring	*tani*	9	-71	139
WL3669	Slab3	3	Basal Newport Fm	Ulster Spring	*tani*	8	-60	146

WL3669 Slab 4	4	Basal Newport Fm	Ulster Spring	*tani*	10	-97	106
WL3669 Slab 1	5	Basal Newport Fm	Ulster Spring	*tani*	9	-193	100
WL3669 Slab 1	6	Basal Newport Fm	Ulster Spring	*tani*	9	-52	119
WL3669 Slab 2a	7	Basal Newport Fm	Ulster Spring	*tani*	7	-51	112
WL3669 Slab 2a	8	Basal Newport Fm	Ulster Spring	*tani*	7	-38	110
WL3669 Slab 2a	9	Basal Newport Fm	Ulster Spring	*tani*	7	-58	
WL3669 Slab 2a	10	Basal Newport Fm	Ulster Spring	*tani*	8	-76	107
WL3669 Slab 2a	11	Basal Newport Fm	Ulster Spring	*tani*	10	-48	129
WL3669 Slab 2a	12	Basal Newport Fm	Ulster Spring	*tani*	8	-42	127
WL3669 Slab 2a	12A	Basal Newport Fm	Ulster Spring	*tani*	10	-51	119
WL3669 Slab 2c	13	Basal Newport Fm	Ulster Spring	*tani*	8	-35	
WL3669 Slab 2b	14	Basal Newport Fm	Ulster Spring	*tani*	8	-48	142
WL3669 Slab 2b	15	Basal Newport Fm	Ulster Spring	*tani*	7	-44	131
WL3669 Slab 2b	16	Basal Newport Fm	Ulster Spring	*tani*	7	-53	113
WL3669 Slab 3A	16	Basal Newport Fm	Ulster Spring	*tani*	8	-35	121
WL3676 N/A	1	Moneague Fm	Ulster Spring	*basraensis*	13	-216	118
WL3676 N/A	2	Moneague Fm	Ulster Spring	*basraensis*	13	-212	91
WL3676 N/A	3	Moneague Fm	Ulster Spring	*basraensis*	17	-212	77
WL3676 N/A	4	Moneague Fm	Ulster Spring	*basraensis*	14	-218	120
WL3807 N/A	1	Moneague Fm	Ulster Spring	*complanatus*	18	-299	59
WL3807 N/A	2	Moneague Fm	Ulster Spring	*complanatus*	17	-221	69
WL3807 N/A	3	Moneague Fm	Ulster Spring	*complanatus*	19	-274	97
WL3807 N/A	4	Moneague Fm	Ulster Spring	*complanatus*	21	-328	85
WL3807 N/A	5	Moneague Fm	Ulster Spring	*complanatus*	17	-279	82
WL3807 N/A	6	Moneague Fm	Ulster Spring	*complanatus*	16	-259	104
WL3807 N/A	7	Moneague Fm	Ulster Spring	*complanatus*	18	-301	138
WL3807 N/A	8	Moneague Fm	Ulster Spring	*complanatus*	21	-344	133
WL3807 N/A	9	Moneague Fm	Ulster Spring	*complanatus*	19	-292	92
WL3807 N/A	10	Moneague Fm	Ulster Spring	*complanatus*	19	-345	69
WL3809 Slab 1 bottom	1	Moneague Fm	Ulster Spring	*thalmanni*	16	-265	100
WL3809 Slab 1 bottom	2	Moneague Fm	Ulster Spring	*thalmanni*	17	-325	133
WL3809 Slab 1 bottom	4a	Moneague Fm	Ulster Spring	*thalmanni*	16	-232	
WL3809 Salb 1 top	5	Moneague Fm	Ulster Spring	*thalmanni*	13	-169	125
WL3809 Salb 1 top	6	Moneague Fm	Ulster Spring	*thalmanni*	14	-226	139
WL3809 Salb 1 top	7	Moneague Fm	Ulster Spring	*thalmanni*	17	-246	
WL3809 Salb 1 top	8	Moneague Fm	Ulster Spring	*thalmanni*	16	-210	97
WL3809 Salb 1 top	9	Moneague Fm	Ulster Spring	*thalmanni*	14	-237	97
WL3809 Slab 2	10	Moneague Fm	Ulster Spring	*thalmanni*	13	-149	110
WL3809 Slab 2	11	Moneague Fm	Ulster Spring	*thalmanni*	19	-420	
WL3809 Slab 2	12	Moneague Fm	Ulster Spring	*thalmanni*	14	-237	100
WL3809 Slab 3	13	Moneague Fm	Ulster Spring	*thalmanni*	15	-159	94
WL3809 Slab 3	14	Moneague Fm	Ulster Spring	*thalmanni*	15	-233	97
WL3809 Slab 3	15	Moneague Fm	Ulster Spring	*thalmanni*	16	-267	116
WL3809 Slab 3	16	Moneague Fm	Ulster Spring	*thalmanni*	14	-257	120
WL3809 Slab 3	17	Moneague Fm	Ulster Spring	*thalmanni*	17	-243	95
WL3809 Slab 4	18	Moneague Fm	Ulster Spring	*thalmanni*	17	-262	111
WL3809 Slab 4	19	Moneague Fm	Ulster Spring	*thalmanni*	17	-242	
WL3809 Slab 4	20	Moneague Fm	Ulster Spring	*thalmanni*	16	-239	86
WL3809 Slab 4	21	Moneague Fm	Ulster Spring	*thalmanni*	14	-199	115
WL3809 Slab 4	21a	Moneague Fm	Ulster Spring	*thalmanni*	14	-157	136
WL3810 Slab 1	1	Moneague Fm	Ulster Spring	*basraensis*	11	-141	113
WL3810 Slab 1	2	Moneague Fm	Ulster Spring	*basraensis*	12	-137	117
WL3810 Slab 1	3	Moneague Fm	Ulster Spring	*basraensis*	13	-209	108
WL3810 Slab 1	4	Moneague Fm	Ulster Spring	*basraensis*	13	-211	119
WL3810 Slab 1	5	Moneague Fm	Ulster Spring	*basraensis*	12	-169	120
WL3810 Slab 1	6	Moneague Fm	Ulster Spring	*basraensis*	12	-224	98
WL3810 Slab 1	7	Moneague Fm	Ulster Spring	*basraensis*	13	-162	133
WL3810 Slab 1	8	Moneague Fm	Ulster Spring	*basraensis*	11	-214	
WL3810 Slab 1	12	Moneague Fm	Ulster Spring	*basraensis*	12	-186	143
WL3810 Slab 1	13	Moneague Fm	Ulster Spring	*basraensis*	13	-145	96
WL3810 Slab 2a	14	Moneague Fm	Ulster Spring	*basraensis*	12	-186	89
WL3810 Slab 2a	15	Moneague Fm	Ulster Spring	*basraensis*	10	-122	147
WL3810 Slab 2b	16	Moneague Fm	Ulster Spring	*basraensis*	14	-195	134
WL3810 Slab 2b	17	Moneague Fm	Ulster Spring	*basraensis*	15	-180	114
WL3810 Slab 3a	18	Moneague Fm	Ulster Spring	*basraensis*	13	-111	131
WL3810 Slab 3a	19	Moneague Fm	Ulster Spring	*basraensis*	13	-163	120

WL3810	Slab 3a	20	Moneague Fm	Ulster Spring	*basraensis*	12	-195	127
WL3810	Slab 3a	21	Moneague Fm	Ulster Spring	*basraensis*	14	-179	
WL3810	Slab 3a	22	Moneague Fm	Ulster Spring	*basraensis*	14	-241	100
WL3810	Slab 3b	23	Moneague Fm	Ulster Spring	*basraensis*	13	-257	113
WL3810	Slab 3b	24	Moneague Fm	Ulster Spring	*basraensis*	12	-178	89
WL3810	Slab 3b	25	Moneague Fm	Ulster Spring	*basraensis*	11	-180	92
WL3810	Slab 3b	26	Moneague Fm	Ulster Spring	*basraensis*	16	-256	122
WL3810	Slab 3b	27	Moneague Fm	Ulster Spring	*basraensis*	12	-150	124
WL3810	Slab 3b	28	Moneague Fm	Ulster Spring	*basraensis*	14	-279	
WL3810	Slab 3b	29	Moneague Fm	Ulster Spring	*basraensis*	15	-188	133
WL4791	Slab4	…	Moneague Fm	St Ann	*complanatus*	18	-150	
WL4791	Slab4	…	Moneague Fm	St Ann	*complanatus*	16	-199	106
WL4791	Slab4	…	Moneague Fm	St Ann	*complanatus*	19	-281	90
WL4791	Slab4	…	Moneague Fm	St Ann	*complanatus*	18	-328	112
WL4791	N/A	…	Moneague Fm	St Ann	*complanatus*	23	-375	95
WL4791	N/A	…	Moneague Fm	St Ann	*complanatus*	22	-395	87
WL4791	N/A	…	Moneague Fm	St Ann	*complanatus*	20	-356	102
WL497	Slab 1	1	Moneague Fm	Prickly Pole	*basraensis*	14	-213	114
WL497	Slab 1	2	Moneague Fm	Prickly Pole	*basraensis*	14	-161	153
WL497	Slab 1	3	Moneague Fm	Prickly Pole	*basraensis*	12	-165	108
WL497	Slab 1	4	Moneague Fm	Prickly Pole	*basraensis*	13	-150	118
WL497	Slab 2	b	Moneague Fm	Prickly Pole	*basraensis*	14	-251	
WL497	Slab 2	5	Moneague Fm	Prickly Pole	*basraensis*	15	-232	88
WL497	Slab 3	1	Moneague Fm	Prickly Pole	*basraensis*	12	-159	113
WL497	Slab 4	1	Moneague Fm	Prickly Pole	*basraensis*	14	-250	104
WL497	Slab 5	1	Moneague Fm	Prickly Pole	*basraensis*	12	-133	116
WL497	Slab 6	1	Moneague Fm	Prickly Pole	*basraensis*	15	-232	92
WL497	Slab 6	2	Moneague Fm	Prickly Pole	*basraensis*	14	-169	108
WL5008	N/A	9	Chester Fm	Hope Bay	*tani*	5	-12	138
WL5008	N/A	10	Chester Fm	Hope Bay	*tani*	6	-39	201
WL5008	N/A	20	Chester Fm	Hope Bay	*tani*	6	9	158
WL5008	N/A	22	Chester Fm	Hope Bay	*tani*	8	-53	148
WL5008	N/A	23	Chester Fm	Hope Bay	*tani*	8	-37	154
WL5008	N/A	33	Chester Fm	Hope Bay	*tani*	7	-2	177
WL5008	N/A	34	Chester Fm	Hope Bay	*tani*	6	14	164
WL5008	N/A	35	Chester Fm	Hope Bay	*tani*	6	14	131
WL5008	N/A	36	Chester Fm	Hope Bay	*tani*	5	15	138
WL531	Slab 1	1	Moneague Fm	Prickly Pole	*complanatus*	19	-335	84
WL531	Slab 1	1	Moneague Fm	Prickly Pole	*complanatus*	17	-288	81
WL5548	Slab 1	1	Newport Fm	Maggotty	*tani*	8	-16	130
WL5548	Slab 1	2	Newport Fm	Maggotty	*tani*	10	-124	110
WL5548	Slab 1	3	Newport Fm	Maggotty	*tani*	6	-12	132
WL5548	Slab 1	4	Newport Fm	Maggotty	*tani*	8	-24	147
WL5548	Slab 1	5	Newport Fm	Maggotty	*tani*	6	-24	159
WL5548	Slab 1	6	Newport Fm	Maggotty	*tani*	7	-21	134
WL5548	Slab 1	7	Newport Fm	Maggotty	*tani*	7	-72	95
WL5548	Slab 1	8	Newport Fm	Maggotty	*tani*	8	-32	132
WL5548	Slab 1	9	Newport Fm	Maggotty	*tani*	10	-24	100
WL5548	Slab 1	10	Newport Fm	Maggotty	*tani*	7	-35	138
WL5548	Slab 1	11	Newport Fm	Maggotty	*tani*	8	-34	130
WL5548	Slab 2	1	Newport Fm	Maggotty	*tani*	7	6	131
WL5548	Slab 2	2	Newport Fm	Maggotty	*tani*	7	-24	145
WL5548	Slab 2	3	Newport Fm	Maggotty	*tani*	8	-28	126
WL5548	Slab 2	4	Newport Fm	Maggotty	*tani*	9	-32	129
WL5548	Slab 2	5	Newport Fm	Maggotty	*tani*	9	-38	119
WL5548	Slab 3	1	Newport Fm	Maggotty	*tani*	8	-43	162
WL5548	Slab 4	1	Newport Fm	Maggotty	*tani*	7	-18	126
WL5548	Slab 4	2	Newport Fm	Maggotty	*tani*	8	-84	107
WL5772	N/A	1	Chester Fm	Rio Bueno	*complanatus*	18	-272	119
WL5772	N/A	1	Chester Fm	Rio Bueno	*complanatus*	19	-344	87
WL5772	N/A	1	Chester Fm	Rio Bueno	*complanatus*	20	-346	93