

Madden–Julian oscillations and Calendar-band frequencies in the geological past

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Evidence of Madden–Julian oscillations and Calendar-band frequencies in the Late Paleogene and Early Neogene recorded by larger foraminifera

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Tests of the larger foraminifera *Lepidocyclina ocalana* CUSHMAN from the Late Paleogene and *Nephrolepidina vauhani* (CUSHMAN) and *Eulepidina undosa* (CUSHMAN) from the Late Oligocene/Early Miocene of the Caribbean region show significant growth-related oscillations in chamberlet-subdivided chamber volumes. These oscillations were modeled as sums of sinusoids after their frequency distributions were decomposed into normally distributed components. Comparable components occur across the species and are expressed by common average sinusoids at 3.0, 5.2, 9.4, 15.3, and 19.4 chambers. Chamber numbers were converted to days using the chamber-building rate of the living *Cycloclypeus carpenteri* BRADY, whose test structure—with hyaline walls and radially arranged chamberlet-divided chambers following a large embryonal apparatus (nepiont)—resembles the equatorial layers (neanic chambers) of the fossil species. The Michaelis-Menten function yielded common averaged sinusoids with dominant periods of 7.8, 13.9, and 26.7 days, and weaker periods of 38.5, 46.1, and 58.6 days. These time-based sinusoids correlate strongly with those based on chamber numbers. The second and third sinusoids correspond to spring-neap tides and synodic lunar cycles, whereas the first, circaseptan oscillation is difficult to interpret. The remaining oscillations fall within the range of atmospheric induced Madden-Julian oscillations. Halving the chamber-building rate shifts the first three dominant sinusoidal peaks to 15.6, 27.8, and 53.0 days, bringing them closer to the spring-neap tide and synodic lunar cycles while strengthening the MJO signal. The Caribbean records suggest that, during the Late Paleogene and Early Neogene, the MJO may have propagated around the

equator without weakening and attenuation by continental barriers, thus strongly influenced paleoclimate in both hemispheres. Future studies should test this interpretation using radial foraminifera from different regions and stratigraphic levels.

Marine protozoa with algal symbionts depend to varying degrees on metabolic products released by these symbionts, forming mixotrophic to autotrophic holobionts. Because their metabolism is governed by light-driven algal photosynthesis, it responds to calendar-band frequencies, including semi-annual, synodic lunar-month and semi-monthly spring-neap tide cycles, as well as larger-scale atmospheric convection.

Today, larger symbiont-bearing foraminifera with calcareous hyaline tests inhabit shallow tropical and subtropical seas down to the base of the photic zone^{1,2,3,4}. Their glassy tests transmit light, and decreasing light intensity from the euphotic to the oligophotic zone⁵ is accompanied by a shift from thick, lenticular tests to large, thin, flattened forms^{2,6}. This morphology increases the surface-to-volume ratio and accommodates more photosymbionts just beneath the glassy walls⁷. In radial foraminifera⁸, this adaptation is enhanced by circularly arranged, flattened chambers divided into chamberlets, enabling sizes exceptional for protozoa. Besides the living genera *Cycloclypeus* and *Heterocyclus*, the fossil lepidocyclinids studied here belong to this morphologic group, although they are not phylogenetically related to those genera.

In polythalamous, or multi-chambered, foraminifera, biomass growth can be estimated from chamber and chamberlet volumes and modeled with limited growth functions⁹. The inflection points of these functions, where chamber volumes begin to decrease, indicate the chamber number at which reproduction occurs in both agamonts (microspheres) and gamonts/schizonts (macrospheres)¹⁰. In temporal terms, chamber construction is recorded by chamber-wall formation, which takes up to 24 hours in larger symbiont-bearing foraminifera¹¹. Each chamber therefore represents the interval, measured in days, between two discrete growth stages marked by wall construction when biomass growth stops. During these multi-day intervals, environmental factors influence biomass accumulation¹². Biomass growth depends on nutrient input remaining after maintenance requirements are met¹³. As maintenance demands increase with size, chamber-building rates decline monotonically, reducing growth velocity¹⁴. Consequently, newborn and juvenile specimens, which have higher mass-specific metabolic rates, form chambers at shorter intervals than mature specimens⁹.

Chamber-building rates have been modeled with power functions for *C. carpenteri*¹² and *Heterostegina depressa*¹⁵, and with Michaelis-Menten functions for *H. depressa*^{10,16} and *Palaeonummulites venosus*^{17,18}. Combining these functions with the inflection points of the Gompertz growth functions yielded longevity estimates of 416 days for *H. depressa*¹⁶ and 432 days for *P. venosus*¹⁷. Both estimates are compared with data obtained by the “natural laboratory” approach¹⁹ and agree broadly with longevities observed in cultures of *P. venosus* with 468 days²⁰, *H. depressa* with 12–13 months^{20,21} and *C. carpenteri* with 12 months²².

Oscillations in chamber volumes along chamber-building trajectories were decomposed into sums of sinusoids using power spectral analyses. Spring–neap tide and synodic lunar-month cycles were identified in *H. depressa*^{10,15,16}, *P. venosus*^{10,12,17,18} and *C. carpenteri*¹². Cross-correlation supported the assignment of sinusoids to calendar-band frequencies¹⁸. Despite differing growth stages, all specimens collected on the same date showed a significant negative correlation between their 14-day sinusoids and tidal stands¹⁸. The bimonthly cycle reported for *P. venosus*^{10,18} and the significant 70- and 75-days cycles found in *H. depressa* from Okinawa and Hawaii¹⁵ as well as weekly cycles observed in *H. depressa*¹⁰, *C. carpenteri*¹² and *P. venosus*⁹ could not be explained by calendar-band frequencies.

Thin sections in the equatorial plane of three lepidocyclinid species from the Late Paleogene and Early Neogene of the Caribbean allow test volumes to be approximated from the areas of chamberlet-divided chambers. Oscillations in chamber numbers that can be converted into days may, for the first time, reveal the influence of calendar-band frequencies and large-scale atmospheric convection on larger, symbiont-bearing foraminifera in the geological past.

Geographical and stratigraphical setting

The lepidocyclinid species studied here were collected from three sections and two spot samples in the Caribbean, ranging from the Late Eocene to the Early Neogene (Fig. 1). During this interval, lepidocyclinids were widespread and dominant in larger benthic foraminiferal communities, occupying diverse settings along the outer margins of carbonate platforms^{23,24}. Well-preserved megalospheric specimens were examined from the following localities (Tab. 1):

In Cuba, specimens of *Lepidocyclina ocalana* CUSHMAN were examined from two spot samples of the Jicotea Formation (P-559 and P-562), northwest of La Esperanza, Villa Clara Province (Tab. 1). The species was also studied in the Loma Vigia section (CA-216) of the

Blanco Formation, near Siguaney, Sancti Spiritus Province (Tab. 1). The Priabonian age of these localities is based on calcareous nannofossils and larger benthic foraminiferal assemblages spanning biozones NP17–NP19 and ABZ15–ABZ16²⁵.

In Panama, specimens of *Nephrolepidina vauhani* (CUSHMAN) were examined from the San Juan section (23PA-SJ) of the Caimito Formation, near San Juan village along the highway between Panama City and Colón (Tab. 1). Calcareous nannofossil assemblages assign this section to the Aquitanian, corresponding to the lower part of zone NN2²⁶ and to subzones CN1b to lower CN1c²⁷.

In Mexico, *Eulepidina undosa* (CUSHMAN) was identified in the Salto de Agua section (23ME-SA) of the Mompuyil Formation (Fig. 1), near Salto de Agua village along the road between Chavalito and Patioja villages, Chiapas (Tab. 1). The studied sediments lack diagnostic calcareous nannofossils. Based on Caribbean occurrences of *E. undosa*, the section can be assigned from the Oligocene to lower Miocene²⁸. In Chiapas, *E. undosa* is characteristic of the Oligocene and is absent from the lower Miocene²⁹; its occurrence in the Mompuyil Formation is therefore also assigned to the Oligocene³⁰.

Methods

Well-preserved tests of lepidocyclinids with clear distinctions between test walls and chamber fillings, needed for Micro CT analysis, are rarely found among fossil larger foraminifera. Therefore, measuring nepiont and chamber volumes of the equatorial layers using Micro CT, a method effective for growth estimation in extant species^{31,32,33}, is largely impractical for fossil specimens. Consequently, cell growth measurement defined by the equatorial layer relies on volumes represented by two-dimensional chamber and chamberlet areas in equatorial thin sections, which is justified by the consistent chamber height during growth shown in axial sections (Fig. 2).

In microspheres (A-generations) of the three species investigated, *Lepidocyclina ocalana*, *Nephrolepidina vauhani*, and *Eulepidina undosa*, neighboring chamberlets are connected within one chamber by short common septulae, making chambers identifiable as circular rows of spatulate to rhombic chamberlets^{34,35}. Due to the incomplete and non-planar, but corrugated to undulated tests of the species, specifically *E. undosa*, only parts of the equatorial layers are observable in thin sections (Fig. 2). This limits the ability to completely measure chamber rows to determine the actual volume of the equatorial layers.

Areas of neanic chamberlets were measured in test sectors³⁵, where chamberlet rows could be identified from the nepiont to the test margin (Fig. 3). The first row ($j = 1$) begins after the peri-embryonal chambers. Sector angles α were kept small to minimize the number of measurements, resulting in slight changes between succeeding rows.

Growth by chamber number

Tests with over 30 chambers were used to determine sufficient periods during growth, leading to the study of 11 *L. ocalana*, 14 *N. vaughani* and 9 *E. undosa* specimens (Supplement 1).

Two areas were measured studying cell growth. The first is the mean chamberlet area cht_j of chamber j defined by

$$cht_j = \frac{1}{n} \sum_{i=1}^n cht_{ij} \quad n = \text{number of measured chamberlets} \quad (1)$$

Using cht_j as representative for the complete chamber j , chamber areas chb_j results from

$$chb_j = 360 \sum_{i=1}^n cht_{ij} / \alpha_j \quad \alpha \text{ in degrees} \quad (2)$$

Both equations allow for the estimation of chamberlets and chamber areas, facilitating growth studies in lepidocyclinids.

The sequences of mean chamberlet areas cht_j exhibit deviations from the average chamberlet area

$$cht_{j,e} = \frac{1}{m} \sum_{j=1}^m cht_{j,o} \quad (3)$$

during growth (e = expected, o = observed, m = number of chambers; Fig. 4A).

Increasing chamber areas chb_j correspond to regression function

$$chb_{j,e} = a + b chb_{j,o} \quad (4)$$

because the circular chamber arrangement expands the mean chamber area (Fig. 4B).

All growth histograms for chamberlet areas cht show clear deviations from the average, which appear as oscillations rather than random variation (Fig. 4A). Similarly, deviations in chamber areas chb (Fig. 4B) can be assessed by calculating residuals d , defined as the difference between observed values (for each j) and those predicted by the regression function¹⁰

$$d_j = chb_{j,o} - chb_{j,e} \quad (5)$$

Cell growth is based on the cumulative distribution of chamber areas

$$cell_{area,j} = \sum_{j=1}^{j=m} chb_j \quad m = \text{number of chambers} \quad (6)$$

Oscillations around the average in chamberlet areas *cht* or from the residuals in chamber and cell areas *chb* (Fig. 4) can be decomposed into k sinusoidal functions, where the sum of these sinusoids approximates the empirical oscillations by

$$d_j = \sum_{s=1}^{s=k} amplitude_{j,s} * \cos(2\pi j / period_{j,s} - phase_{j,s}) \quad (7)$$

Oscillating functions were broken down into k sinusoids with the Lomb Periodogram³⁶ and the matching pursuit algorithm³⁷. Although both techniques produced comparable results, the matching pursuit algorithm showed a higher correlation with the observed data and was therefore selected.

A comparison of significant periods between chamberlet and chamber areas indicates a pronounced similarity, especially for shorter periods attributable to their functional relationship in equation (2). This is exemplified by the mapped *N. vaughani* (in Fig. 2) shown in the correspondence between fitted sinusoids for residuals in single rows and sums of chamberlet areas, as well as single rows and sums of chamber areas (Figs. 5, 6). As a result, further analyses concentrated on oscillatory patterns within the rows of chamberlet areas, since this approach is based on direct measurements and avoids the need to calculate residuals from a regression function, linearize data, or standardize residuals¹⁰.

Growth by time

The second step in analyzing fossil foraminiferal growth considers external factors causing changes in chamber volumes. Beyond genetic influences, environmental conditions must be considered. Consequently, chamber count should be converted to time (days) to evaluate the effects of ongoing (e.g. tides, seasons) or sudden temporal factors (e.g. tropical cyclones, tsunamis).

Cell growth in extant larger benthic foraminifera, measured by test volume V , can be described with various functions⁹. For *C. carpenteri* as one of two living representatives

belonging to larger foraminifera with radial tests, relationship between chamber number and days was assessed using the power function

$$n = 1.289t^{0.698} \quad (8)$$

based on laboratory cultures^{12,22} (Fig. 7). Trying to approximate natural conditions at the best, laboratory conditions can result in behaviors unrepresentative of the natural environment (e.g., *Peneroplis* and *Heterostegina*¹⁹; *Palaeonummulites*³⁸). This is also documented in the cell growth of *Cycloclypeus* gamonts with strong excentric positions of the nepionts and irregular radial growth in all cultured specimens²². Therefore, the “natural laboratory” approach¹⁹ was adopted for *Palaeonummulites venosus*¹⁷ and *Heterostegina depressa*¹⁶, facilitating the study of growth using the Michaelis-Menten function

$$n = L_{\infty}t/(k + t) \quad (9)$$

L_{∞} = upper limit, k = velocity constant describing time when $L_{\infty}/2$ arrived

The "natural laboratory" method could not be applied by sampling difficulties to *C. carpenteri*, the extant large benthic foraminifer with hyaline walls, a large nepiont, and circular, chamberlet-divided chambers comparable to the equatorial layer in lepidocyclinids. Laboratory cultures show that daily (t) chamber growth in *C. carpenteri* can better be described using the inverse Michaelis-Menten function

$$t = (277.91n/(126.95 - n)) \quad (10),$$

fitted to the laboratory data²² rather than an inverse power function (Fig. 7).

When modeling the cumulative chamber areas (y) for each species using the Gompertz function

$$y = ae^{-be^{-cn}} \quad (11)$$

the inflection point—where the chamber areas begin to decrease—can be determined at

$$n_{infl} = \ln(b) / c \quad (12)$$

This pattern occurs in many foraminifera with hyaline shells, as surpassing the inflection point leads to what are called ‘kummerformen’^{39,40}. Reproduction usually starts at or before this growth threshold, though it occasionally occurs after surpassing it⁹.

In the case of lepidocyclinids, with a maximum (mean) inflection point occurring at approximately 68 chambers, applying the Michaelis Menten Function (Eq. 9) corresponds to a lifespan of 320.6 days prior to reproduction.

Significance of growth measurements

Primarily it has been assumed that a single shell sector is representative of the overall specimen's growth. To prove this hypothesis, specimen 23Pa-SJ (867) from the Lower Miocene of Panama was analyzed using two opposing sectors (Fig. 8).

In each sector, the areas of five adjacent chamberlets were calculated for every chamber, starting with the first chamber that fully surrounds the inner chambers. This established a time consistent point for growth in all directions. In both sectors, the five chambers found between the chambers where measurements started and the nepiont did not surround their preceding chambers or the nepiont. Notably, these chambers are much smaller in sector 2 than in sector 1 due to the noncircular form of the nepiont (Fig. 8). In total, 42 chambers could be measured per sector.

During growth, chamberlet areas show strong oscillations in both sectors, with sharp peaks followed by strong drops, clearly expressed in sector 2 (Fig. 9A). To document the consistency of chamberlet areas within a single chamber, the coefficient of variation was used, which relates the standard deviation to the mean. This coefficient shows an opposite trend to the average chamberlet area: low coefficients indicate uniform chamber areas, while high coefficients point to greater variability. This relationship is supported by strong negative correlations between chamberlet areas and their coefficients of variation, clearly observed in sector 2 (Fig. 9A). High variability in chamberlet areas with low means arises from pronounced increases or decreases in the measurement series, depending on the measuring direction. Consequently, the absolute slope of the regression line was calculated and correlated with the coefficient of variation. In both sectors, this correlation is highly significant (Fig. 9B).

Both growth functions of chamberlet areas were modeled as sums of sinusoids using the matching pursuit algorithm³⁷, yielding a highly significant fit with eight sinusoids for both sectors (Fig. 10A). Although the frequency functions differ between sectors, decomposition into sinusoids produced comparable outcomes. Six of the eight sinusoids

exhibit similar periods in both sectors but vary in phase and amplitude (Fig. 10A). The concordance observed for the longest period, corresponding to 41.86 chambers, reflects the chamber number analyzed. For this sinusoid, a marked difference in amplitude with similar phases accounts for the substantial increase in sector 1. Sinusoids with a common period of 10.75 chambers share amplitudes of similar magnitude but display considerable differences in phase. Among the remaining sinusoids with shorter periods, only the one with a period of 4.70 chambers demonstrates both similar amplitudes and negative phases across sectors, while those with shorter periods possess comparable amplitudes yet exhibit opposing phases. These common sinusoids, along with two additional ones in each sector, contribute to pronounced discrepancies in fitting the distinct frequency distributions in both sectors through the sums of sinusoids.

Fitting both sectors' frequency distributions reduced to the six shared period sinusoids yielded strong results, with coefficients of determination of 74.6% explaining variance for sector 1 and 58.5% for sector 2 (Fig. 10B). These results support the assumption that a single sector's sinusoids can represent overall test growth.

Results

Oscillations in chamber numbers

Using sums of sinusoidal oscillations fitted to growth functions of chamberlet areas based on chamber numbers produced high significant results across all three species examined. This is documented for all specimens by graphical representations (Supplement 1), where, as well as in Fig. 10, the intersection points between observed functions shown as discrete events combined by lines and the sums of sinusoids as continuous functions indicate how closely the theoretical model matches the empirical data, quantifiable by correlation. Figure 11 demonstrates that modelling discrete growth patterns in the selected specimens of *L. ocalana*, *N. vaughani*, and *E. undosa* in Fig. 2 using summed sinusoid intersections, both represented as bars, effectively estimate growth and predict values beyond current limits.

Each specimen's initial sinusoid covers the total chamber number by its period, defining the oscillating function (Supplement 2). This can be assessed by the proportion of explained variance among all amplitudes. Furthermore, the minimum average chamberlet area can be identified within the chamber number sequence as Lag (n_{min}).

Analysis shows that 8 of 9 *L. ocalana* and 12 of 14 *N. vauhani* specimens exhibit a strong influence of the first sinusoid on overall oscillation, while this effect is less common in *E. undosa*, occurring in only 5 of 11 specimens. The impact of the first sinusoid on overall oscillation is quantified by its proportion (Supplement 2). Among the species examined, *L. ocalana* exhibits the highest mean proportion at 33.7%, which is significantly greater than the values for *N. vauhani* (24.2%) and *E. undosa* (15.5%). Additionally, the position of the minimum within the first significant sinusoid, determined by chamber number (n_{min}), also varies among the three species (Tab. 2). Specifically, *N. vauhani* demonstrates a mean minimum (n_{min}) at chamber number 13.5, which differs significantly from both *E. undosa* ($n_{min} = 21.5$) and *L. ocalana* ($n_{min} = 22.5$).

Linear regression analysis shows significant positive relationships between periods and amplitudes across all species (Fig. 12). *Lepidocyclina ocalana* and *N. vauhani* have similar intercepts, but the former species displays a steeper slope. While *L. ocalana* and *E. undosa* share comparable slopes, the latter possess a much higher intercept. *Nephrolepidina vauhani* differs from *E. undosa* in both having a lower intercept and a weaker slope (Fig.12).

As only specimens with over 30 chambers were considered, the search for significant sinusoids below the first was restricted to fewer than 30 chambers. 44 significant periods were found among 9 specimens of *L. ocalana*, 82 periods among 14 specimens of *N. vauhani*, and 62 periods among 11 specimens of *E. ocalana*. The frequency distributions of periods by chamber numbers were very similar across all three species. Rather than showing a continuous decline, these distributions exhibited distinct peaks. When the frequency distributions were broken down into normally distributed components, similar results emerged: period lengths clustered around 3, 5, and 9.5 chambers (Fig.13). Period concentrations at around 15 and 19 chambers were less prominent due to their low frequencies.

Further comparisons between the three species using analyses of variance and the following Tukey tests based on pairwise comparisons revealed agreement in the period concentrations with shared means of 9.44 and 15.25 chambers, attributed to their broad standard deviations (Tab. 3). The concentration near a mean of 5.17 chambers was almost in accord; however, there were significant differences between the peripheral members *L. ocalana* (5.87 chambers) and *E. undosa* (4.75 chambers; Tab. 3). For concentrations with a common mean of 2.99 chambers, significant differences existed, largely due to smaller standard deviations in all

species and a higher mean of 3.37 chambers in *L. ocalana* compared to the matchable 2.71 chambers in *N. vaughani* and 2.94 chambers in *E. undosa* (Fig.13, Tab. 3).

Oscillations in days

Oscillations in chamberlet areas by chamber number represent a static perspective of growth. To ensure an accurate dynamic analysis, it is essential to quantify the intervals between chamber constructions in terms of days. The timing of chamber construction is influenced by metabolism, with mass-specific metabolic rates determining growth velocities¹⁴. The Michaelis-Menten Function in equation (9), adapted from growth studies of the living *Cycloclopeus* and using the common inflection point of the Gompertz Function at 60 and 68 chambers, was applied for the three lepidocyclinid species.

Like growth functions related to chamber numbers, the primary sinusoidal oscillation represents the recorded lifespan of each specimen, rather than the actual lifespan of the specimen. The proportion of the first sinusoid's amplitude relative to all sinusoids mirrors what is seen in chamber numbers, again revealing significant differences among species, where *E. undosa* displays notably lower proportions (13.1%) than *N. vaughani* (23.2%) and *L. ocalana* (24.0%). Species differences in minimum area position for chamber numbers also appear in day lags, though values are higher; *N. vaughani* reaches the minimum area sooner (day 46) than *E. undosa* (day 67) and *L. ocalana* (day 70.7).

Regression analysis further reinforced differences in amplitudes between species, confirming significance in regressions (Fig.14). However, unlike regressions based on chamber numbers, the slopes do not significantly differ among the three species. The intercepts reveal that the relationships between amplitudes based on either chamber number or days are the same, with significantly higher values found for *E. undosa* (Fig.14).

Frequency distributions of periods below the largest sinusoid are limited to a 70-day range, comprising 58 sinusoids for *L. ocalana*, 93 for *N. vaughani*, and 72 for *E. undosa* (Supplement 2). Looking at frequency distributions based on days instead of chamber number, the results are more alike among the three species. Breaking the data into normally distributed components shows six for *L. ocalana* and *N. vaughani*, clustering near 7.7, 14, 27, 38, 45.5 and 60 days. The 45.5-day component is less pronounced in *E. undosa* (see Fig.15).

This close resemblance between species in the frequency distributions of periods was tested by analyses of variance. The distributions with shared means of 7.8, 13.9, 38.5 and 58.6 days

do not exhibit significant differences between species above the 5% error threshold. For the component with a common mean of 26.7 days, interspecies differences are not significant above 1% error probability (Tab. 4). Notably, *E. undosa* demonstrates a mean of 28.7 days, which is marginally higher significant compared to *L. ocalana* (25.4 days) and *N. vauhani* (26.1 days) (Fig.15).

Frequency distributions of the three species are mainly driven by components with mean periods of 7.8, 13.9, and 26.7 days, accounting for an average of 78.7% split into 20.6%, 39.2%, and 18.9%. The 7.8-day component has a common standard deviation of 0.99 days, while the longer periods (13.9 and 25.4 days) have wider deviations (3.53 and 2.93 days). The components with higher averages in periods are less important with mean proportions of 8.7% for 38.5 days and 6.5% for 58.6 days period.

Relations between oscillations

The apparent similarity in period frequency distributions among the three species, based on both chambers and days, can be evaluated using correlation analyses (Fig.16). The resulting correlation checking interdependence between periods based on chambers and days without regarding dependencies was highly significant, with probability of uncorrelation $p(H_0) = 2.08E-09$ (Fig.16A). To investigate the underlying causes of chamber periods in respect to growth, regression analysis showed that chamber periods depend significantly on the timing of chamber construction (Fig.16A). Consequently, environmental factors influencing these periods in days are responsible for the observed oscillations in chamberlet and chamber areas.

When dependency is focused on the three main periods making 80.6% in chambers and 78.7% in days, the regression through the origin remains highly significant (Fig.16B). By calculating the dependence of common chamber periods from the common day periods, correlation further increased (Fig.16C). Therefore, the average number of periods in chambers can be determined by multiplying the average number of periods in days by a factor of 0.359 (Fig.16C).

Discussion

The significant oscillations in the three lepidocyclinid species of 7.8, 13.9, 26.7, 38.5 and 58.6 days closely resemble the primary periodicities identified in laboratory cultures on

*Heterostegina depressa*²¹, from which significant peaks at 8.2, 13.8, 19.3, and 31.8 days are reported¹⁰. In tests involving *H. depressa* gamonts and schizonts obtained from nature during a single event, the average discernible periods derived using the power function based on laboratory cultures are 14.8, 28.6, 75.9, 129.8, and 176 days for samples from Okinawa, and 14.1, 27.8, 76.5, and 130.5 days for those from Hawaii¹⁵. Concurrent investigations on tests from laboratory cultures display analogous cycles of 14.8, 27.8, and 69.9 days¹⁵. Combined with the initial research on laboratory cultures²¹, these findings indicate that the tidal and lunar modulation of light intensity may be partially retained in laboratory settings through intrinsic, endogenous mechanisms.

For *P. venosus*, living specimens were studied using the “natural laboratory” approach, with monthly sampling over 15 months¹⁸. The significant periods averaged 7.7, 14.1, 30.4, 64.6, and 91.6 days, with the first three dominating, closely match the primary periods observed in the studied lepidocyclinids. *Palaeonummulites venosus* fits a Michaelis-Menten function reaching an expected upper limit L_{∞} of 109.4 chambers and a halftime k at 154.7 days. The mean inflection point of the Gompertz function is at 85.2 chambers, which results in an estimated average lifespan of 18 months¹⁷. This indicates that *P. venosus* has a significantly longer lifespan compared to the studied lepidocyclinids with L_{∞} of 126.95 chambers and k at 277.9 days (Eq. 10), whose estimated mean lifespan becomes roughly one year (11 months).

The closest counterpart to the growth cycles observed in lepidocyclinid species is *C. carpenteri*, the large benthic foraminifer with hyaline tests and radially arranged, chamberlet-divided chambers. Calculations for natural samples from Ishigaki Jima, Okinawa, identified four distinct oscillation periods of 13.3, 28.6, 48.3, and 62.7 days¹². Recalculation of the first three sinusoids for the Okinawa specimens¹² shifted the main periods to means of 8.9, 15.4, and 25.7 days, with standard deviations of 0.96, 2.24, and 0.82, respectively. The mean lifespan at the 68-chamber inflection point is 42 weeks (294 days)²².

Regarding chamber construction resulting from biomass growth, these cycles do not act strictly at the time interval of chamber formation. Instead, they represent the cumulative influence on biomass exerted over the interval between the formation of successive chamber walls. Thus, chamber growth can be divided into a biomass-growth phase and a chamber-formation phase. The latter, an immobile phase, begins with anchoring of the outer protective envelope, continues with chamber formation by the globopodium, and ends with biomineralization of the chamber walls^{41,42}. Complete fixation of chamber walls takes 6 to 12 hours in the smaller hyaline foraminifer *Ammonia beccarii*^{41,43}, < 24 hours in the symbiont-

bearing foraminifer *Amphistegina lessonii*⁴² and 24 hours in *H. depressa*^{44,45}. After this immobile phase, the organism returns to a mobile phase of biomass growth that lasts for a cell-size-dependent interval and can be approximated by the Michaelis-Menten or similar chamber-building functions⁹. During this interval, environmental factors influence biomass growth and are recorded at the end of the mobile phase in the chamber volume enclosed by the wall.

In *C. carpenteri*, chamber building begins after the two-chambered young schizonts or gamonts are released from the pseudopodial network of the mother individual into the surrounding seawater. This process takes 66.5 hours²². The third chamber, which completes the nepiont, is formed within 24 hours, corresponding to the time required for chamber construction and indicating that no fresh produced biomass was used; instead, the remaining parental protoplasm was partitioned. The next day is devoted to biomass growth, and chamber construction resumes on the following day. The rate of chamber formation is nearly three chambers per week during the first weeks, decreases to two chambers per week until week 17, and then declines to one chamber per week until week 24²². After that, the average rate falls below one chamber per week and continues at that level until week 46.¹²

Using the power function in equation (8) and including the day after nepiont completion, the daily increase is given in Tab. 5. This function predicts the formation of five chambers within the first week, which is considerably higher than reported²². Thereafter, chamber numbers align with the generalized prediction, and *C. carpenteri* reaches a mean inflection point of 68 chambers on the Gompertz curve after 294.4 days, or about 10 months, corresponding to a final rate of 0.89 chambers per week.

Based on the Michaelis-Menten function in Eq. 10, which is also used to model chamber-building rates in the lepidocyclinid species, the weekly chamber-building rates closely match observations from cultured *C. carpenteri*, beginning with three chambers in the first weeks²² (Tab. 5). *Cyclocypeus carpenteri* completes growth after 320.6 days, or about 11 months (Tab. 5), whereas reproduction in cultured specimens began after 10.5 months²².

Nephrolepidina vaughani, which shares a Gompertz inflection point of 68 chambers with *C. carpenteri*, also completed growth after about 11 months. In contrast, *L. ocalana* and *E. undosa*, with similar inflection points at 60 chambers, completed growth after 250 days, or about eight months.

Following these characteristics, chamber construction proceeds under stable environmental conditions at rates that can be modeled by the Michaelis-Menten and related functions⁹.

Changes to a differing stable environmental condition modify the function parameters leading to an increase or decrease of the chamber building rate^{21,38}.

The dominant common periods of 7.8, 13.9, and 26.7 days of the three investigated lepidocyclinid species correspond to the 7.4-day (weekly), 14.8-day (semilunar), and 29.5-day (lunar) cycles. It appears that variations in light intensity caused by the moon's gravity and rotation combined with its position to the sun are the primary factors contributing to the observed peaks in lepidocyclinid growth. In living symbiont-bearing larger foraminifera, which depend to varying extents on organic carbon from their symbiotic algae, light serves as the primary factor governing cell growth. Like modern nummulitids with similar test construction (*Cycloclypeus*, *Heterocyclus*), extinct lepidocyclinids seem to depend solely on organic carbon waste produced by their symbiotic microalgae, as their porous hyaline tests lack openings for the uptake of larger organic particles, thus working as autotrophic organisms. In combination with symbiotic bacteria, they can be regarded as holobionts^{46,47,48}. All living symbiont-bearing larger foraminifera with hyaline walls, such as Amphisteginidae, Calcarinidae, and Nummulitidae, utilize Bacillariophyta (diatoms) as endosymbionts, enabling them to occupy the deepest regions of the euphotic zone. Thus, diatoms as photosynthesizing symbionts can also be expected for the lepidocyclinids. Acting as endosymbionts within nummulitids, diatoms show peak photosynthetic activity at relatively low light levels, specifically around 110 PAR (Photosynthetically Active Radiation)⁴⁹. Variations in PAR levels are affected through seasonal changes in surface irradiation, water transparency and cloudy weather. For *P. venosus* the average PAR values¹⁸ are 22.5 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ and 14 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ for *C. carpenteri*⁴⁹. The corresponding distribution optima are located at 45 m for *P. venosus* and 80 m for *C. carpenteri*⁵⁰. A decrease in sea level of 1.5 m during neap tide results in an increase in PAR ranging from 5 to 20 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$.¹⁸ This moderate rise in PAR leads to a significant boost in photosynthetic activity, as shown by a strong increase in the relative Electron Transport Rate (rETR) response curve between 0 and 120 PAR¹⁸. These results help explain how circasemilunar (spring–neap tide) cycles affect symbiont-bearing larger foraminifera living in the middle and lower part of the euphotic zone. Based on substrate preference and test morphology, the fossil lepidocyclinids with lenticular tests are thought to have occupied mid-ramp environments (~30 to 60 m), whereas larger, flatter species appear to have inhabited the outer ramp (60 to 100 m)⁵¹. This corresponds with the depth distribution observed for the lenticular *P. venosus* and the flat *C. carpenteri* in relation to light availability⁵², further supporting the significant impact of circasemilunar cycles on extinct species.

There are two principal explanations for circalunar rhythms observed in marine organisms. The first involves the effect of moonlight during the full-moon phase, mediated by specialized receptors, and is referred to as stimulus-controlled rhythms⁵³. The second explanation pertains to clock-controlled mechanisms, whereby an endogenous oscillator regulates these rhythms⁵³. In diatoms as endosymbionts in hyaline larger foraminifera, the cryptochrome gene family is mainly implicated in the absorption of blue light, either directly through moonlight influencing the circalunar rhythm or indirectly via modulation of an internal clock⁵⁴. The latter explanation appears to be more probable, as circalunar rhythm has been observed in laboratory cultures even without the direct influence of moonlight^{10,15,21}. The second explanation appears probable for the lepidocyclinid species since all of them possess the circalunar rhythm with similar intensities, regardless of their geological age. This suggests that the rhythm is an inherited evolutionary trait, stimulated by the factual changes in moonlight.

The main peak with the smallest standard deviation corresponds to the circaseptan oscillation (7.4 days). Because no known environmental weekly cycle accounts for it, this rhythm seems to be internally generated. Coral experiments show that it persists regardless of the day of the week, thus excluding external weekly events as its cause⁵⁵. Circaseptan oscillations seem to reflect an endogenous biological timing mechanism, possibly modulated by activity of the cell nucleus together with environmental stimulus⁵⁵ and/or by regulation for metabolism⁵⁶. In all cases, they are not driven directly by external weekly events. Such cycles are extremely rarely reported in marine organisms and therefore cannot explain their importance in *H. depressa* and *C. carpentieri* laboratory cultures¹⁰ and in natural grown *P. venosus* populations¹⁸.

Lower-proportion sinusoids have mean periods of 38.5 days (8.7%) and 58.6 days (6.5%), yet they occur in all species investigated. Because of their heterogeneity, interpreting these oscillations is difficult. A plausible explanation is that they reflect Madden–Julian oscillations (MJO), a large-scale coupling of atmospheric circulation and tropical deep convection^{57,58}. In tropical oceans, the MJO alternates between phases of heavy rainfall and dry conditions on timescales of 30 to 90 days^{59,60}. It typically develops today over the Indian Ocean, where very warm sea-surface temperatures and high humidity promote low-level wind convergence and strong upward motion, forming large thunderstorm clusters. In the upper troposphere, this rising air diverges, while air farther east sinks, warms, and dries, suppressing cloud formation. The mechanism driving the MJO's eastward propagation is not fully understood, and different explanations are given^{59,60}. Primarily it is thought to involve Kelvin waves that promote eastward movement and Rossby waves that oppose it. As the MJO moves from the warm

Indian Ocean and Indo-Pacific into the cooler eastern Pacific, its moist convection weakens strongly. However, the associated atmospheric pressure wave can continue rapidly across South America and the Atlantic as a dry Kelvin wave. When it reaches the Indian Ocean again, it can trigger renewed air ascent and initiate the next MJO cycle. Interference between differences in propagation have been attributed to two modes: a roughly 45-day “fast MJO” and a 70-day “slow MJO”⁶¹.

Using chamber-building rates from cultured *C. carpenteri* to interpret fossil lepidocyclinids is problematic because the fossil species hosted symbiotic microalgae with different light adaptations. In cultures²², *C. carpenteri* was exposed continuously to 6.4–7.7 PAR, close to the reported 5.0 PAR optimum⁴⁹. Even small departures from this optimum reduce rETR, with stronger effects under lower than under higher PAR^{18,49}. Consequently, chamber building rates decline, especially when PAR falls below the optimum.

Because the identity and light requirements of the symbiotic microalgae remain unknown, lepidocyclinids may have built chambers more slowly than *C. carpenteri*. While *C. carpenteri* reaches its optimum at 5.0 PAR, the symbionts of lepidocyclinids may have had different light optima. This difference could have reduced chamber-building rates without altering the Gompertz growth parameters, including the upper limit of 126.9 chambers and the inflection point at 68 chambers. Doubling the velocity constant k in Eq. 10 also doubles the sinusoid means and standard deviations (Tab. 6). The shared means and standard deviations confirmed by analyses of variance are 15.6 days (20.6%), 27.8 days (39.2%), and 53.4 days (18.9%), together accounting for 78.7% of the total oscillations.

At this lower chamber-building rate, *L. ocalana* and *E. undosa*, with Gompertz inflection points at 59.8 and 60.5 days, completed chamber building after 497 days, equivalent to 16.5 months (1 year and 4.5 months; Tab. 5). The larger *N. vauhani*, with an inflection point at 68 days, reached the end of growth after 641 days, or about 21 months (1 year and 9 months; Tab. 5). Comparable longevity ranging around 1.5 years has been reported for the extant species *P. venosus*^{20,17,62} and *H. depressa*^{16,20,21}.

Using the lowered chamber-building rate, the common sinusoids are easier to interpret physically. The first, pronounced sinusoid has a mean period of 15.6 days and a small standard deviation, closely matching the circasemilunar (neap–spring tide) cycle of 14.77 days. The second common sinusoid, with a mean period of 27.8 days and broader variance, corresponds to the circalunar cycle of 29.5 days, equivalent to a synodic month. The third

sinusoid has a common mean of 53.0 days and a standard deviation of 5.84, thus fully spanning the 30 to 90 days range of the Madden–Julian Oscillation (MJO).

This raises the question of whether the MJO, inferred from the common chamber-building rates, also affected the Caribbean in the Late Eocene and Early Miocene, when these lepidocyclinid species lived, although it is blocked today in the eastern Pacific by the Panama Land Bridge. In the Late Eocene, broad marine connections linked the Indian Ocean and the Atlantic through the Tethys Ocean, where Europa remained as an archipelago⁶³. Warm surface waters could flow into the Atlantic as a broad front. At the same time, the wide seaway between the Caribbean and the eastern Pacific⁶⁴ may have allowed these waters to warm the eastern Pacific, thereby weakening the present-day barrier to MJO propagation. A similar configuration existed in the Early Miocene, when circulation from the Indian Ocean to the Atlantic remained open⁶³ and the Caribbean–East Pacific connection was still broad⁶⁴. This continuous belt of warm water may therefore have favored MJO development around the equator, consistent with the significant oscillations recorded in lepidocyclinid shells from the Caribbean Late Eocene and Late Oligocene/Early Miocene.

Conclusion

Growth oscillations in chamber volumes were identified in three lepidocyclinid species, one from the Late Eocene of Cuba and two from the Oligocene to Early Miocene of Panama and Mexico. In these radial foraminifera, the circularly arranged equatorial-layer chambers are subdivided into chamberlets that remain nearly constant in area and height from the embryonal apparatus to the test margin. This allows chamberlet-volume oscillations to be measured as deviations from mean area, even within restricted test sectors. Oscillations along chamber-number sequences were decomposed into sums of sinusoids using power spectral analyses. The resulting frequency distributions are highly similar among the species and, after decomposition into normally distributed components, yield common periods with means of 3.0, 5.2, 9.4, 15.3, and 19.4 chambers in decreasing abundance.

To assess the influence of continuous or abrupt environmental factors, chamber numbers were converted into time (days) using the chamber-building rate of *Cycloclypeus carpentieri*, one of the two living representatives with hyaline walls and radially arranged, chamberlet-divided chambers. This rate was derived from laboratory growth studies by applying the Michaelis-Menten function, with an upper limit of 127 chambers and a half-life of 278 days. Similar

oscillation-frequency distributions among the lepidocyclinid species yielded dominant common mean periods of 7.8, 13.9, and 26.7 days, along with weaker periods of 38.5, 46.1, and 58.6 days. These time-based periods correlate strongly with those derived from chamber numbers. Halving the chamber-building rate shifts the three dominant sinusoidal peaks to 15.6, 27.8, and 53.0 days. The first two can be interpreted as spring-neap tide and synodic lunar-month cycles, whereas the third peak with broader variance corresponds to the atmospherically driven Madden-Julian Oscillation.

This study provides the first evidence from marine organisms for circasemilunar (spring-neap tide) and circalunar (synodic lunar-month) cycles in the geological past. The third oscillations around 50 days, rarely observed in recent symbiont-bearing foraminifera from the subtropical West Pacific, may reflect the Madden-Julian Oscillation (MJO), as suggested by their large variances. During the Late Paleogene and Early Neogene, open Atlantic-Pacific seaways allowed warm Caribbean waters to enter the eastern Pacific, limiting equatorial cooling and reducing MJO attenuation. A comparable configuration connected the Indian and Atlantic oceans through the wide Neotethys seaway in the Paleogene and through open connections between the Indo-Pacific and the Mediterranean Sea in the Early Neogene. Under these conditions, the MJO may have propagated eastward around the equator at an average speed of 5 m s^{-1} , without major obstruction or weakening, possibly with wider latitudinal extension than the recent between 6.8°N and 6.8°S ^{59,60} thereby influencing paleo-weather in both hemispheres.

Thus, growth oscillations in fossil larger Foraminifera with hyaline test walls and radially arranged, chamberlet-divided chambers provide a means of detecting not only calendar-band frequencies but also past MJO signals. In addition to Lepidocyclinidae, which appeared in the Americas during the middle Eocene and persisted in the Late Miocene in Southeast Asia^{65,66}, Orthophragminidae may also be suitable for such analyses. This group originated in the Late Paleocene, spread into the Mediterranean, and disappeared there by the Late Eocene⁶⁵.

Because orthophragminids also have chamberlet-divided radial chambers, their growth patterns can be tested for oscillations using the same approach described above. Since both groups occur in the Caribbean and Mediterranean, and except orthophragminids in the Indo-Pacific regions, published thin sections can be examined for calendar-band oscillations and large-scale atmospheric convection. Placed in stratigraphic and paleogeographic context, these records may help identify large-scale atmospheric oscillations at every Cenozoic stage and paleogeographic position and clarify their influence on global paleoclimate.

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Author Contributions

J.H. wrote the manuscript, performed the statistical analyses, and prepared the figures and tables. A.T.S. conducted the sampling, prepared thin sections, took photographs, and performed the measurements. S.Ć. assisted with sampling, prepared figures, and carried out the stratigraphic determinations. All authors reviewed the manuscript.

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Table 1. Geographical location and stratigraphical position of the lepidocyclinid species

Site	Section name	Section label	Latitude	Longitude	Formation
Panama	San Juan	23PA-SJ	9° 14' 04" N	79° 37' 52" W	Caimito
Mexico	Salto de Agua	23ME-SA	17° 55' 75" N	92° 35' 12" W	Mompuyil
Cuba	Spot sample	P-559	22° 30' 00" N	79° 46' 00" W	Jicotea
Cuba	Spot sample	P-562	22° 30' 00" N	79° 46' 00" W	Jicotea
Cuba	Loma Vigía	CA-216	21° 59' 11" N	79° 16' 36" W	Blanco

Table 2. Comparison of species based on the average percentage of total amplitudes accounted for by the first significant sinusoid, as well as the location of its minimum value (Lag), both evaluated using Analysis of Variance.

	<i>Lepidocyclina ocalana</i>			<i>Nephrolepidina vauhani</i>			<i>Eulepidina undosa</i>		
	Number	Mean	Stdev	Number	Mean	Stdev	Number	Mean	Stdev
%	9	33.7	10.59	14	24.2	11.98	11	15.5	7.14
Lag	9	22.5	2.43	14	13.5	5.65	11	21.5	8.61

ANOVA Proportion %

Mean = 23.89

 $F_0 = 7.781$ $p(H_0) = 0.0011$

ANOVA Lag

Mean = 18.47

 $F_0 = 18.47$ $p(H_0) = 0.0012$

Table 3. Comparison of species using their component distributions of periods based on chamber numbers. The analysis after ANOVA used Tukey's q-Test for pairwise differences when variances were homogeneous; if variances were not homogeneous, pairwise T-tests with unequal variances were used. Shaded areas indicate significant differences.

common mean 2.99	<i>L. ocalana</i> 3.37	<i>N. vauhani</i> 2.71	<i>E. undosa</i> 2.94
<i>Lepidocyclina ocalana</i>		t = 3.739	t = 2.122
<i>Nephrolepidina vauhani</i>	p(H ₀) = 0.0007		t = 1.572
<i>Eulepidina undosa</i>	p(H ₀) = 0.0445	p(H ₀) = 0.1160	
common mean 5.17	<i>L. ocalana</i> 5.87	<i>N. vauhani</i> 5.34	<i>E. undosa</i> 4.75
<i>Lepidocyclina ocalana</i>		t = 1.131	t = 2.823
<i>Nephrolepidina vauhani</i>	p(H ₀) = 0.2068		t = 1.989
<i>Eulepidina undosa</i>	p(H ₀) = 0.0111	p(H ₀) = 0.0573	
common mean 9.44	<i>L. ocalana</i> 9.54	<i>N. vauhani</i> 10.18	<i>E. undosa</i> 8.80
<i>Lepidocyclina ocalana</i>		t = 0.852	t = 0.949
<i>Nephrolepidina vauhani</i>	p(H ₀) = 0.2687		t = 1.979
<i>Eulepidina undosa</i>	p(H ₀) = 0.2475	p(H ₀) = 0.0597	
common mean 15.25	<i>L. ocalana</i> 14.36	<i>N. vauhani</i> 14.32	<i>E. undosa</i> 16.04
<i>Lepidocyclina ocalana</i>		t = 0.041	t = 1.818
<i>Nephrolepidina vauhani</i>	p(H ₀) = 0.376		t = 1.872
<i>Eulepidina undosa</i>	p(H ₀) = 0.0808	p(H ₀) = 0.0754	
common mean 19.39	<i>L. ocalana</i> 19.95	<i>N. vauhani</i> 18.01	<i>E. undosa</i> 23.65
<i>Lepidocyclina ocalana</i>		q = 3.414	q = 5.242
<i>Nephrolepidina vauhani</i>	p(H ₀) = 0.0465		q = 9.969
<i>Eulepidina undosa</i>	p(H ₀) = 0.0689	p(H ₀) = 0.0002	

Table 4. Comparison of species using their component distributions of periods based on days. The analyses after ANOVA used Tukey's q-Test for pairwise differences when variances were homogeneous; if variances were not homogeneous, pairwise T-tests with unequal variances were applied. Shaded areas indicate significant differences.

common mean 7.77	<i>L. ocalana</i> 7.79	<i>N. vauhani</i> 7.85	<i>E. undosa</i> 7.79
<i>Lepidocyclina ocalana</i>		t = 0.151	t = 0.415
<i>Nephrolepidina vauhani</i>	p(H ₀) = 0.3908		t = 0.581
<i>Eulepidina undosa</i>	p(H ₀) = 0.3600	p(H ₀) = 0.3330	
common mean 13.93	<i>L. ocalana</i> 13.12	<i>N. vauhani</i> 13.78	<i>E. undosa</i> 14.55
<i>Lepidocyclina ocalana</i>		q = 1.216	q = 1.986
<i>Nephrolepidina vauhani</i>	p(H ₀) = 0.8730		q = 0.851
<i>Eulepidina undosa</i>	p(H ₀) = 0.1669	p(H ₀) = 0.5499	
common mean 26.66	<i>L. ocalana</i> 25.37	<i>N. vauhani</i> 26.08	<i>E. undosa</i> 28.74
<i>Lepidocyclina ocalana</i>		q = 0.859	q = 3.867
<i>Nephrolepidina vauhani</i>	p(H ₀) = 0.5493		q = 3.225
<i>Eulepidina undosa</i>	p(H ₀) = 0.0124	p(H ₀) = 0.0318	
common mean 38.49	<i>L. ocalana</i> 36.22	<i>N. vauhani</i> 39.25	<i>E. undosa</i> 39.05
<i>Lepidocyclina ocalana</i>		t = 1.929	t = 2.717
<i>Nephrolepidina vauhani</i>	p(H ₀) = 0.0693		t = 0.154
<i>Eulepidina undosa</i>	p(H ₀) = 0.0204	p(H ₀) = 0.3850	
common mean 58.64	<i>L. ocalana</i> 59.08	<i>N. vauhani</i> 61.16	<i>E. undosa</i> 56.97
<i>Lepidocyclina ocalana</i>		t = 0.870	t = 0.683
<i>Nephrolepidina vauhani</i>	p(H ₀) = 0.2431		q = 1.608
<i>Eulepidina undosa</i>	p(H ₀) = 0.2973	p(H ₀) = 0.1095	

Table 5. Chamber-building rates of *Cyclocypeus carpenteri* in laboratory cultures, modeled with a power function and two Michaelis-Menten functions; the second doubles the time intervals of the first. Shaded areas mark weeks. Inflection points in growth are marked for *C. carpenteri* and the lepidocyclinid species.

Power Function		Michaelis Menten		Michaelis Menten	
chamber = 1.289 day ^{0.689}		chamber = 277.91 / (126.95 + day)		chamber = 555.82 / (126.95 + day)	
chamber	day	chamber	day	chamber	day
1	1.7	1	2.2	1	4.4
2	2.9	2	4.4	2	8.8
3	4.4	3	6.7	3	13.4
4	6.0	4	9.0	4	18.0
5	8.0	5	11.4	5	22.8
6	10.1	6	13.8	6	27.6
7	12.3	7	16.2	7	32.4
8	14.7	8	18.7	8	37.4
9	17.2	9	21.2	9	42.4
10	19.8	10	23.8	10	47.6
11	22.6	11	26.4	11	52.8
12	25.4	12	29.0	12	58.0
13	28.4	13	31.7	13	63.4
14	31.5	14	34.4	14	68.8
15	34.7	15	37.3	15	74.6
.	.	.	.	.	.
.	.	.	.	.	.
.	.	.	.	.	.
59	240.4	59	241.3	59	482.6
60	246.2	60	249.1	60	498.2
61	252.1	61	257.1	61	514.2
62	285.0	62	265.3	62	530.6
63	264.0	63	273.8	63	547.6
64	270.0	64	282.5	64	565.0
65	276.0	65	291.6	65	583.2
66	282.1	66	300.9	66	601.8
67	288.2	67	310.6	67	621.2
68	294.4	68	320.6	68	641.2

*Cyclocyp.
carpenteri*

*E. undosa
L. ocalana*

*Nephrolep.
vaughani*

Table 6. Parameters of the significant common periods in the three lepidocyclinid species after doubling the time intervals in the Michaelis-Menten function.

<i>Eulepidina undosa</i>			<i>Nephrolepidina vauhani</i>			<i>Lepidocyclina ocalana</i>		
Prob	Mean	Stdev	Prob	Mean	Stdev	Prob	Mean	Stdev
0.178	15.3	1.62	0.229	15.7	2.24	0.211	15.6	2.07
0.426	29.1	7.32	0.349	28.0	7.20	0.400	26.2	6.69
0.181	57.5	5.97	0.176	52.1	6.18	0.211	50.7	5.40
0.113	78.1	3.55	0.078	78.4	5.65	0.071	72.4	2.71
0	0	0	0.055	94.0	4.18	0.053	89.3	4.08
0.102	113.9	9.144	0.041	122.3	5.16	0.054	118.2	7.64

Figure 1. Location of sections and sampling spots

Figure 2. Representatives of lepidocyclinid species: *Lepidocyclina ocalana* (Ind. Ca-126-E3(12A)), *Nephrolepidina vauhani* (Ind. 23Pa-SJ (875)), *Eulepidina undosa* (Ind. 23ME-SA (885)). Axial sections are from different individuals than the equatorial sections shown.

Figure 3. Measuring four consecutive chamberlet areas in chamber 23 using sector angle α and radii r from the nepiont center of specimen 23Pa-SJ (862).

Figure 4. Growth histograms for specimens shown in Fig. 1. **(A)** Chamberlet area histograms with red lines marking means. **(B)** Chamber area histograms with red regression lines.

Figure 5 Regression analysis of the mean chamberlet area, its cumulative values, and the chamber and cell areas of *N. vauhani* specimen 23Pa-SJ (875) with their adjusted residuals.

Figure 6. Lomb periodograms highlighting significant peaks from Fig. 5 residuals.

Figure 7. Growth of *Cyclocypeus carpenteri* in laboratory cultures²², based on mean chamber numbers, fitted by Power and Michaelis-Menten function.

Figure 8. Measurements of five consecutive chamberlet areas within chambers located in opposing sectors of *N. vauhani* specimen 23Pa-SJ (867).

Figure 9 **(A)** Sector comparison by frequency distributions of mean chamberlet areas and coefficient of variation during growth. **(B)** Sector comparison using coefficient of variation and regression slope of chamberlet areas within a single chamber during growth.

Figure 10. **(A)** Comparing sectors by fitting frequency distributions of mean chamberlet areas using sinusoidal oscillations. **(B)** Fitting mean chamberlet areas from both sectors with shared sinusoidal oscillations.

Figure 11. Mean chamberlet growth for specimens in Fig. 1 fitted with summed sinusoid curves, enabling growth prediction.

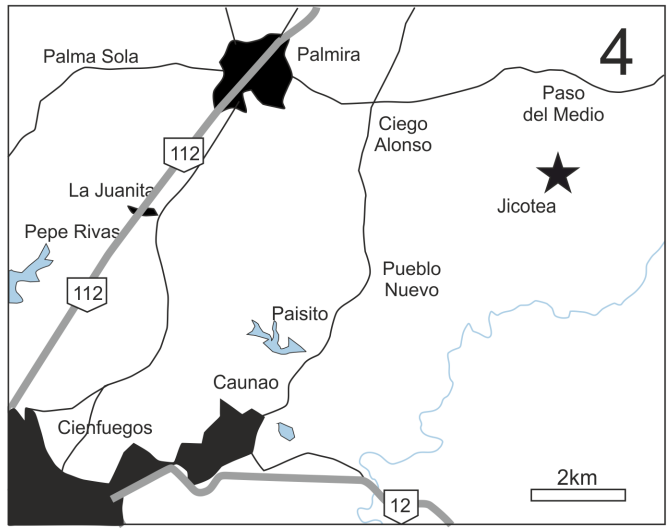
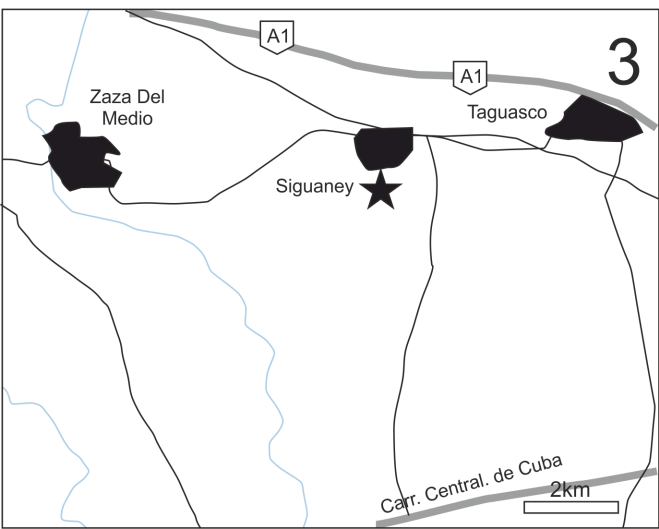
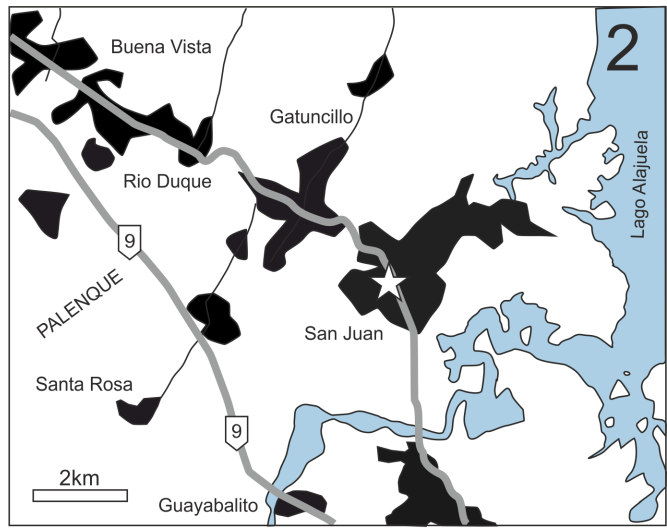
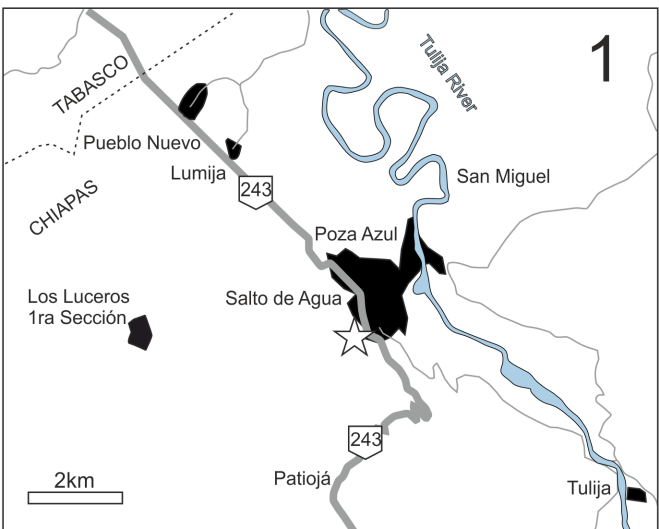
Figure 12. Linear regressions of amplitude on chamber period, with 95% confidence limits for the regression line and forecast. Intercepts and slopes between species were compared using T-Tests.

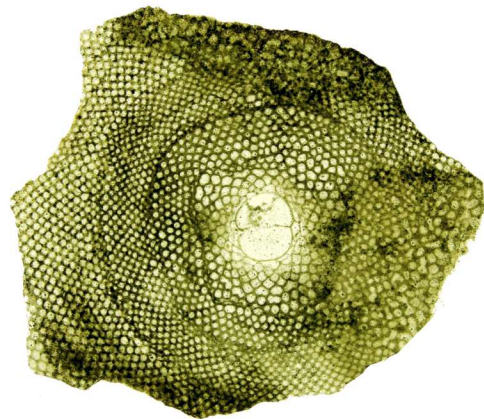
Figure 13. Frequency distributions of periods in chamber numbers and their normal distribution components.

Figure 14. Linear regressions of amplitude on period in days, with 95% confidence limits for the forecast. Intercepts and slopes between species were compared using t-tests.

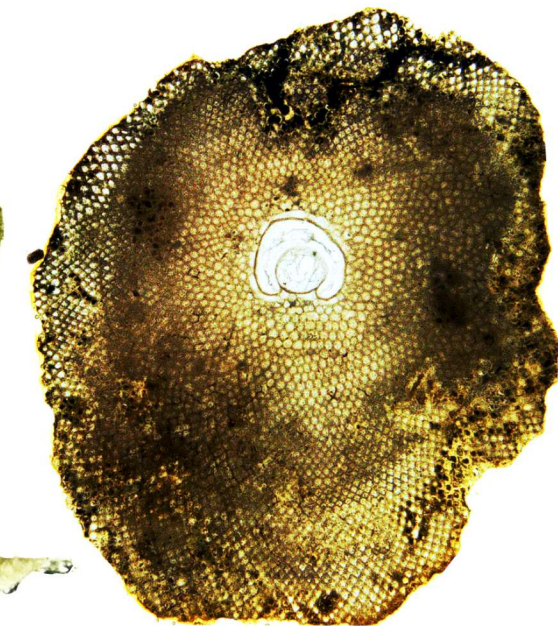
Figure 15. Frequency distributions of periods in days and their normal distribution components.

Figure 16. Relationships between mean periods in chamber numbers and days. **(A)** Correlation determined by RMA (reduced major axis), and the dependence of chamber periods on periods in days determined by regression line passing through the origin. **(B)** Relationship between the first dominant mean periods in chamber numbers and in days using regression line through the origin. **(C)** Dependence of the initial common periods in chamber numbers and periods in days depicted by regression line passing through the origin.





Lepidocyclina ocalana



Nephrolepidina vauhani



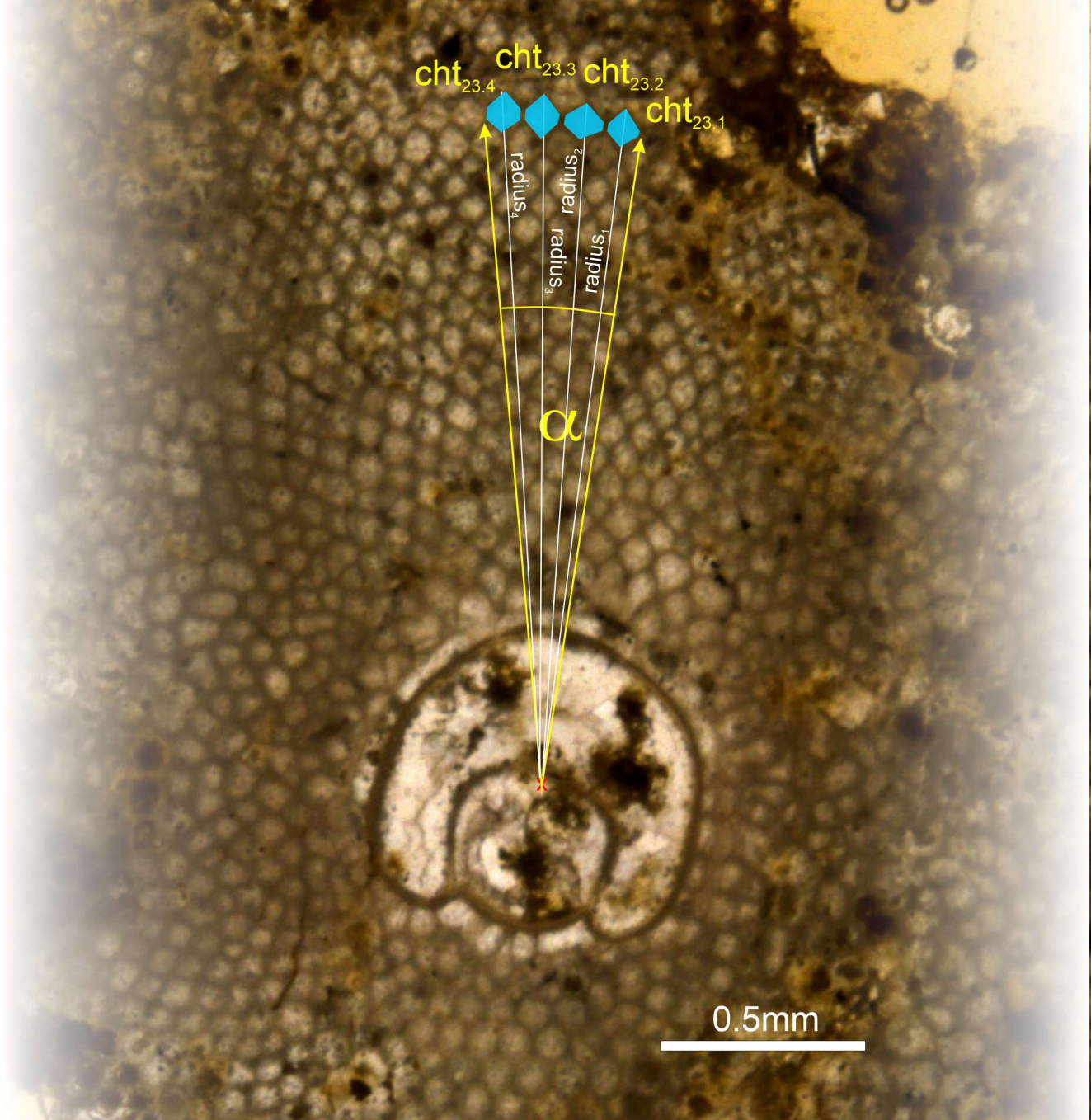
Eulepidina undosa

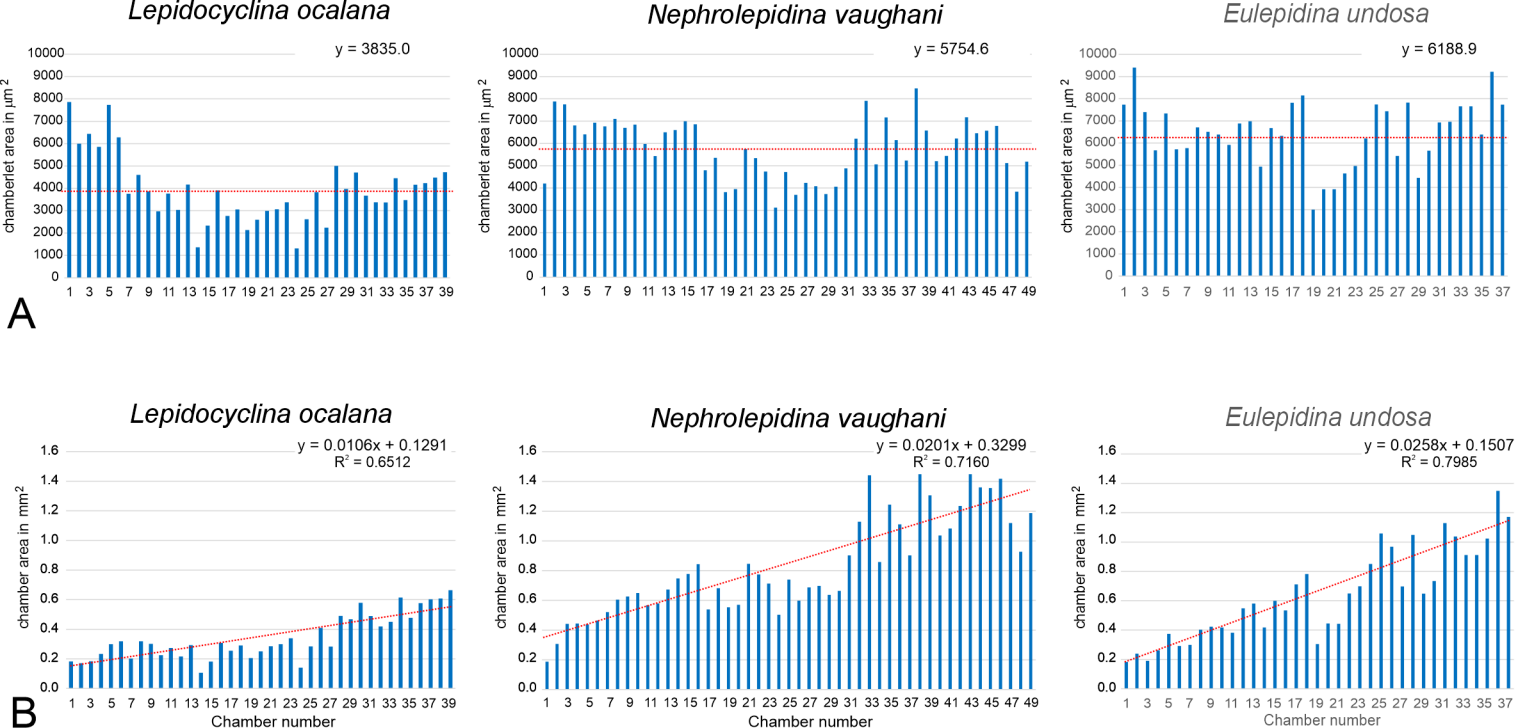
cht_{23.4} cht_{23.3} cht_{23.2} cht_{23.1}

radius₄
radius₂
radius₁

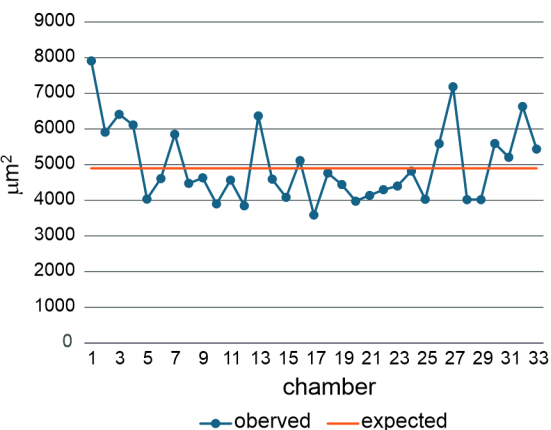
α

0.5mm

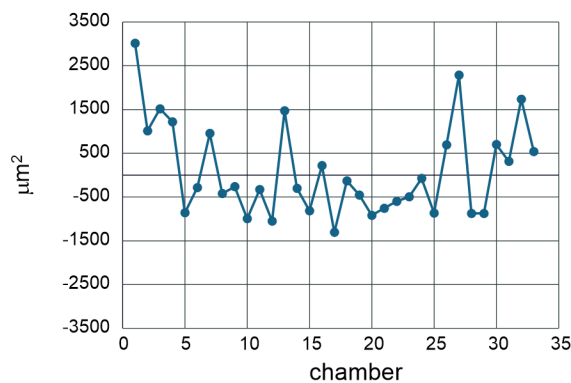




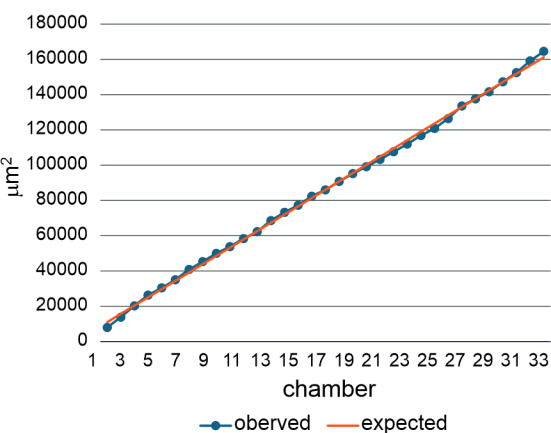
mean chamberlet area



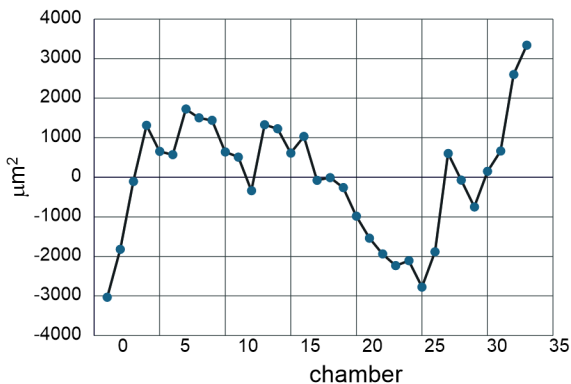
residual



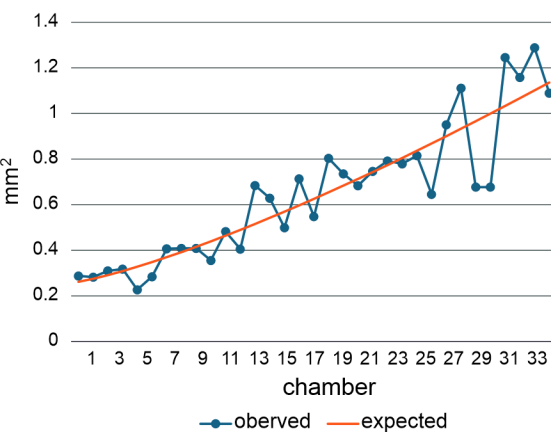
sum of mean chamberlet area



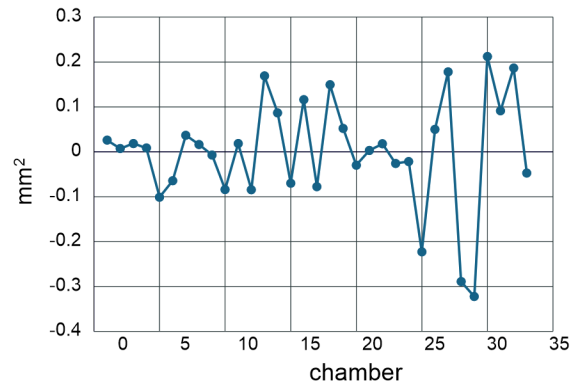
residual



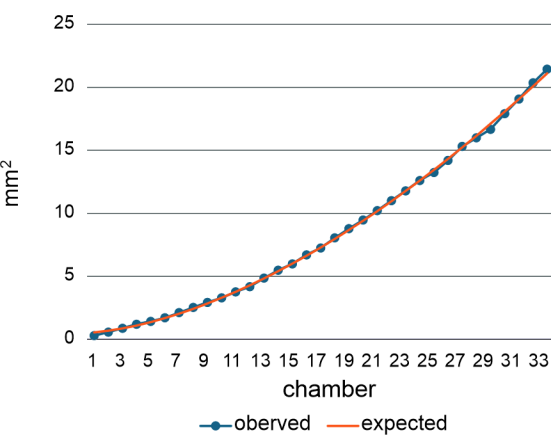
chamber area



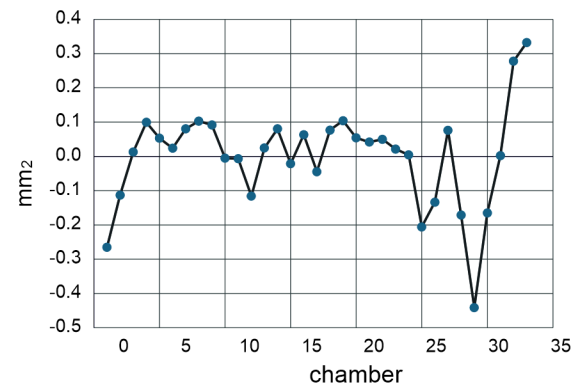
residual



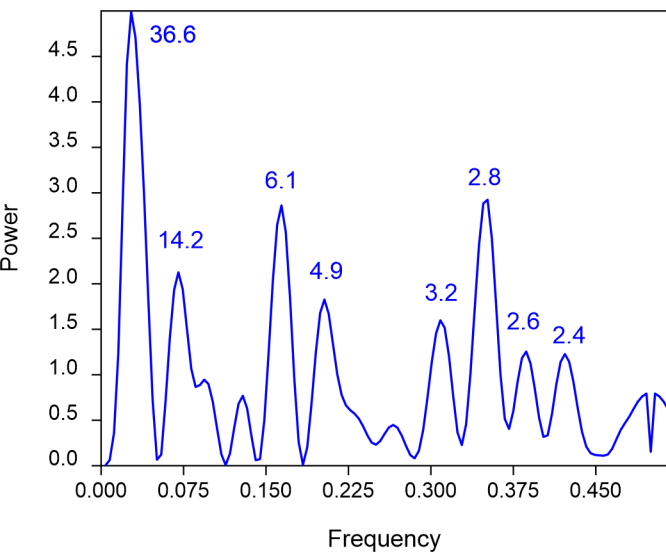
cell area



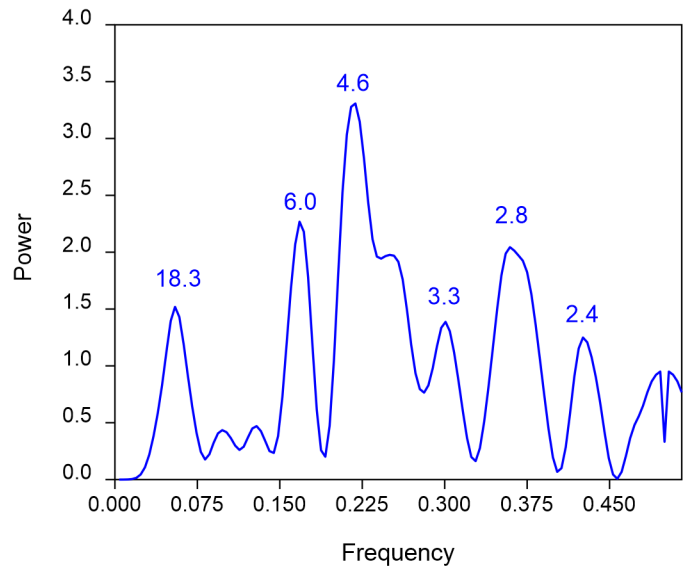
residual



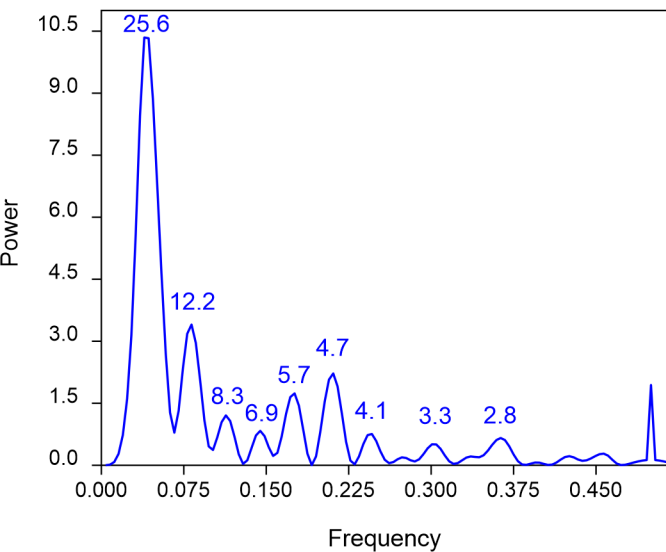
chamberlet areas



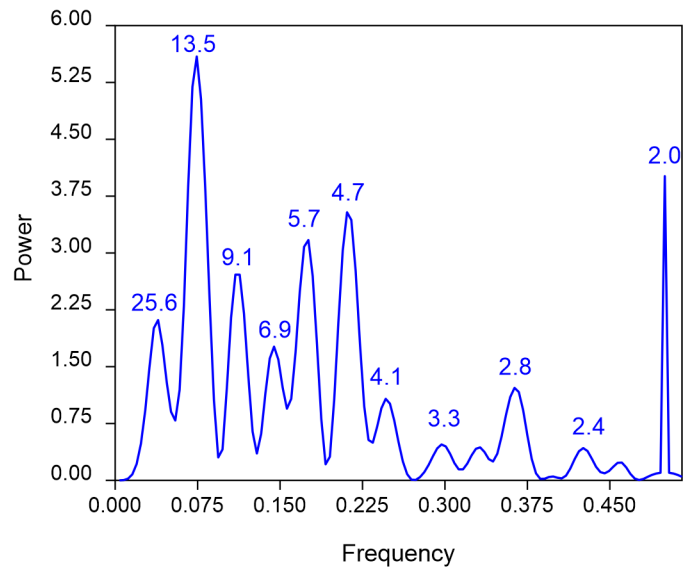
sum of chamberlet areas



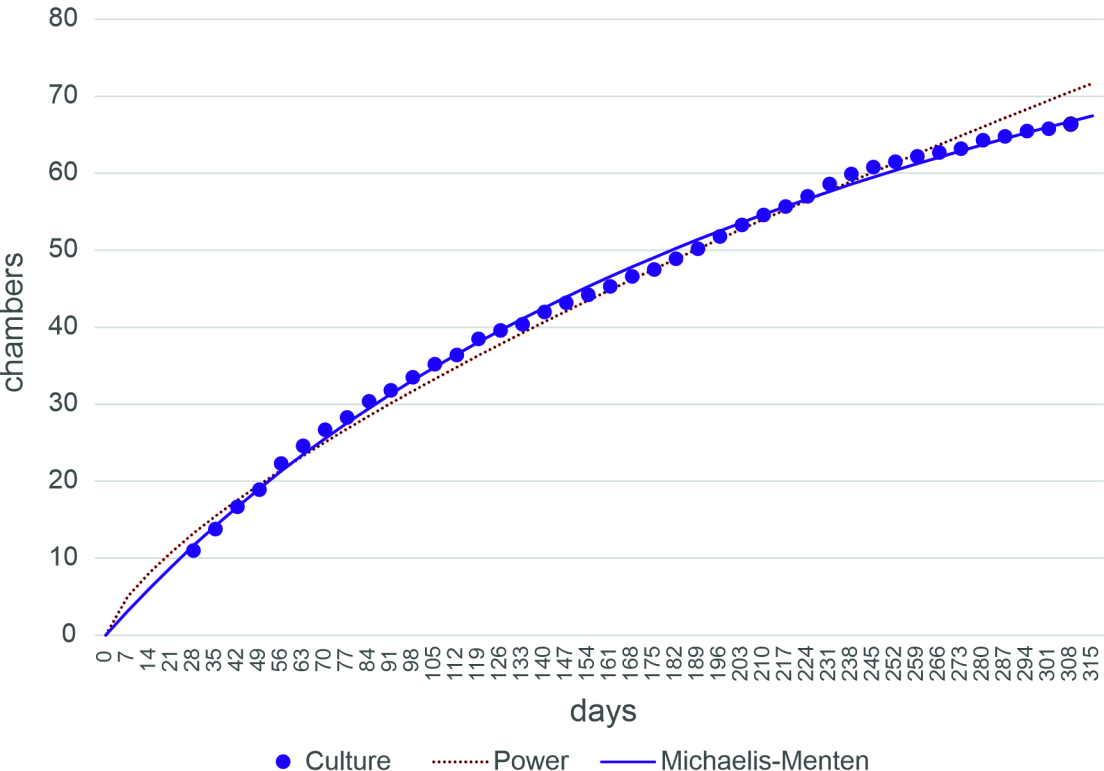
chamber areas

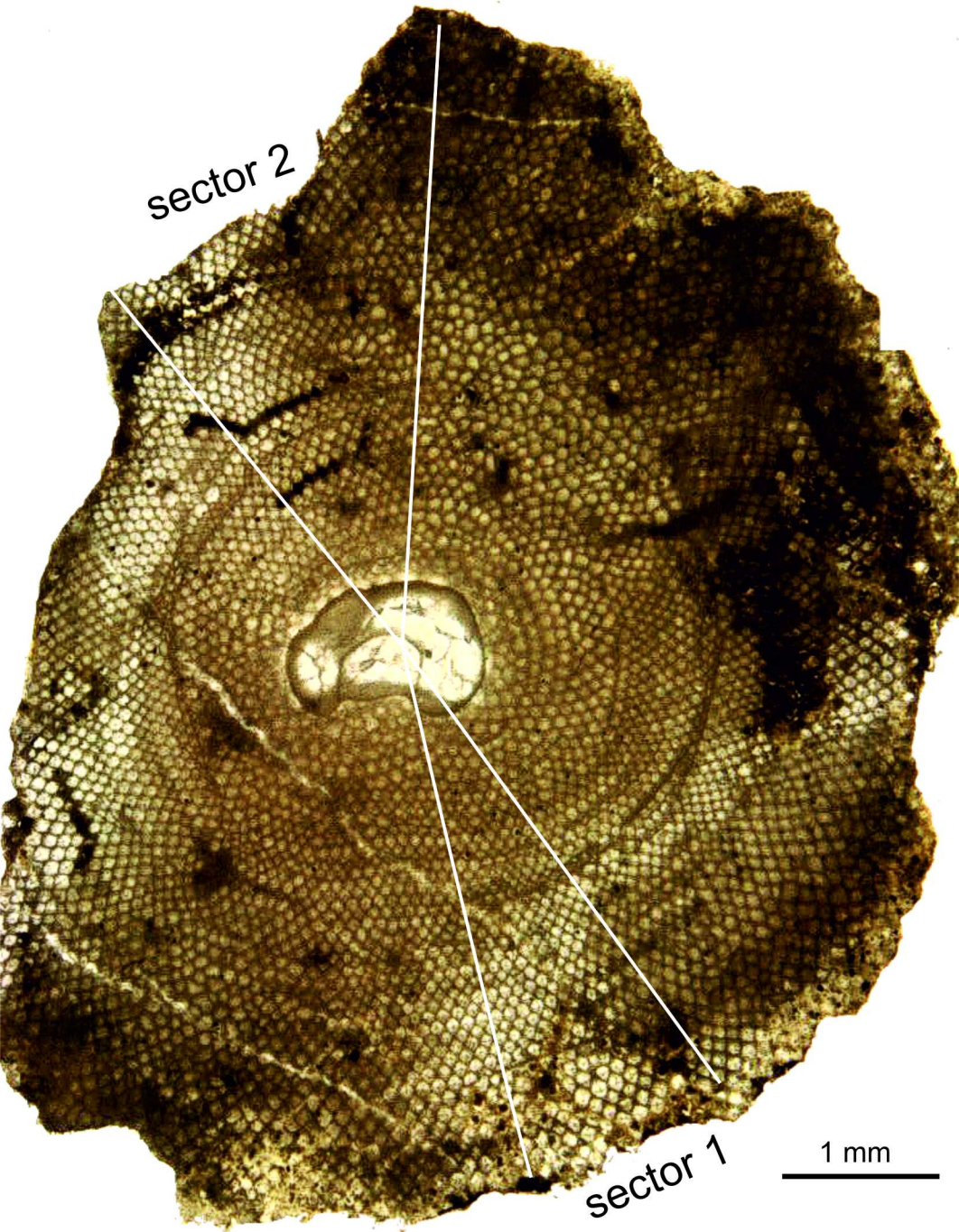


cell areas



Cycloclypeus carpentieri

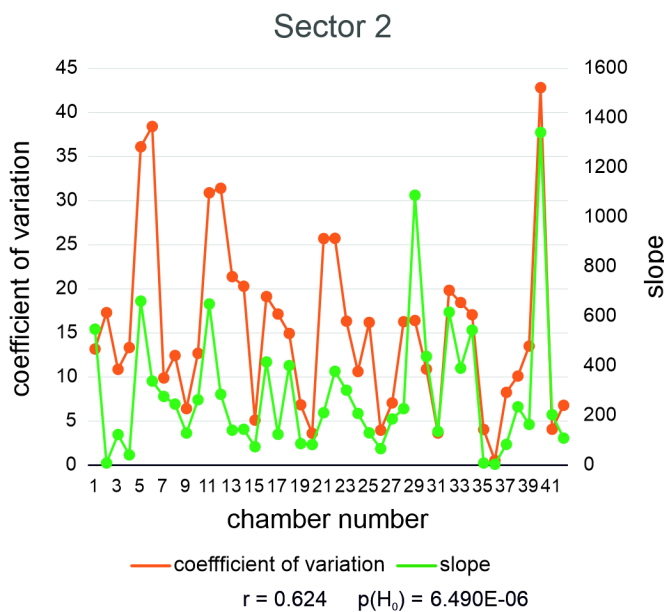
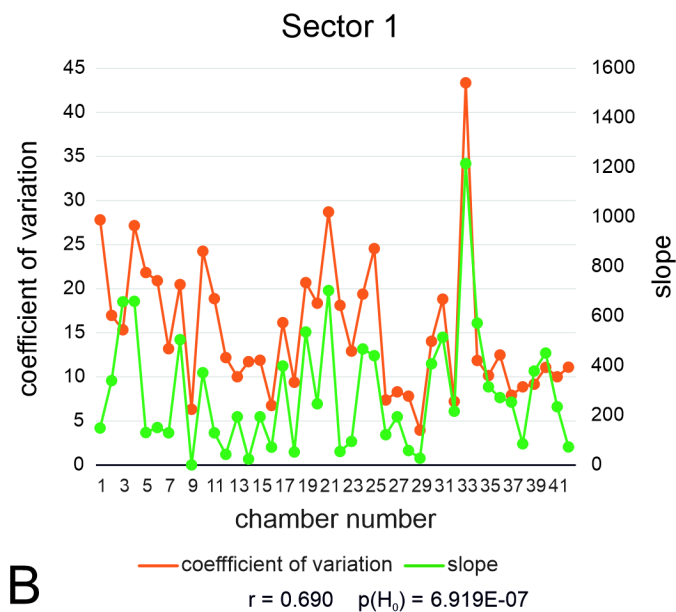
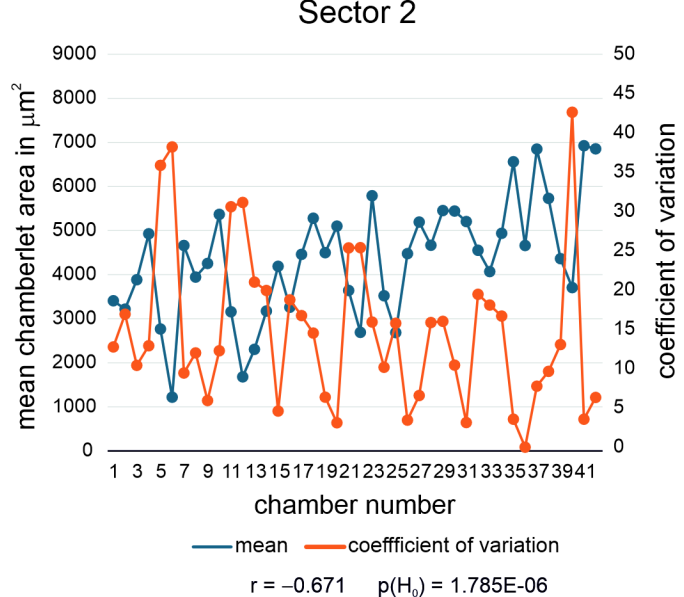
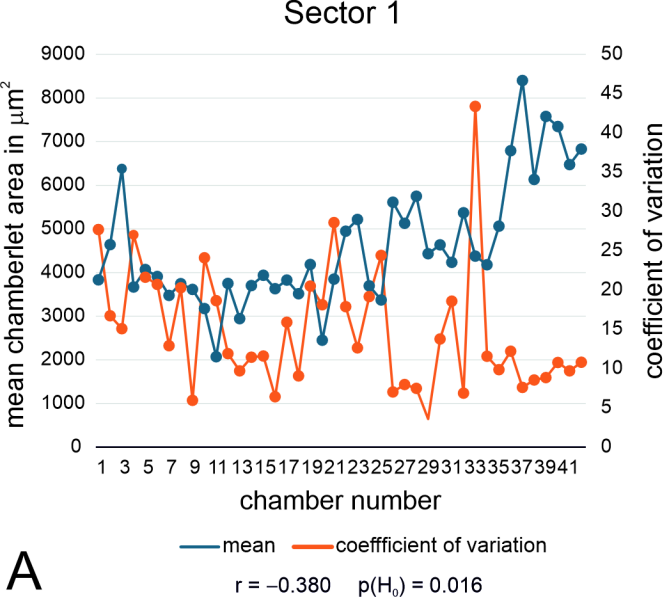




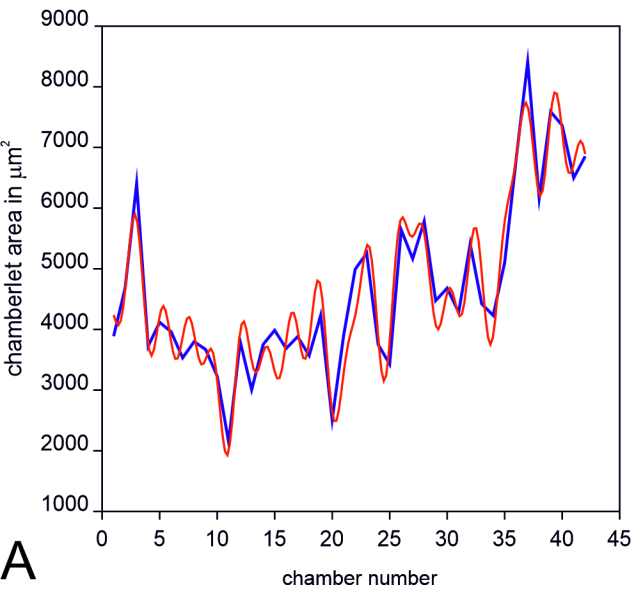
sector 2

sector 1

1 mm



Sector 1



A

Amplitude	Phase	Period
2578	-0.743	41.86
1497	-2.665	31.03
403	-1.466	13.00
594	2.525	11.06
595	-3.090	4.75
270	2.280	4.10
411	2.512	3.38
469	-0.859	2.27

 $R^2 = 0.944$ $p(H_0) = 1.790E-11$

common Periods

41.86

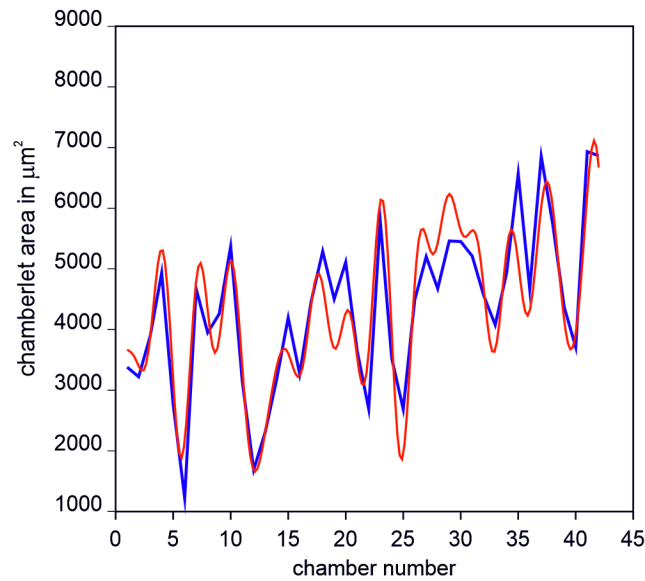
10.75

4.695

3.955

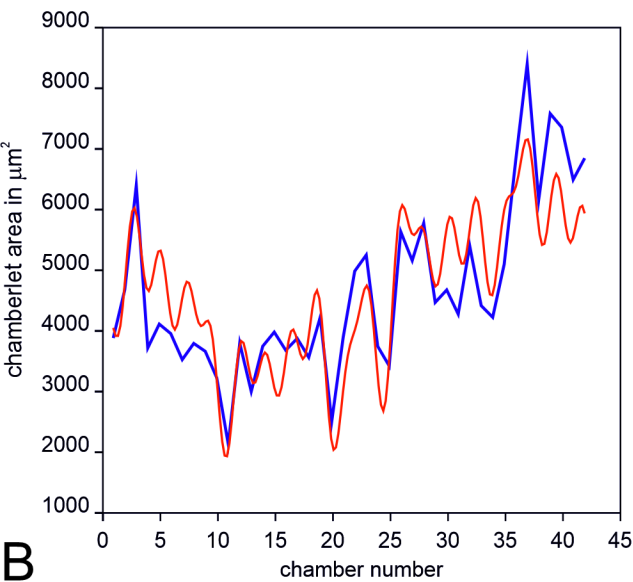
3.415

2.495



Sector 2

Amplitude	Phase	Period
901	-1.435	41.86
635	-2.007	10.44
599	1.888	6.53
485	-1.668	4.64
603	-2.082	3.81
513	-2.342	3.45
488	1.025	3.08
494	1.315	2.72

 $R^2 = 0.848$ $p(H_0) = 1.580E-06$


B

Amplitude	Phase
1377	-0.996
473	0.832
619	-2.733
254	2.747
388	2.002
463	-1.405

 $R^2 = 0.746$ $p(H_0) = 7.698E-06$

common Periods

41.86

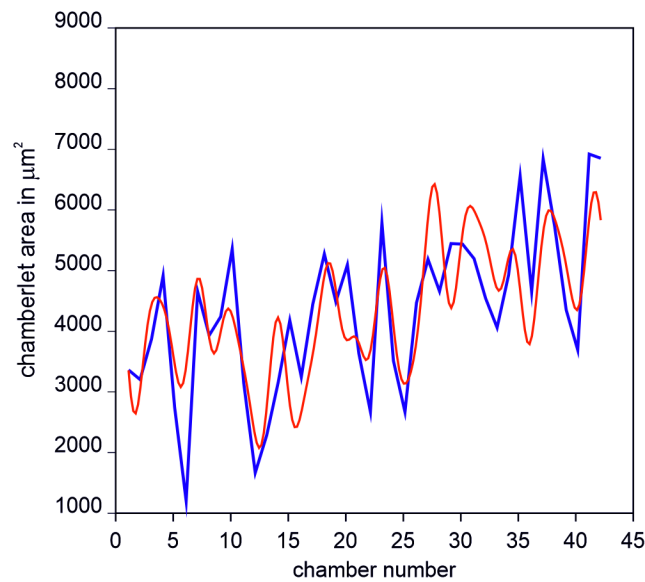
10.75

4.695

3.955

3.415

2.495

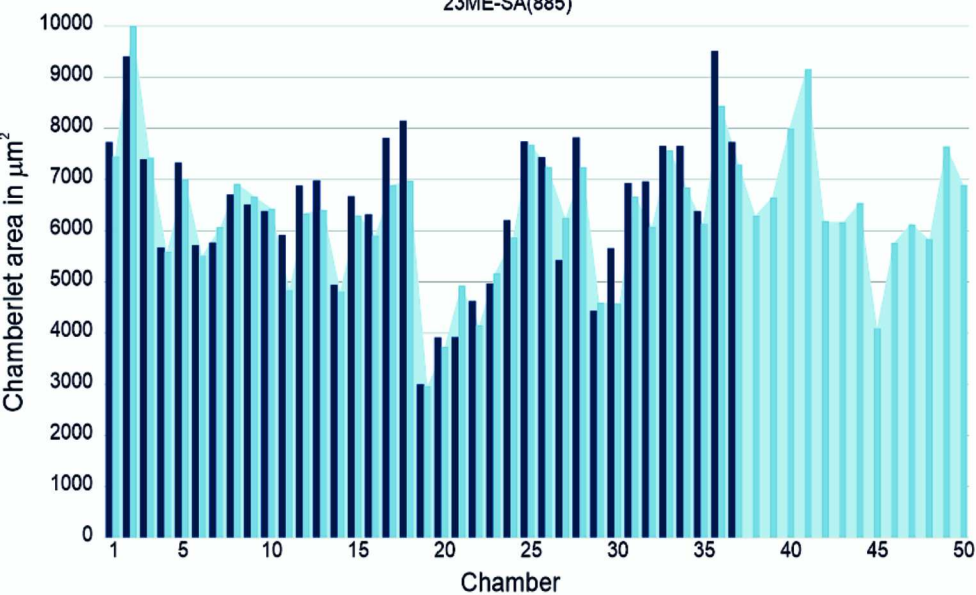


Amplitude	Phase
934	-1.347
549	-2.124
590	-1.971
451	3.057
479	-1.691
250	-2.338

 $R^2 = 0.585$ $p(H_0) = 0.0032$

Eulepidina undosa

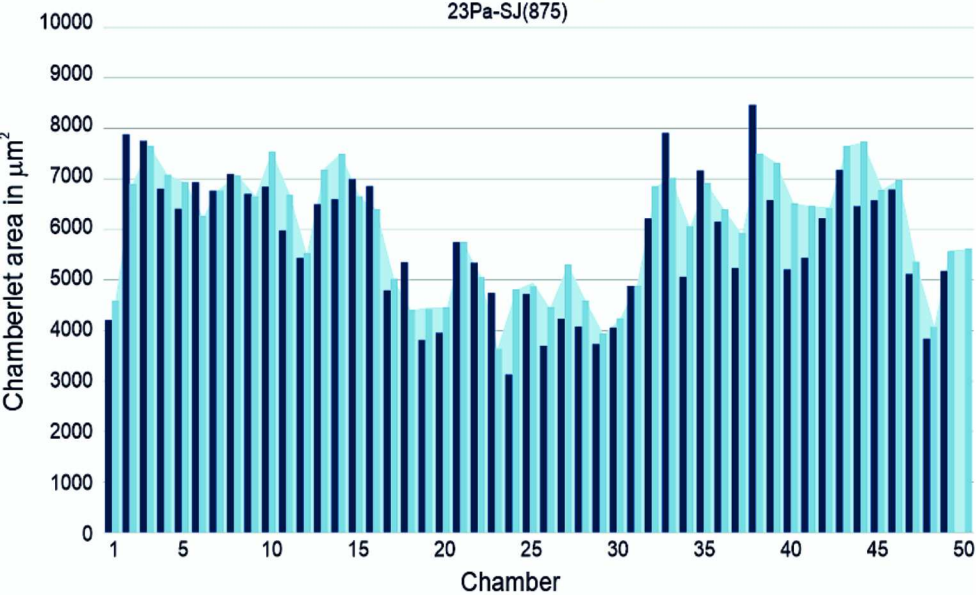
23ME-SA(885)



Amplitude	Phase	Period
897	0.022	36.66
740	0.654	11.92
894	-0.223	8.17
502	2.326	4.79
551	0.957	3.86
453	2.412	3.17
741	2.935	2.60

Nephrolepidina vaughani

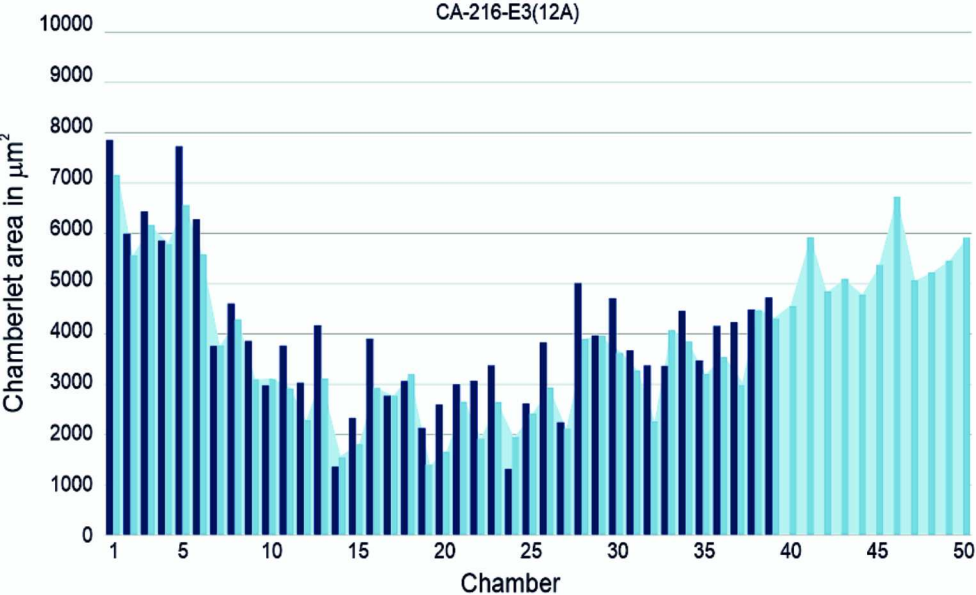
23Pa-SJ(875)



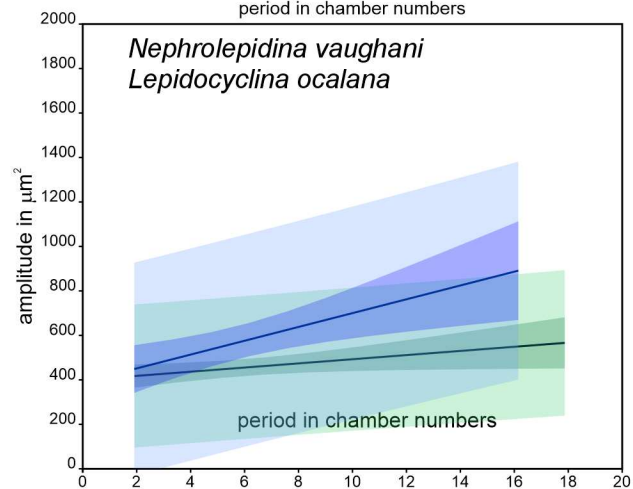
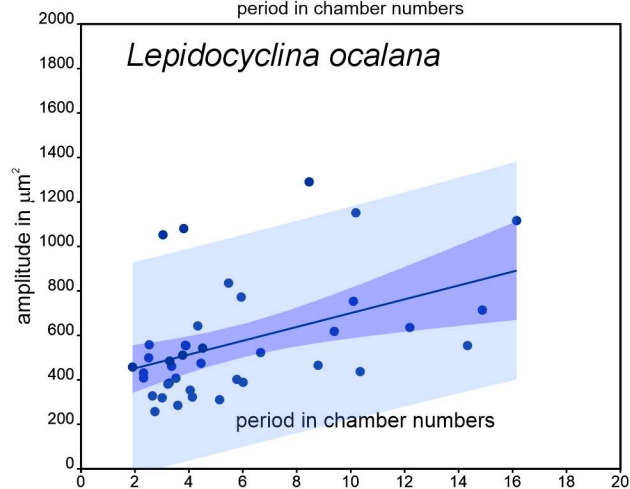
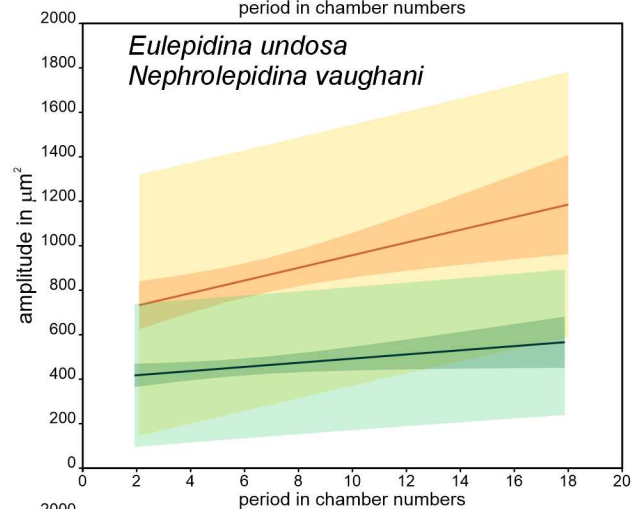
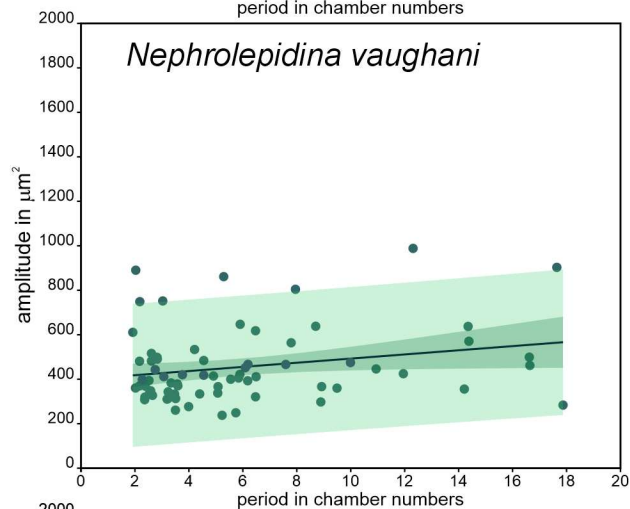
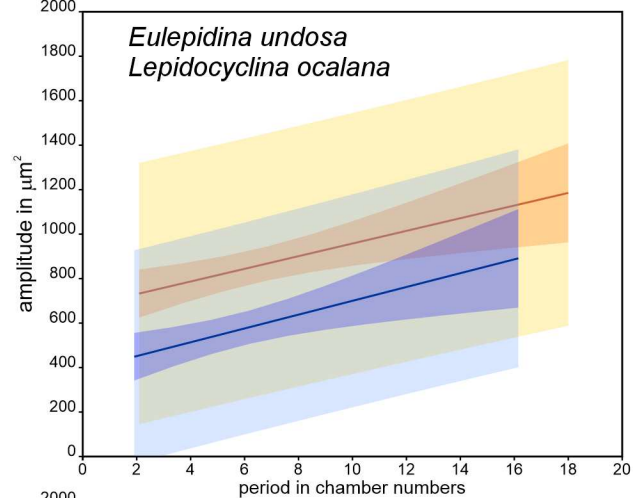
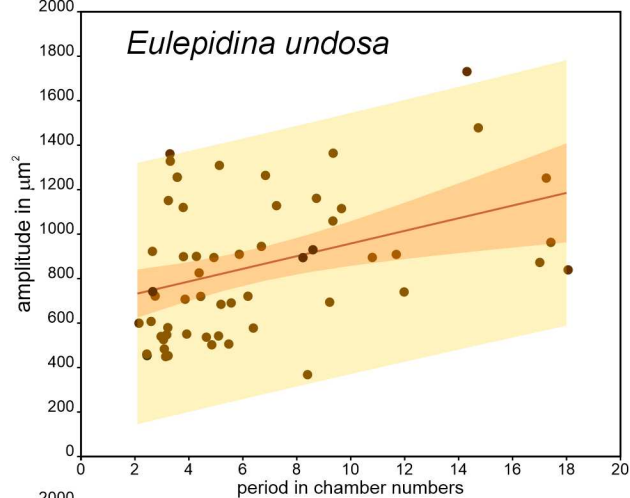
Amplitude	Phase	Period
1340	1.505	31.52
476	1.817	10.00
647	2.204	5.91
371	-2.829	3.60
444	2.713	2.76

Lepidocyclina ocalana

CA-216-E3(12A)



Amplitude	Phase	Period
9131	0.597	38.73
7899	-2.189	36.07
367	1.982	12.18
431	-1.412	5.77
384	-0.624	4.12
544	-1.350	2.52



Lepidocyclus ocalana *Nephrolepidina vaughani* *Eulepidina undosa*

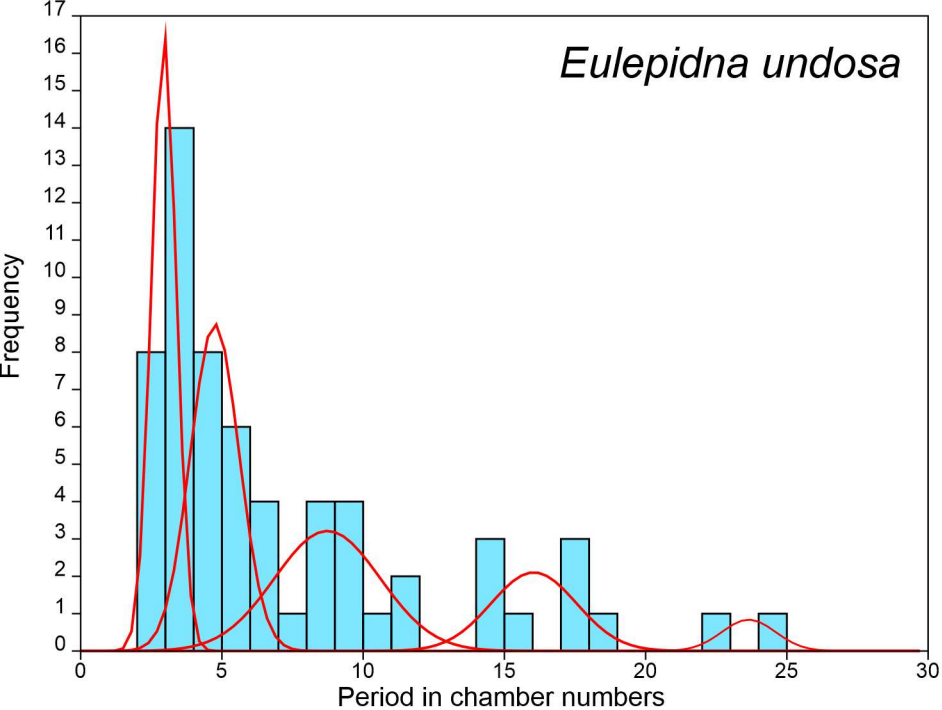
slope: 31.07 15.53 30.52

Lepidocyclus ocalana *Nephrolepidina vaughani* *Eulepidina undosa*

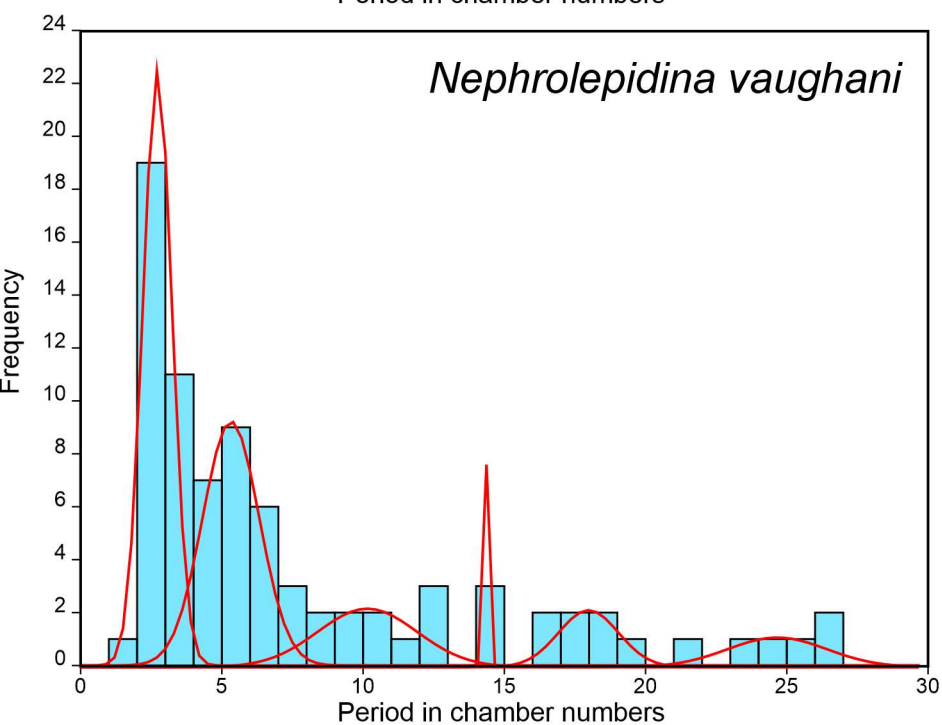
intercept: 387.4 372.0 648.1

<i>Lepidocyclus ocalana</i>		$t = 2.168$	$t = 0.081$
<i>Nephrolepidina vaughani</i>	$p(H_0) = 0.039$		$t = 2.275$
<i>Eulepidina undosa</i>	$p(H_0) = 0.396$	$p(H_0) = 0.031$	

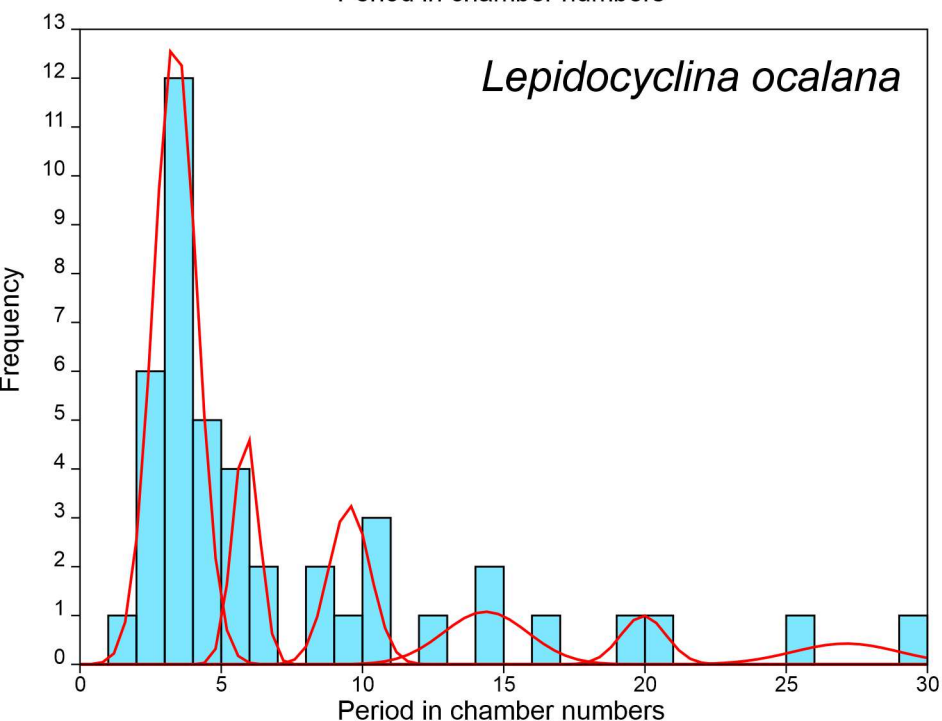
<i>Lepidocyclus ocalana</i>		$t = 1.459$	$t = 2.223$
<i>Nephrolepidina vaughani</i>	$p(H_0) = 0.137$		$t = 2.257$
<i>Eulepidina undosa</i>	$p(H_0) = 0.036$	$p(H_0) = 7.6\text{E-}05$	



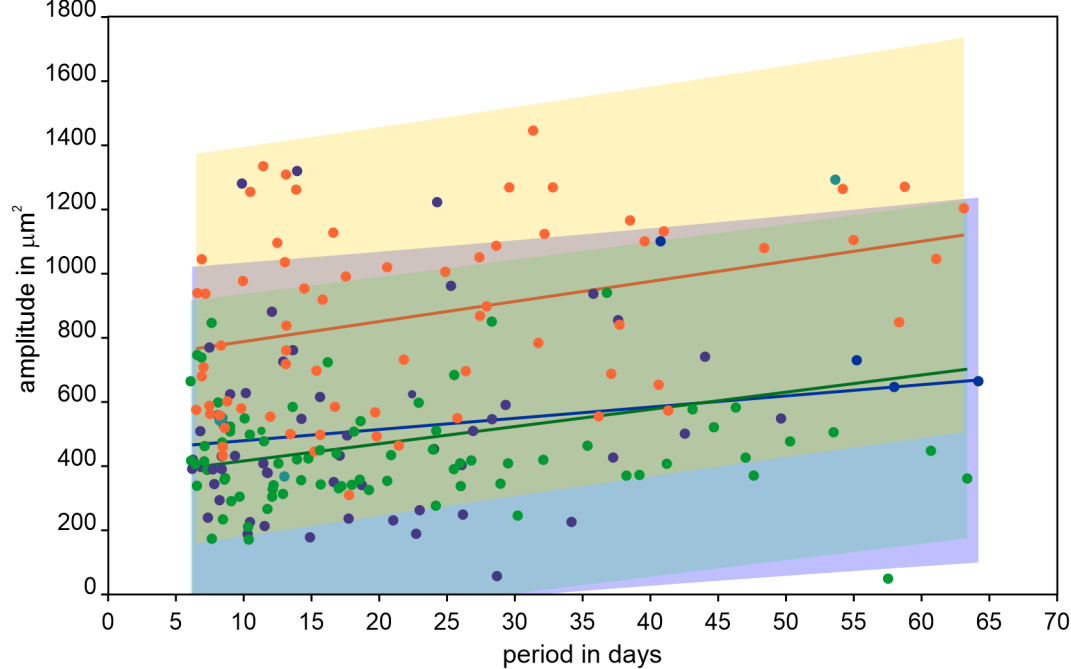
Sinusoids		
Prob	Mean	Stdev
0.287	2.94	0.433
0.315	4.75	0.891
0.237	8.80	1.819
0.129	16.04	1.514
0.032	23.65	0.950



Sinusoids		
Prob	Mean	Stdev
0.351	2.71	0.512
0.309	5.34	1.065
0.144	10.18	1.754
0.035	14.32	0.074
0.085	18.01	1.060
0.073	24.69	1.759



Sinusoids		
Prob	Mean	Stdev
0.557	3.37	0.761
0.125	5.87	0.461
0.136	9.53	0.735
0.092	14.36	1.492
0.045	19.95	0.795
0.046	27.13	1.876



$R^2 = 0.094$ $p(H_0) = 0.0103$

$R^2 = 0.233$ $p(H_0) = 1.030\text{E-}05$

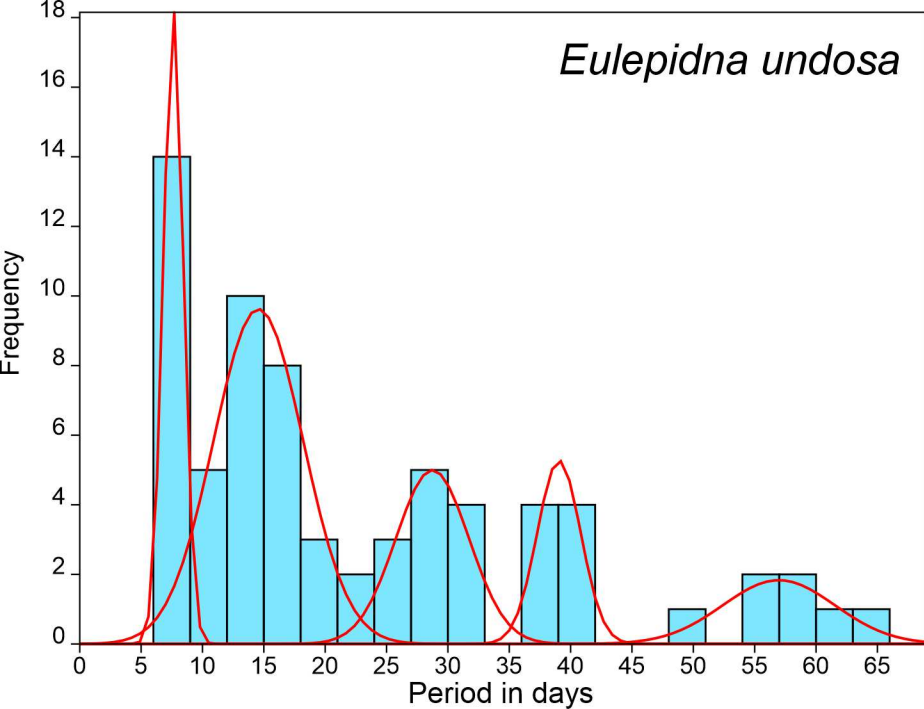
$R^2 = 0.205$ $p(H_0) = 0.0033$

	<i>Lepidocyclina ocalana</i>	<i>Nephrolepidina vaughani</i>	<i>Eulepidina undosa</i>
slope:	3.487	5.362	6.252

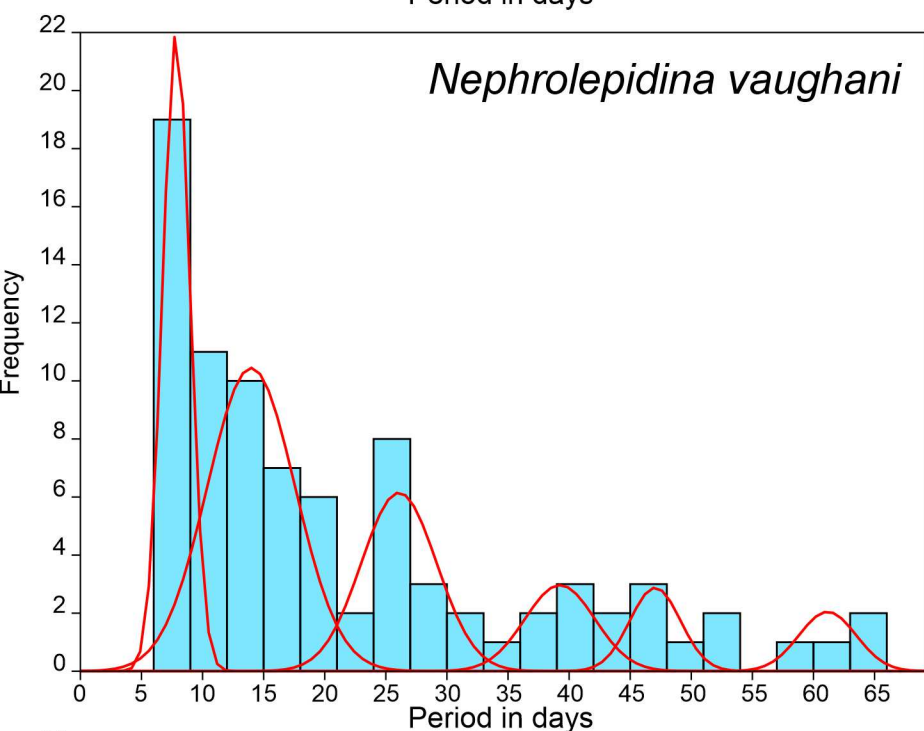
	<i>Lepidocyclina ocalana</i>	<i>Nephrolepidina vaughani</i>	<i>Eulepidina undosa</i>
intercept:	444.6	362.6	725.8

<i>Lepidocyclina ocalana</i>		t = 0.731	t = 1.530
<i>Nephrolepidina vaughani</i>	p(H ₀) = 0.3045		t = 0.407
<i>Eulepidina undosa</i>	p(H ₀) = 0.1236	p(H ₀) = 0.3664	

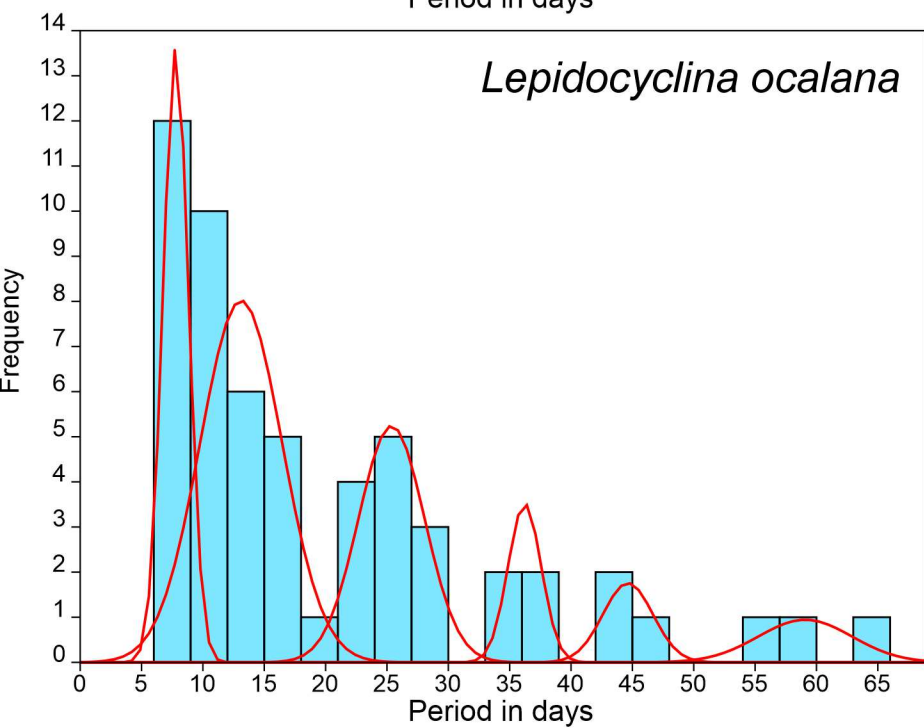
<i>Lepidocyclina ocalana</i>		t = 0.617	t = 3.070
<i>Nephrolepidina vaughani</i>	p(H ₀) = 0.3288		t = 4.433
<i>Eulepidina undosa</i>	p(H ₀) = 0.0045	p(H ₀) = 3.64E-05	



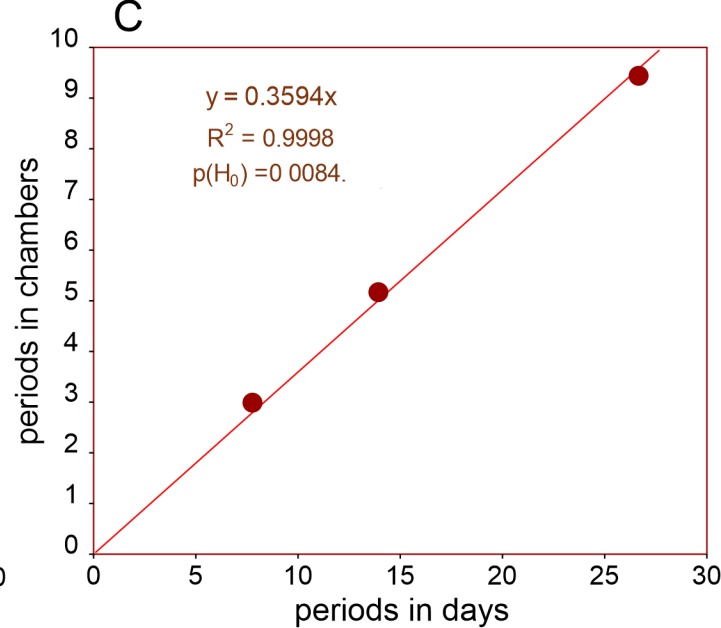
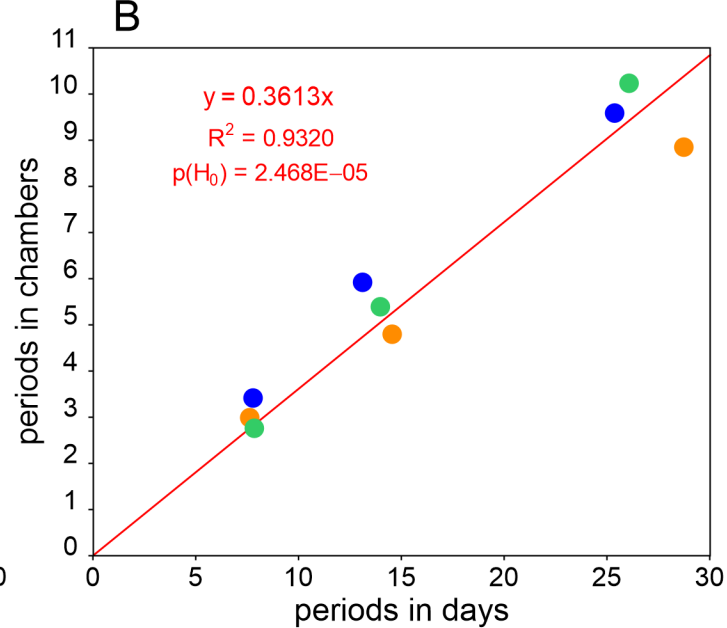
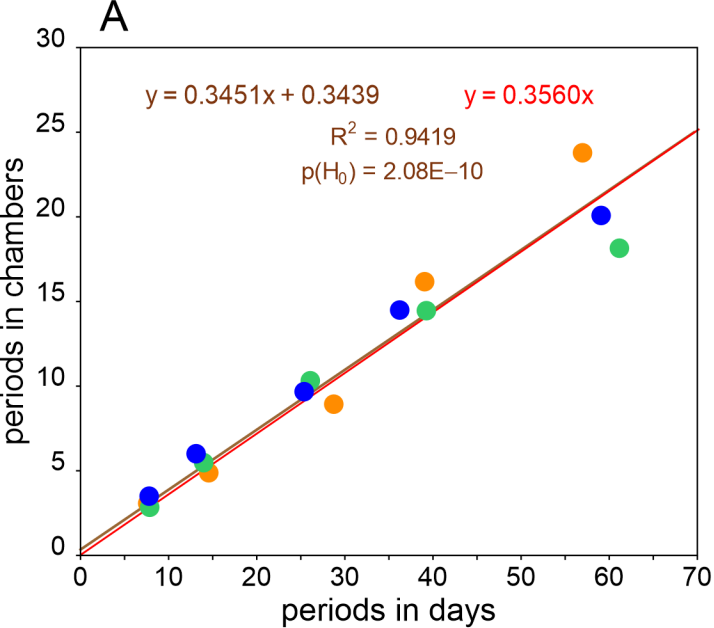
Sinusoids		
Prob	Mean	Stdev
0.178	7.63	0.808
0.426	14.55	3.658
0.180	28.74	2.983
0.113	39.05	1.775
0.101	56.97	4.572



Sinusoids		
Prob	Mean	Stdev
0.229	7.85	1.119
0.349	13.98	3.602
0.176	26.07	3.092
0.078	39.22	2.825
0.055	47.01	2.090
0.041	61.16	2.580



Sinusoids		
Prob	Mean	Stdev
0.211	7.79	1.036
0.400	13.12	3.344
0.211	25.37	2.701
0.071	36.22	1.353
0.053	44.63	2.038
0.054	59.08	3.821



— reduced major axis
— regression line

● *Lepidocyclina ocalana*
● *Nephrolepidina vauhani*
● *Eulepidina undosa*

— regression line
● common periods

Supplementary Files

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- [Supplement1.2.tif](#)
- [Supplement1.3.tif](#)
- [Supplement2.xlsx](#)
- [Supplement2.xlsx](#)
- [Supplement1.1.tif](#)