Session 25

Indicator taxa: what can they tell us about the past, present and future for coral reefs?

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Narayan GR, Westphal H (2016) Are Zanzibar's reefs undergoing ecological change? Foraminifera bio-indicators for monitoring and assessment of reef ecosystems in the west Indian Ocean. Proceedings of the 13th International Coral Reef Symposium, Honolulu: 207-215

Wöger J, Briguglio A, Eder W, Kinoshita S, Hohenegger J (2016) First results of a long-term cultivation experiment of different species of Nummulitidae (Foraminifera) from the island of Sesoko (Okinawa, Japan). Proceedings of the 13th International Coral Reef Symposium, Honolulu: 216-227

Morphometry of the larger foraminifer *Heterostegina* explaining environmental dependence, evolution and paleogeographic diversification

W. Eder, J. Hohenegger, A. I. Torres-Silva, Antonino Briguglio

Abstract The cosmopolitan, symbiont-bearing, larger benthic foraminifer (LBF) *Heterostegina sensu lato* prefers oligotrophic environments in tropical and warm-temperate seas. Harboring diatoms enables this species to be found across a wide illumination gradient from intertidal pools, where *H. depressa* protects against strongest illumination by occupying cryptic habitat, down to the base of the euphotic zone. Sheltered cryptic habitat, such as in holes of boulders, allows this species to live in highly energetic zones down to the fair-weather wave base. Dependence on light for photosynthesis of its endosymbionts is managed by increasing surface/volume ratios of the test correlated with decreasing light, resulting in test flattening. Hydrodynamics also influences reproductive strategies. In high energy environments, asexual reproduction by schizogony dominates, while sexual reproduction (gametogony) is the dominant mode under low energy conditions. Thus, there is a shift in proportions between schizonts with smaller proloculi and gamonts with larger proluculi along the hydrodynamic gradient. Because there is a negative correlation between proloculus size and the number of chambers undivided by septula (operculinid chambers), the latter character shows negative dependence along the hydrodynamic gradient. Both proloculus size and number of operculinid chambers have been used as metric characters not only in the evolution of *Heterostegina* lineages starting in the middle Eocene, but also in many other nummulitds (e.g., *Nummulites*, *Spiroclypeus*, *Cycloclypeus*), totally neglecting the environmental dependence. Additionally, proloculus size can differ between biogeographically different populations (e.g., Okinawa and Hawaii) taken under similar hydrodynamic conditions. Using growth-independent and growth-invariant characters to describe the internal test morphology can enhance interpretation of evolutionary tendencies as distinct from environmental and paleogeographic diversification.

Keywords larger foraminifera, paleogeography, ecology, bathymetry, morphometry

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Introduction

The genus *Heterostegina* d'Orbigny, 1826 with first appearance in the late Middle Eocene (late Bartonian) belongs to the informal group of symbiont-bearing larger benthic foraminifera (LBF) with planispirally enrolled, chambered tests that follow a logarithmic spiral. The hyaline tests are characterized by a complete division of chambers into chamberlets, at least after an embryonal part (nepiont) consisting of a proloculus and deuteroloculus followed by a series of undivided 'operculinid' chambers. Whorls completely embrace the lateral test parts (involute tests) leading to alar chamber prolongations. Final whorls can lose this complete embracement, then named 'maturo-evolute' (Banner and Hodgkinson 1991). Beside molecular genetic differences (Holzmann et al. 2003), this test construction differentiates *Heterostegina* from the completely evolute genus *Planostegina* (Banner and Hodgkinson 1991). In fossil representatives, the division into the subgenera *H. (Heterostegina)* and *H. (Vlerkina)* Eames et al. 1968 is solely based on the difference between maturo-evolute and involute tests (sensu Banner and Hodgkinson 1991), where the latter are regarded as typical for Paleogene representatives. The genus *Gryzbowskia* Bieda (1949) is characterized in equatorial sections by irregular-polygonal chamberlets, thus differentiated from *Heterostegina* possessing rectangular chamberlets (Banner and Hodgkinson 1991; Lunt and Renema 2014). The transition from complete involute into maturo-evolute tests in Paleogene species (e.g., Less et al. 2008) and the change from rectangular to polygonal chamberlets within one specimen makes a division based on chamberlet outline needless. This is followed by Less et al. (2008) in the work on the evolution of Paleogene Tethyan *Heterostegina*.

Today, the cosmopolitan single representative *Heterostegina depressa* d'Orbigny, 1826 is restricted to oligotrophic tropical and warm-temperate seas (Langer and Hottinger 2000). It has reinvaded the Mediterranean as a Lessepsian immigrant (e.g., Hyams et al. 2002). Molecular genetic homogeneity of the species is documented by Holzmann et al. (2003) checking specimens from the Caribbean and Red Sea, and the Indian and Pacific Oceans.

Light

Specific *Thalassionema*-like diatoms harbored by *Heterostegina depressa* are clearly differentiated from related diatoms found in all other extant nummulitids (Holzmann et al. 2006), enabling one of the broadest distributions along the light gradient within diatom-bearing LBF. Optimum photosynthetic rates are obtained at low light levels with a maximum around 150 PAR µmol m^{-2} s^{-1} (e.g., Nobes et al. 2008). This allows the distribution from intertidal pools, where *H. depressa* protects against strongest illumination in the shadow of boulders (cryptic habitat), to the
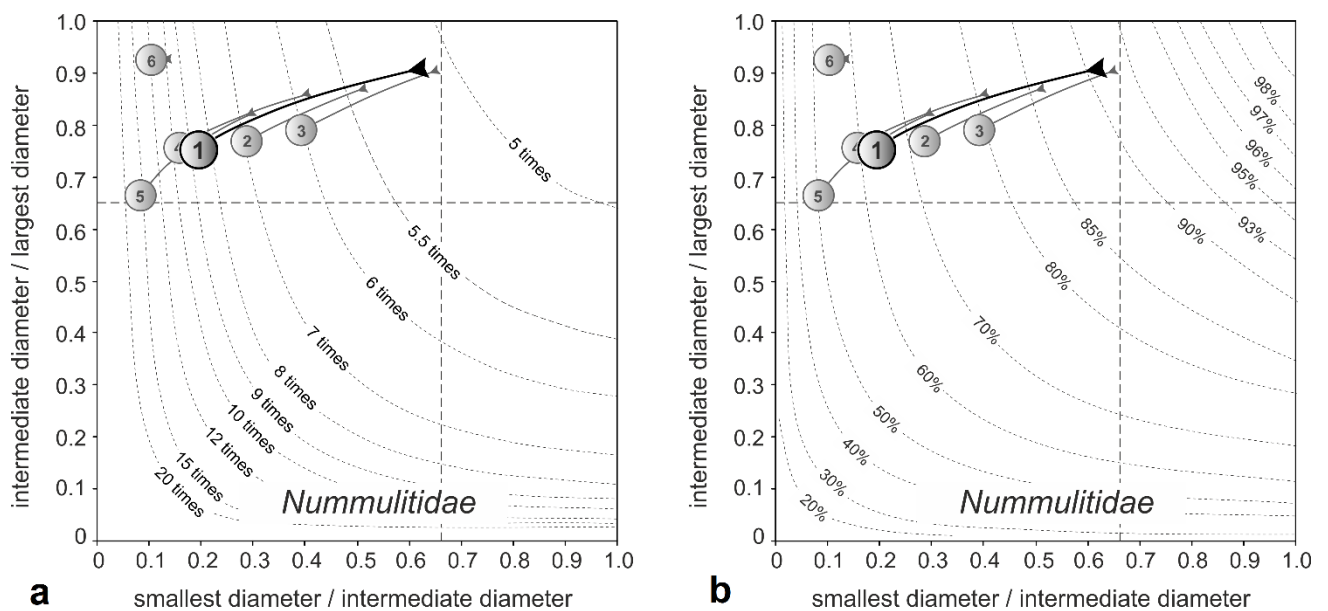

Fig. 1 The response of test shape in nummulitids to light and hydrodynamics represented in Zingg-diagrams. A) isolines represent surface/volume-ratios of triaxial ellipsoids with identical volumes. The surface/volume-ratio of a sphere is 4.836. B) isolines represent settling velocities expressed as percentages of the velocity of an equivalent sphere. Species are represented as trajectories indicating form changes, starting from thick lenticular to thin lenticular tests. 1. *Heterostegina depressa*, 2. *Operculinella cumingii*. 3. *Palaeonummulites venosus*, 4. *Operculina complanata*, 5. *Planostegina operculinoides*, 6. *Cycloclypeus carpenteri* (modified after Hohenegger 2009)

deep euphotic zone (e.g., Hohenegger 2004). The often used thickness/diameter-ratio (or the inverse D/T ratio) for determining the reaction to decreasing light intensities, is primarily understood as a depth estimator (e.g., Hansen and Buchardt 1977; Renema 2005). But it can only be used for tests where flattening is obtained by thinning of the wall lamellae in combination with a constant test diameter, (e.g., *Amphistegina* by Hallock et al. 1986). This ratio is not useful where flattening is obtained by increasing test diameters and constant

volumes (e.g., Röttger and Hallock 1982). Here, the surface/volume ratios (e.g., Hohenegger 2009) are better indicators to demonstrate the influence of decreasing light (Fig. 1a).

An equivalent parameter compared to the thickness/diameter ratio, but growth independent, is used to demonstrate the dependence of test flattening from light intensity. Measuring thickness at diverse radii for fitting a power function representing growth, thickness is calculated for the jth specimen at a radius of 3000 µm by

$$th_j = a_j b_j^{3000} + c_j \qquad (1)$$

Where a is the multiplicative constant, b the growth rate and c the offset from the equatorial plane.

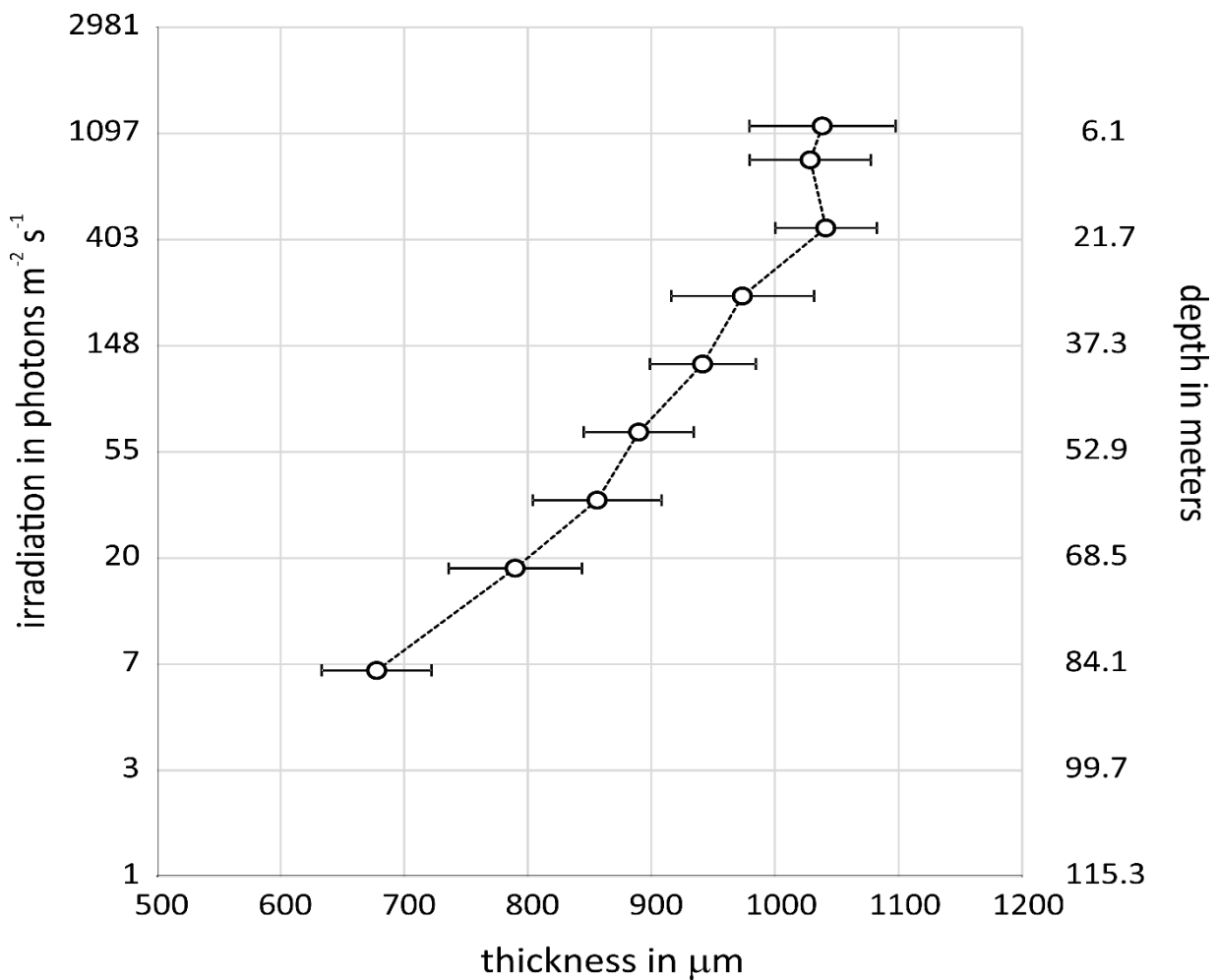The correspondence of this growth invariant character with light intensity and depth is shown in Fig. 2.

Fig. 2 Test thickness at a constant marginal radius of 3000 µm in dependence of light intensities correlating with depth. Bars indicate standard errors of the mean

Hydrodynamics

While test flattening allows light absorption in low-illuminated environments, because a large number of symbionts can be positioned in 'egg holders' of the test wall (e.g., Hottinger 1977), it weakens resistance against hydrodynamics (Fig. 1b). Therefore, thick lenticular *Heterostegina* can be found in high energy environments down to the fair-weather wave base protected in holes of coral rocks and boulders against entrainment and transport. The continuous flattening with depth allows settlement on middle to fine grained sand in deeper, lower-energy environments (e.g., Hohenegger 2004).

Hydrodynamics are thus the second important factor for the distribution of *H. depressa*. Beside the effect of entrainment and transport of 'adult' tests, the hydrodynamic regime is extremely important for reproduction. A trimorphic life cycle in LBF as postulated by Leutenegger (1977) was first documented for LBF in *H. depressa* by Röttger (1990). Morphological differences between the asexually reproduced schizonts and gamonts are expressed in proloculus size (e.g., Biekart et al. 1985), where proloculi of schizonts are significantly smaller than proloculi of gamonts. According to investigations at two depth transects NW of Sesoko Jima, Japan (Yordanova and Hohenegger 2002), the test characters 'proloculus size' and 'number of operculinid chambers' (e.g., Less et al. 2008) are negatively correlated, independent of their partial correlation with water depth. Decomposition of the bimodal frequency distribution of proloculus size, combining all depth samples into normally distributed components, resulted in two groups, one with smaller and the other with larger proloculi, thus interpreted as schizonts and gamonts. Fitting depth samples using parameters of both distributions resulted in dominance of schizonts from 5 m to 35 m expressed in unimodal distributions, followed by bimodal distributions between 35 and 55 m, where both generations are present. Below 55 m the unimodal frequency distributions correspond to the distribution parameters of gamonts. Analyses of variance confirmed the stability in parameters of each generation with depth, thus explaining the depth trend as a sequence of two stable intervals, apogamic schizogeny at hydrodynamically exposed depths (5 to 35m) and gametogamy in quiet water (55 to 90 m), connected by a transition zone where both reproduction modes are present showing decreasing schizogeny and increasing gametogamy (Eder et al. 2016b). This distribution pattern can be explained by hydrodynamics hindering sexual reproduction in shallow environments exposed to strong water movement by destroying tiny gametes (Eder et al. 2016b).

Evolutionary lineages

The depth trends in increasing proloculus size and decreasing number of undivided (operculinid) chambers of *H. depressa* perfectly mirrors the evolutionary lineages proposed by Less et al. (2008) for the Western Tethyan *Heterostegina armenica* and *H. reticulata* (Fig. 3; Eder et al. 2016b). This is an argument for an intense environmental dependence of these lineages and may explain setbacks that have been documented also for *Nummulites*, where "more evolved" species occurred together with unreworked "primitive" species (Racey 1992). Hence, the distributional pattern influenced by environmental factors might pose a problem for the explanation of continuous character changes as evolutionary tendencies.

Additionally, biogeographic differences may tangle the explanation as evolutionary lineages. Investigation on cell growth by chamber volumes using generalized logistic functions (Richards 1959) showed that chamber growth in the initial test part up to chamber 25 can best be fitted by exponential function:

$$V_{test} = ae^{bi} \qquad i = \text{chamber number} \qquad (2)$$

with the multiplicative constant *a* explaining proloculus size and the multiplicative constant *b* determining the growth rate (Eder et al. 2016a).
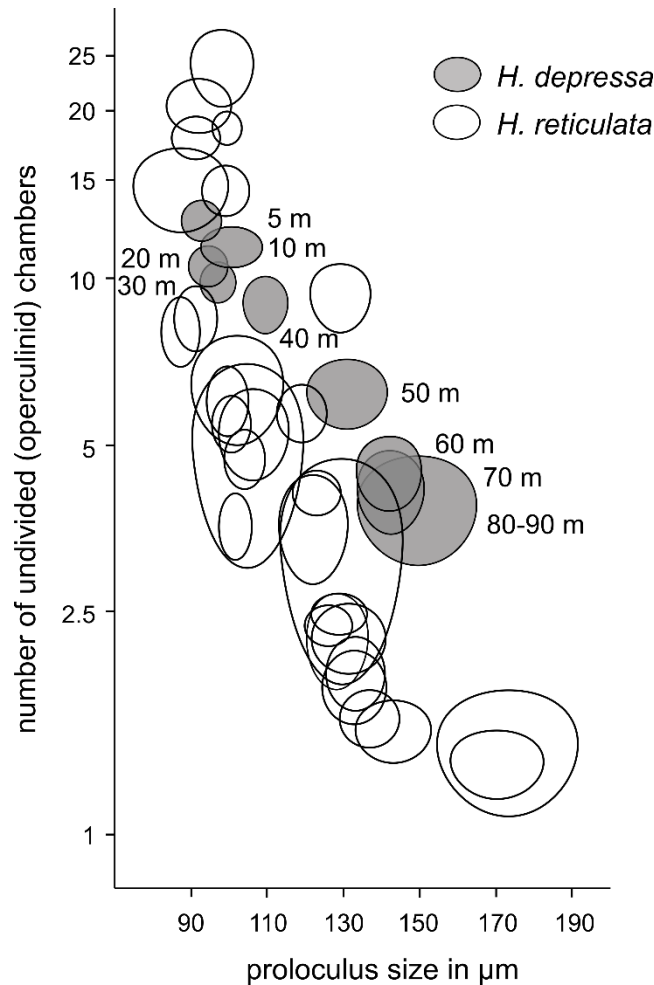
Fig. 3 Depth trend in proloculus size versus number of undivided postembryonic chambers in *Heterostegina depressa* from Sesoko Island, Okinawa with ellipses marking standard errors (95%). This depth trend completely fits the proposed evolutionary lineage of the late Eocene *Heterostegina reticulata* with the subspecies (from top to the bottom) *H. reticulata tronensis*, *H. reticulata hungarica*, *H. reticulata multifida*, *H. reticulata helvetica*, *H. reticulata reticulata*, *H. reticulata mossanensis* and *H. reticulata italica* (modified after Less et al. 2008)

Differences in initial growth between populations from Sesoko, Japan 20 m (collection Hohenegger) and Maui, Hawaii 40 m (collection Röttger) are expressed in proloculus size (constant *a* in equation 2), where individuals from Sesoko correspond to schizonts and individuals from Hawaii with larger proloculi correlate to gamonts (Fig. 4). Individuals from both natural populations have the same growth rates expressed in parameter *b* of equation 2. Cultured specimens originating from the natural population of Hawaii differ in both growth parameters from their natural population
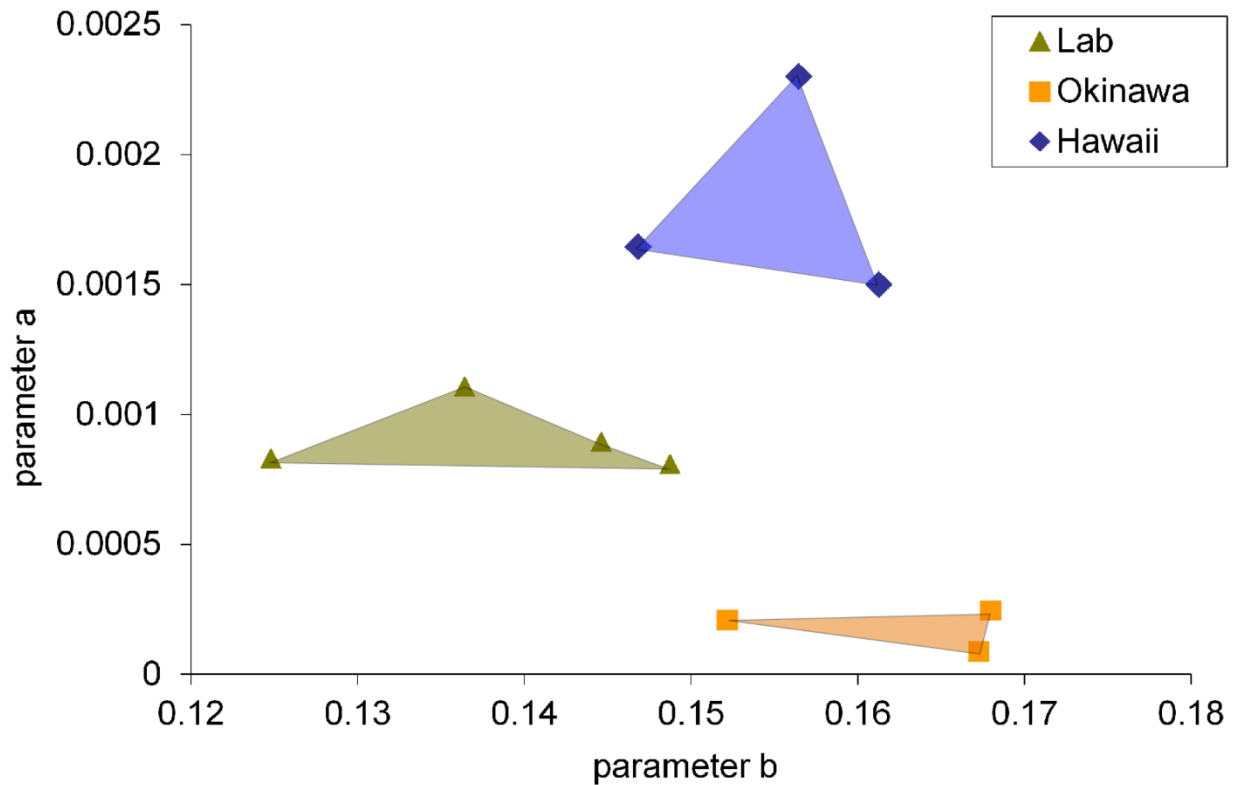
Fig. 4 Scatter plot of the constants *a* (indicating proloculus volume) and *b* (indicating growth rate) for the exponential fit of the first 25 chambers, comparing megalospheres from Sesoko and Maui with laboratory cultures (after Eder et al. 2016b)

(Fig. 4; Eder et al. 2016a).This difference in parameter *a* indicates that they are also schizonts. Hence, schizonts from Hawaii have larger proloculi than those from Japan. Parameter *a* has to be studied on a larger scale to establish a reliable biogeographic trend, while parameter *b* gives more information about individual growth.

The above mentioned difficulties in explaining evolutionary lineages by a small set of internal test characters as used for stratigraphic purpose (e.g., Less et al. 2008) can be avoided using growth-independent and growth-invariant characters enabling a more or less general description of the complete test (e.g., Hohenegger 2011, 2016). Using these methods, constants of equations fitting the character change during growth act as "supergenes" (e.g., Thompson and Jiggins 2014). Their effect on individuals can then be used as characters to classify fossil individuals in populations by multivariate analyses. After determining populations using classification analyses, they can be interpreted as populations within an evolutionary lineage or as paleobiogeographically separated populations (subspecies; Hohenegger 2013). Significant differences between populations can be obtained by discriminant analysis. The Late Eocene *Heterostegina ocalana* Cushmann, 1921 from Cuba

and Panama (Cole 1952) can be used as an example for interpretation of populations. Here, the differentiation between paleogeographic distinct populations from Cuba and Panama is expressed in the first discriminant axis that is highly loaded by the character "number of undivided (operculinid) chambers" (Fig. 5). Evolutionary tendencies in populations from Cuba that are stratigraphically supported are also demonstrated in the first axis by a weak increase in the number of operculinid chambers, but strongly documented by the second discriminant axis with decreases in the "expansion rate of the marginal spiral", the "number of chamberlets" and the "backward-bend angle of chambers" (Fig. 5). This evolutionary tendency is not coupled with an increase in "proloculus size" (here proloculus height and width), yet is regarded as the most prominent indicator for evolutionary changes in heterostegines (Less et al. 2008).
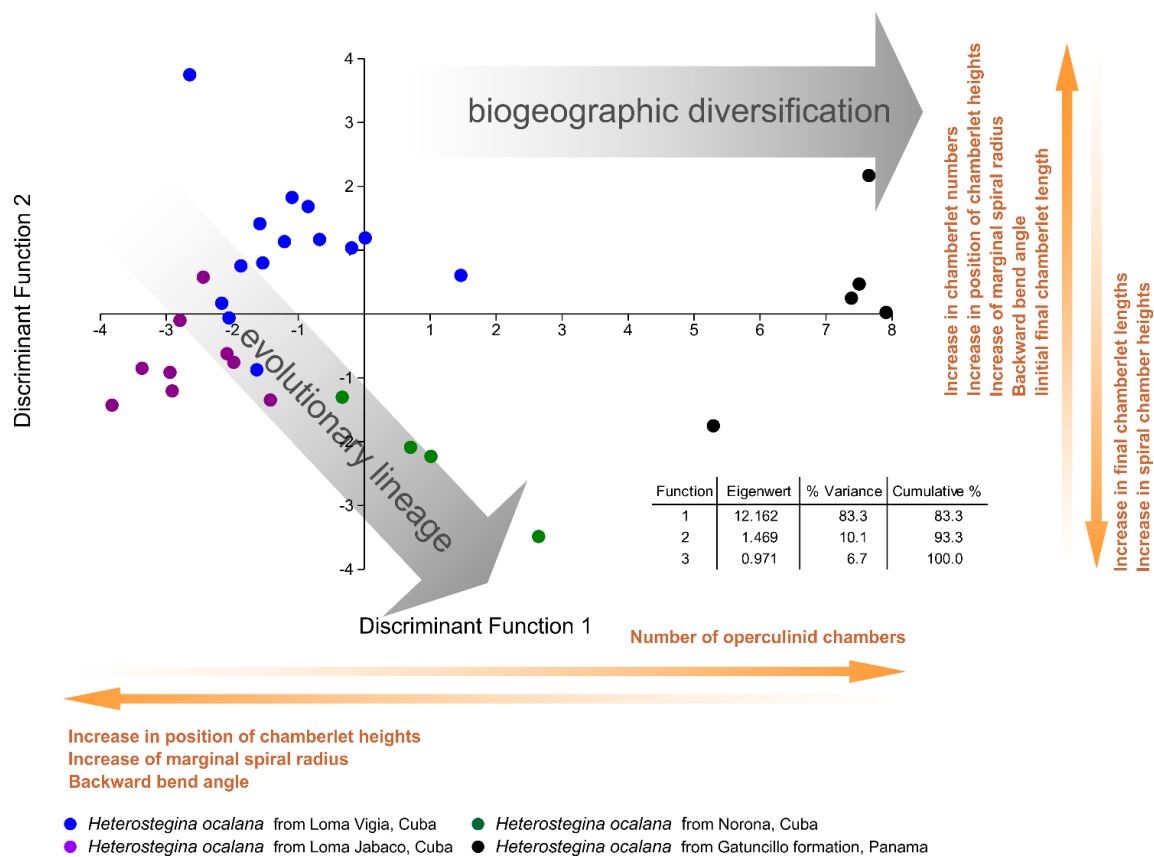

Function	Eigenwert	% Variance	Cumulative %
1	12.162	83.3	83.3
2	1.469	10.1	93.3
3	0.971	6.7	100.0

Fig 5 Discriminant analysis of *Heterostegina ocalana* populations from Cuba and Panama based on growth independent and growth invariant characters, where loadings of the important characters are shown (after Hohenegger and Torres-Silva 2016)

Paleogeographical differences leading to subspecies, together with transport, reworking and time-averaging, could obscure the clear dependence of fossil *Heterostegina* species on hydrodynamics and light, possibly leading to erroneous interpretations regarding evolutionary

lineages. Using growth-independent and growth-invariant characters describing the internal test morphology more or less completely allows a much better interpretation of evolutionary tendencies separated from paleogeographic diversification.

Acknowledgements

References

Banner FT, Hodgkinson, RL (1991) A revision of the foraminiferal subfamily Heterostegininae. Rev Esp Micropal 23: 101-140

Biekart JW, Bor T, Röttger R, Drooger CW, Meulenkamp JE (1985) Megalospheric *Heterostegina depressa* from Hawaii in sediments and laboratory cultures. Palaeontology, Proc Koninklijke Nederlandse Akademie Wetenschappen B Phys 1:20

Cole WS (1952) Eocene and Oligocene larger foraminifera from the Panama Canal Zone and vicinity: U.S. Geol Survey Prof Paper 244: 1-41

Eder W, Briguglio A, Hohenegger J (2016a) Growth of *Heterostegina depressa* under natural and laboratory conditions. Mar Micropaleontol 122: 27-42

Eder W, Hohenegger J, and Briguglio, A (2016b) Depth-related morphoclines of megalospheric tests of *Heterostegina depressa* d'Orbigny. biostratigraphic and paleobiological implications: Palaios [doi.10.2110/palo.2015.098]

Hallock P, Forward LB, Hansen, HJ (1986) Environmental influence of test shape in *Amphistegina*. J Foraminiferal Res 16:224-231

Hansen HJ, Buchardt B (1977) Depth distribution of *Amphistegina* in the Gulf of Elat, Israel. Utrecht Micropaleontol Bull 15: 205–224

Hohenegger J (2004) Depth coenoclines and environmental considerations of Western Pacific larger foraminifera. J Foraminiferal Res 34: 9-33

Hohenegger J (2009) Functional shell geometry of symbiont-bearing benthic foraminifera. Galaxea, Journal of Coral Reef Studies 11: 1-9

Hohenegger J (2011) Growth-invariant meristic characters: tools to reveal phylogenetic relationships in Nummulitidae (Foraminifera). Turk J Earth Sci 20: 655-681

Hohenegger J (2013) Species as the basic units in evolution and biodiversity: recognition of species in the recent and geological past as exemplified by larger foraminifera. Gondwana Res 25: 707-728

Hohenegger J, Torres-Silva AI (2016) Growth-invariant and growth-independent characters in equatorial sections of *Heterostegina* shells relieve phylogenetic and paleobiogeographic interpretations: Palaios [doi. 10.2110/palo.2015.092]

Holzmann M, Hohenegger J, Pawlowski J (2003) Molecular data reveal parallel evolution in nummulitid foraminifera. J Foraminiferal Res 33: 277–284

Holzmann M, Berney C, Hohenegger J (2003) Molecular identification of diatom endosymbionts in nummulitid foraminifera. Symbiosis 42: 93-101

Hottinger L (1977) Foraminifères operculiniformes. Mémoires muséum national d'histoire naturelle, series C: 1–159

Hyams O, Almogi-Labin A, Benjamini C (2002) Larger foraminifera of the South Eastern Mediterranean shallow continental shelf off Israel. Isr J Earth Sci 51: 169–179

Langer MR, Hottinger L (2000) Biogeography of selected "larger" foraminifera. Micropaleontology 46 (1): 105-126

Less G, Özcan E, Papazzoni CA, Stockar R (2008) The middle to late Eocene evolution of nummulitid foraminifer *Heterostegina* in the Western Tethys. Acta Palaeontol Pol 53: 317–350

Leutenegger S (1977) Reproduction cycles of larger foraminifera and depth distributions of generations. Utrecht Micropaleontol Bull 15: 27–34

Lunt P, Renema W (2014) On the *Heterostegina – Tansinhokella – Spiroclypeus* lineage(s) in SE Asia. B Sedimentologi 30: 6-31

Nobes K, Uthike S, Henderson R (2008) Is light the limiting factor for the distribution of benthic symbiont bearing foraminifera on the Great Barrier Reef? J Exp Mar Biol Ecol 363: 48-57

Racey A (1992) The relative taxonomic value of morphological characters in the genus *Nummulites* (Foraminiferida). J Micropalaeontol 11: 197-209

Renema W (2005) Depth estimation using diameter-thickness ratios in larger benthic foraminifera. Lethaia 38: 137–141

Richards FJ (1959) A flexible growth function for empirical use. J Exp Bot 10: 290–300

Röttger R (1990) Trimorphism in foraminifera (Protozoa) – Verification of an old hypothesis. Eur J Protistol 25: 226-228

Röttger R, Hallock P (1982) Shape trends in *Heterostegina depressa* (Protozoa, Foraminiferida). J of Foraminiferal Res 12: 197–204

Thompson, MJ, Jiggins, CD (2014) Supergenes and their role in evolution. Heredity 113: 1-8

Yordanova, EK, Hohenegger J (2002) Taphonomy of larger foraminifera: relationships between living individuals and empty tests on flat reef slopes (Sesoko Island, Japan). Facies 46: 169–204