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# Functional morphology of *Melonis* barleeanum and *Hoeglundina elegans*: a proxy for water-mass characteristics

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Morphometric study of Melonis barleeanum and Hoeglundina elegans was carried out on 15 core top samples from the Indian Ocean. Length to breadth ratios and wall and septal thicknesses of the largest tests of both the species from each sample, along with  $\delta^{13}C$ and  $\delta^{18}$ O values of *Cibicides wuellerstorfi* were measured. Both the species show equal growth rates of the test in their normal habitat. However, the high organic carbon preference species M. barleeanum shows more elongation of the test during food scarcity. This effect is not evident in *H. elegans*, which varies in its wall and septal thicknesses with bottom-water oxygen levels of the deep water mass up to 2000 m, probably to maintain the required rate of osmosis for the intake of dissolved O<sub>2</sub>. Below this depth both parameters show parallel relationship with deviation indicating that oxygenation may play some role in the variation of wall and septal thicknesses. Thinning or thickening of the wall and septa in *M. barleeanum* and *H. elegans* has no relation with the water depth, indicating no relation with either the overlying pressure effect or nutrients as each deep water mass has a different nutrient budget. Depletion in  $\delta^{13}$ C and enrichment in  $\delta^{18}$ O below 2000 m water depth suggests that up to 2000 m depth, the Indian Ocean is bathed by the welloxygenated, low-nutrient North Atlantic Deep Water (NADW), whereas below 3000 m cold, nutrient-rich Antarctic Bottom Water (AABW) is dominant. Between 2000 and 3000 m water depths, the water mass in the Indian Ocean is a mixture of NADW and AABW.

**Keywords:** Benthic foraminifera, *Hoeglundina elegans*, *Melonis barleeanum*, osmosis, septal thickness.

THE distribution of benthic foraminifera on the ocean floor is mainly controlled by the bottom-water oxygenation, and input and quality of organic carbon on the sea floor  $^{1-4}$ . The epifaunal and shallow infaunal benthic

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foraminifera are more influenced by the bottom-water hydrography than the deep infaunal forms, whose distribution pattern is mainly controlled by the pore water chemistry. However, the morphological variations of benthic foraminifera can be used to infer their mode of habitat as well. It is well established that some deep infaunal species with increased body volume and evenly distributed pores on the surface indicate preference for low oxygen environments facilitated possibly by enhanced gas exchange capacity<sup>5</sup>. High surface area to volume ratio and surface pore-bearing forms are mainly deep infaunal<sup>5</sup>; spherical, planoconvex, lenticular morphologybearing forms prefer oxygenated environment<sup>6</sup>; elongateflattened, unornamented, thin-walled, cylindrical, tapered forms with pores on their surface indicate anoxic environment<sup>6,7</sup>; numerous biserial and triserial calcareous forms generally indicate oxygen-poor environment<sup>1</sup>; presence of thin wall and small test indicates stressful dysoxic environment<sup>8,9</sup>; and abnormal tests indicate presence of toxic/polluted environment<sup>10-13</sup>. The size of some trochospiral benthic foraminiferal tests also varies with the temperature minima and maxima as well as bottomwater oxygenation<sup>14,15</sup>. Morphometric study by Caralp<sup>16</sup> reveals that high food supply may cause increase in mean size as well as abnormality (kummerform) in the tests of M. barleeanum.

However, very little is known about the functional morphology of benthic foraminiferal tests, particularly about the function of wall and septal thicknesses. According to Marszalek<sup>17,18</sup> and Murray<sup>19,20</sup>, there are six possible functions of the test of foraminifera. These include: (i) to provide shelter, (ii) help as receptacle for excretory materials, (iii) aid in reproduction, (iv) control buoyancy, (v) protection of protoplasm and (vi) growth of cell. Some studies indicate that test wall thinning might be an indicator of reducing/toxic environments<sup>9,21</sup>.

The present study measures test dimension, wall thickness and septal thickness of recent specimens of *M. barleeanum* and *H. elegans* to understand the growth of test, function of wall and septa along with variation of wall and septal thickness to accommodate the overlying hydrostatic pressure.

Fifteen Ocean Drilling Programme (ODP) core top samples were analysed from the Indian Ocean having different bathymetries and coordinates as given in Table 1 and Figure 1. Each sample was taken from the top 2 cm of each Hole representing Holocene age<sup>22,23</sup>.

In general, the Indian Ocean is bathed by three types of water masses. Shallower depth (up to ~ 1200 m) is dominated by the Antarctic Intermediate Water  $(AAIW)^{24}$ . Depths between 1200 and 2000 m are mostly dominated by a mixture of the well-oxygenated North Atlantic Deep Water (NADW) and North Indian Deep Water (NIDW)<sup>24-26</sup>. The deeper part (> 3000 m) is bathed by nutrient-rich cold water of Antarctic origin – the Antarctic Bottom Water (AABW)<sup>24</sup>. Between 2000 and 3000 m, the

water mass has the characteristic of both NADW and AABW due to mixing.

Each sample having 10 cm<sup>3</sup> volume of unconsolidated sediments was soaked in water overnight and wet-sieved at 63 µm. Residue collected over the sieve was transferred to a beaker and dried in a hot-air oven at a temperature of 50°C. Oven-dried samples were then transferred into labelled glass vials. Benthic faunal analyses were carried out under a microscope using  $\geq 150 \ \mu m$ fractions to avoid juvenile and small-sized forms. M. barleeanum and H. elegans were chosen for the present study as an experiment to understand the role of environmental parameters on functional morphology of these species. The largest specimens of each species from each sample were picked for image analysis. Microscopic images of the largest individuals from both the species were taken with the help of Leica MZ 16 trinocular microscope. The maximum length of test of each specimen was measured by calibrating the scale using stage micrometer and eye-piece reticule. Breadth perpendicular to the maximum length was also measured in a similar way for each specimen. This was followed by breaking of the same specimens and measurement of their wall and septal thicknesses (Figure 2). Length-breadth ratios were determined for each specimen. All the measured values are given in Table 2.

Carbon and oxygen isotope analyses were performed on pre-cleaned specimens (1–5 individuals) of *Cibicides wuellerstorfi* picked from >150  $\mu$ m size fraction.



Figure 1. Location map of the 15 studied ODP Holes. *Melonis barleeanum* and *Hoeglundina elegans* are not recorded at Holes 757A and 756B.

Table 1.	Locations of ODP Hol	es with present-day water	depth
Sample number	Water depth (m)	Latitude	Longitude
115-708A, 1H-1, 0-2	4109.3	5°27.35′S	59°56.63′E
115-709B, 1H-1, 0-2	3040.8	3°54.90'S	60°33.10′E
115-710A, 1H-1, 0-2	3824.3	4°18.70′S	60°58.80'E
115-711A, 1H-1, 0-2	4429.8	2°44.56′S	61°09.78'E
115,712A, 1R-1, 0-2	2904.3	4°12.99′S	73°24.38′E
115-714A, 1H-1, 0-2	2038.3	5°03.60′N	73°47.20′E
115-715A, 1R-1, 0-2	2266.3	5°04.89′N	73°49.88'E
115-716A, 1H-1, 0-2	544.3	4°56′N	73°17′E
117-721A, 1H-1, 0-2	1944.8	16°40.636′N	59°51.879′E
117-725C, 1H-1, 0-2	311.5	18°29.2′N	57°42.030'E
117-728B, 1H-1, 0-2	1427.8	17°40.790'N	57°49.553'E
117-729A, 1R-1, 0-2	1398.5	17°38.715′N	57°57.221′E
117-731A, 1H-1, 0-2	2365.8	16°28.229′N	59°42.149'E
121-756B, 1H-1, 0-2	1518.1	27°21.33′S	87°35.805′E
121-757A, 1H-1, 0-2	1650.2	17°01.458'S	88°10.90'E



Figure 2. Photomicrographs showing measurement of different morphometric parameters of whole and broken specimens of M. barleeanum and H. elegans. L represents length of the test, whereas B indicates breadth measured perpendicular to the length.

Samples were run at Brown University, USA in batches of ~40 on a Finnigan MAT 252 mass spectrometer equipped with a carbonate (Kiel) III auto-sampler where the samples reacted in individual reaction vessels at 70°C using H<sub>3</sub>PO<sub>4</sub>. Reproducibility based on repeated analysis of Carrara marble (N=12) and Brown Yule marble (BYM; N=10) was  $\pm 0.02\%$  and  $\pm 0.06\%$  for  $\delta^{13}$ C and  $\delta^{18}$ O respectively (1 $\sigma$ ). The Carrara and BYM in-house standards were calibrated to NBS-19 for conversion to the Vienna Pee Dee Belemnite (VPDB) scale. All data have been reported in % units relative to VPDB. We also adopted published bottom-water oxygen data from the nearest GEOSECS station<sup>26</sup> of each studied Hole for comparison (Table 2).

One hundred thirty-six specimens of M. barleeanum from 11 sites and 42 specimens of H. elegans from 10 sites are reported (Table 2). No specimen of M. barleeanum and H. elegans was recorded in the core top samples of Holes 756B and 757A. None of the specimens shows any abnormality and thus indicates the absence of stressful environmental conditions. Scatter plots using measured values of test length and breadth of M. barleeanum and H. elegans on 11 and 10 specimens respectively, show good correlation (Figure 3). It is possible

		5d 2000		concen	tration measu	ured in differe	ent GEOSECS	stations			moord num (	i iion oo (m	
Sample ID	117-725C, 1H-1, 0-2	115-716A, 1H-1, 0-2	117-729A, 1R-1, 0-2	117-728B, 1H-1, 0-2	117-721A, 1H-1, 0-2	115-714A, 1H-1, 0-2	115-715A, 1R-1, 0-2	117-731A, 1H-1, 0-2	115,712A, 1R-1, 0-2	115-709B, 1H-1, 0-2	115-710A, 1H-1,0-2	115-708A, 1H-1, 0-2	115-711A, 1H-1, 0-2
Water depth (m) <i>M. barleeanum</i> maximum length (µm)	311.5 ×	544.3 ×	1398.5 542.22	1427.8 461.90	1944.8 635.25	2038.3 337.63	2266.3 351.08	2365.8 467.92	2904.3 424.28	3040.8 245.83	3824.3 425.26	4109.3 444.18	4429.8 414.88
M. barleeanum breadth perpendicular to maximum length (µm)	×	×	449.70	402.32	590.33	286.24	283.69	399.22	375.91	197.04	380.94	374.18	356.09
<i>M. barleeanum</i> length/breadth	×	×	1.21	1.15	1.08	1.18	1.24	1.17	1.13	1.25	1.12	1.19	1.17
<i>M. barleeanum</i> wall thickness (μm)	×	×	31.00	14.00	14.00	8.00	24.13	20.17	19.00	4.00	10.00	47.00	24.00
<i>M. barleeanum</i> septal thickness (μm)	×	×	15.00	16.00	12.00	9.00	16.00	17.24	17.00	9.00	17.77	19.00	12.00
<i>H. elegans</i> maximum length (μm)	323.48	732.56	275.17	753.78	678.87	374.85	1211.95	849.73	363.27	×	×	582.77	×
<i>H. elegans</i> breadth perpendicular to maximum length (μm)	272.14	640.30	244.30	667.09	586.83	376.11	1077.62	789.76	308.72	×	×	515.38	×
H. elegans length/breadth	1.19	1.14	1.13	1.13	1.16	1.00	1.12	1.08	1.18	×	×	1.13	×
<i>H. elegans</i> wall thickness (μm)	17.00	25.00	18.00	56.00	50.00	49.00	37.00	26.00	30.55	×	×	49.00	×
<i>H. elegans</i> septal thickness (μm)	12.00	22.85	11.00	15.00	27.58	53.00	14.29	17.00	19.00	×	×	31.03	×
GEOSEC station number	415	418	421	415	415	418	418	415	449	421	421	420	421
Oxygen (µm/kg)	2	52	24	24	73	121	133	106	166	163	178	179	192
δ <sup>13</sup> C of C. wuellerstorfi δ <sup>18</sup> O of C. wuellerstorfi	0.27 0.72	0.65 2.32	0.23 1.49	0.16 2.07	0.2 3.39	× ×	0.52 2.47	0.17 3.95	<b>-0.04</b> 2.77	0.24 3.27	-0.17 4.01	<b>0.1</b> 3.19	0.37 2.55
Bold faced carbon isotope	values are p	ublished in Bł	haumik <i>et al.</i> <sup>2</sup>	23.									

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Figure 3. Scatter plots with correlation coefficient (R) and probability test values (P) on measured length and breadth of M. barleeanum (a) and H. elegans (b).

that the correlation values derived with small number of observations may not significantly represent the larger community. To test the high correlation (*R*) value of 0.99 in case of *M. barleeanum* and R = 0.99 in case of *H. elegans*, *P* test was performed. *P* value is the probability of obtaining a correlation and is used here for testing the hypothesis of no correlation. Significantly high *P* value indicates low correlation, whereas very low *P* value indicates high correlation. In the present study, the measured *P* values for *M. barleeanum* and *H. elegans* are  $53 \times 10^{-10}$  and  $4 \times 10^{-10}$  respectively, indicating that the high correlation values obtained are quite significant.

The rate of expansion of chambers of foraminifera in terms of increase in size of the test follows a fairly constant logarithmic trend<sup>27</sup>. The study of Caralp<sup>16</sup> on growth of *M. barleeanum* shows that high correlation values are recorded (within 0.97–0.99) between greatest test diameter and diameter measured at right angles to this as well as between greatest test diameter and maximum width. Thus, our result corroborates the observation of Caralp<sup>16</sup> and indicates growth rate of both the species along both directions following a constant linear pattern in normal environment.

Figures 4 and 5 show composite plots for both species using wall thickness, septal thickness, length-breadth ratio,  $\delta^{13}$ C and  $\delta^{18}$ O of *C. wuellerstorfi* and published bottom-water oxygen data. Plots of wall (R = 0.45, P = 0.43) and septal (R = 0.94, P = 0.01) thicknesses of *H. elegans* with bottom-water O<sub>2</sub> shows parallelism up to a water depth 2000 m (Figure 4 *a* and *b*) and below this depth the two parameters deviate significantly. Plot of length-breadth ratio of *H. elegans* with  $\delta^{13}$ C does not show any particular trend up to a depth of 2500 m and below that the two values show opposite relation (Figure 4*c*). However, the same parameter does show a positive correlation with  $\delta^{18}$ O values below 2500 m (Figure 4*d*). On the other hand, wall and septal thicknesses of *M. bar*- *leeanum* with bottom-water oxygen do not show any similarity (Figure 5*a* and *b*). Rather, the length-breadth ratio of *M. barleeanum* is better correlated with  $\delta^{13}$ C values (R = 0.58, P = 0.08) compared to  $\delta^{18}$ O (R = -0.33, P = 0.35; Figure 5*c* and *d*). The  $\delta^{13}$ C values are depleted and  $\delta^{18}$ O values enriched below 2500 m water depth (Figures 4*c*, *d* and 5*c*, *d*).

*C. wuellerstorfi* is a raised epifaunal benthic foraminifer<sup>28</sup> and widely used for isotopic study owing to its capacity to record  $\delta^{13}$ C and  $\delta^{18}$ O in equilibrium with marine water<sup>29</sup>. The  $\delta^{13}$ C and  $\delta^{18}$ O values are reliable indicators of organic carbon flux to the sea floor and bottomwater temperature respectively.

*H. elegans* having both epifaunal and shallow infaunal microhabitats, prefers to live within the top 2 cm of the sediment<sup>5</sup> and bears fine perforation on its test surface<sup>30</sup>. This species is generally recorded in low oxygen conditions and has been defined as an 'oxygen minimum zone' species<sup>28,31,32</sup>. *M. barleeanum* is considered a shallow infaunal benthic foraminifer that prefers to live within 1–2 cm below the sediment surface and has evenly distributed large pores on its surface suggest enhance gas exchange in low oxygen conditions<sup>4,5,16</sup> as well as during high food supply<sup>33,34</sup>.

A parallelism between septal and wall thicknesses of *H. elegans* and bottom-water  $O_2$  up to a water depth of 2000 m indicates a regulated intake of dissolve oxygen through fine pores present in calcitic wall and septa to the soft body by osmoregulatory processes (Figure 4 *a* and *b*). It is well established that during osmosis the size of the pores and thickness of the media play an important role. Larger pore size indicates enhanced osmosis rates, whereas thicker medium indicate more sluggish rates<sup>35</sup>. *H. elegans* test surface contains small-sized pores and hence the wall and septa thicknesses may be a vital factor to make the pores more effective for the exchange of dissolve gas by reducing the travel path distance. Probably owing to



Figure 4. Composite plot of wall thickness, septal thickness and length-breadth ratio of *H. elegans* with  $\delta^{13}$ C and  $\delta^{18}$ O values of *Cibicides wuellerstorfi* and published bottom-water O<sub>2</sub> data.

osmoregulatory controlling factors, the septal and wall thickness of H. elegans varies directly with increased or decreased amount of dissolved  $O_2$  in the surrounding water. However, numerous large-sized pores on the test of M. barleeanum may be sufficient for the exchange of gas and thus the role of wall and septal thicknesses becomes negligible. Hence, M. barleeanum does not show regular variation in the wall and septa thicknesses with variation of dissolved O<sub>2</sub>. The study of Marszalek et al.<sup>17,18</sup> also reveals that the septal and wall thicknesses in foraminiferal tests are mainly related to the physicochemical stress factors as well as osmoregulatory processes. Though these parameters in *H. elegans* show more deviation below 2000 m, the parallelism between wall and septal thicknesses with dissolved oxygen indicates that oxygen may play some role in the variation of wall and septal thicknesses. However, changes in water mass may also influence such deviations.

Increased length-breadth ratio indicates test elongation along the length with respect to the breadth. Similar variation in lower and higher values of length-breadth ratio of *M. barleeanum* with depleted and enriched  $\delta^{13}$ C of *C. wuellerstorfi* is observed in the present study (Figure 5 c). Depleted values of both parameters indicate that the test becomes more circular in outline when sufficient food supply is available and higher values indicate elongation of test along the length during the scarcity of food. It is evident that with increased food supply the test of M. *barleeanum* becomes larger<sup>16</sup>. Laboratory experiments also show that scarcity of food is responsible for the generation of small-sized and deformed species<sup>36</sup>. *M. barleeanum* is more dependent on the amount and quality of food compared to *H. elegans*, which is mainly dependent on bottom-water oxygenation. Thus, *M. barleeanum* shows variability in the length–breadth ratio with the supply of food, whereas *H. elegans* shows variation in wall and septa thicknesses to monitor osmoregulatory process with the local oxygen profile.

Similar trends in the length-breadth ratio of both the species with  $\delta^{18}$ O may indicate the production of more circular test (normal growth of spire) during cold times (Figures 4 *d* and 5 *d*). Temperature-dependent size variation of trochospiral benthic forms has been reported earlier<sup>14,15</sup>. We also assessed the relation of wall and septal thicknesses with variation of water depth. It is quite expected that the deep-dweller forms require more robust test in terms of increased septal and wall thickness to accommodate overlying pressure compared to the shallow-dwellers. To understand this problem, we converted all measured test size dimensions into a standard size to



**Figure 5.** Composite plot of wall thickness, septal thickness and length-breadth ratio of *M. barleeanum* with  $\delta^{13}$ C and  $\delta^{18}$ O values of *C. wuellerstorfi* and published bottom-water O<sub>2</sub> data.

establish uniformity. Then septal and wall thickness were recalculated with respect to these converted test sizes. We could not find any increasing trend of wall and septal thicknesses with increase in water depth. This may be either due to their infaunal habitat or these parameters are independent of overlying pressure.

Deviation of carbon and oxygen isotopes below 2500 m water depth reflects the variation in downward water mass characteristic (Figures 4c, d and 5c, d). Depleted  $\delta^{18}$ O ( $\leq 2.5\%$ ) and enriched  $\delta^{13}$ C ( $\geq 0.2\%$ ) values up to water depth 2500 m indicate presence of relatively warm and nutrient-poor water mass of mixed NADW and NIDW. Whereas water mass below this depth is characterized by enriched  $\delta^{18}$ O (up to 4.01‰) and depleted  $\delta^{13}$ C (up to -0.17‰), indicating the presence of the cold, the nutrient-rich AABW. As mentioned earlier, in the Indian Ocean, shallower depths (up to 1200 m) are dominated by AAIW and depths below 3000 m are bathed by AABW. The transition zone between 2000 and 3000 m depths is bathed by a mixture of NADW above and AABW below. Shifts in all morphometric characters along with isotopic values also suggest the presence of a transition zone within this water depth, which affects the variations in all these parameters.

thicknesses of pore-bearing benthic foraminifera are indicative of their habitat. The deep infaunal benthic foraminifera are affected by pore water, while the bottom-water character influences shallow infaunal fauna. In unstressed environments, both species show equal growth rates along the long axis and perpendicular to the long axis of the test. However, M. barleeanum can produce a more elongated test along the long axis during low food supply. H. elegans does not show any such change as this species is mainly dependent on dissolved O<sub>2</sub>. Rather, the finely perforated test-bearing H. elegans uses its wall and septal thicknesses to control the osmoregulatory process for intake of dissolved oxygen. This species makes its test wall and septa thinner to increase the effectiveness of osmosis by reducing the travel path. On the other hand, larger pore-bearing test does not require any such mechanism as the large size pores themselves are sufficient for osmosis. Thinning or thickening of wall and septa of these two species does not show any linear relation with water depth. This may result from their infaunal nature or their septal and wall thicknesses are independent of the effect of the overlying pressure. A major shift in all the

Morphometric parameters of *H. elegans* and *M. bar-leeanum* reveal that the test size, and septal and wall

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measured parameters between 2500 and 3000 m water depth indicates presence of transition zone which is overlain by a nutrient-poor, well-oxygenated water mass (NADW) and underlain by a cold, nutrient-rich water mass (AABW).

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